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**Analysis and detection of *Ips typographus* L.
infestations using remote sensing methods**

Ph.D., Dissertation thesis (Diss T)

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Field of study: Global Change Forestry

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Place & Year: Prague, 2025

Ph.D. THESIS ASSIGNMENT

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Global Change Forestry

Thesis title

Analysis and detection of *Ips typographus* L. infestations using remote sensing methods

Objectives of thesis

1. Analysing the influence of solar radiation and canopy temperature on the spruce predisposition to *Ips typographus* infestation using LiDAR and thermal data. Solar radiation has direct influence on bark beetle outbreaks and canopy temperature serves as an indicator of tree stress. Potential heat load on every tree can be calculated using a 3D model of forest, which is created by LiDAR data. Heat load on the trees depends on their position in the stand and the crown geometry. Stand and tree crown characteristics can be assessed by LiDAR data. These data are closely related to tree resistance to bark beetle attack. Integrating solar radiation load, crown temperature and stand structure data into one model will make it possible to identify areas of the forest most susceptible to bark beetle outbreaks.

2. Analysis of areas affected by *Ips typographus* infestations using satellite, aerial or UAV imagery. Conifer forests affected by water stress are potential areas for bark beetle outbreak or these areas have already been infested. Water stress is one important parameter of the predisposition to attack by bark beetles. Remote sensing data can be useful for detection of these areas because water stress has influences to the spectral signature. Detection of these changes with high accuracy needs high spatial resolution and bands in the red and infrared ranges. Identification of bark beetle attack needs to compare the spectral characteristics of attacked and non-attacked trees. Methods for detection of green stage attack need to include spectral analyses and meteorological data such as temperature and precipitation. Spatial distribution of bark beetle infestation is influenced by various stand and site factors.

Methodology

Field data will be collected in experimental plots in Kostelec nad Černými Lesy and other plots affected by bark beetle outbreaks in the Czech Republic or in other areas with high bark beetle population. Field data will be collected according to a developed method based on knowledge obtained from a literature review. Key data are the infested trees detected in field work. During remote sensing campaigns, various platforms and sensors will be used to obtain data for the study area.

Remote sensing data will be used to detect trees infested by the bark beetle. One of the signs of the bark beetle attack is a change in the chlorophyll and the water content of the needles. These parameters can be used to identify infested trees.

The proposed extent of the thesis

70-120 pages

Keywords

Ips typographus, modelling of outbreak, solar radiation, voxel approach, thermal data

Recommended information sources

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Expected date

2024/25 SS – FFWS – State Doctoral Examinations

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Annotation

This thesis investigates the response of Norway spruce to drought and thermal stress at the stand level. It assesses the risk of bark beetle infestation using drought indices and models the phenology of the Eurasian spruce bark beetle (*Ips typographus* L.) within study areas in the Czech Republic. The thesis studies the outbreak of bark beetles on Kunashir Island, examining it in phases and identifying the drivers of the outbreak. This thesis is based on four scientific articles.

The results of the first study (Karpov et al., 2025a) show how variation in crown temperature is explained by gap area, crown openness on the south side, tree height and canopy density. These analyses are then compared with solar radiation simulations.

The second study (Karpov et al., 2025b) combines aerial thermal-hyperspectral surveys, LiDAR canopy indices, landscape parameters, sap flow and other sensor data to reflect the microclimate conditions of spruce stands. It investigates the sensitivity of thermal data and vegetation spectral indices to detect conditions of drought and thermal stress.

The third study (Karpov et al., 2024) uses satellite imagery to quantify conifer mortality between 2017 and 2021 in the southern part of the Kurilskiy Nature Reserve and analyses the drivers of bark beetle outbreaks. The study demonstrates that the composition and age structure of stands influence the severity and spatial patterns of conifer stand loss.

The fourth study (Pirtskhalava et al., 2024) applies the TANABBO II model, combining phenology simulations with simulated drought conditions based on meteorological data and potential solar radiation. This produces a spatial layer indicating areas at high risk of spruce stand infestation on a daily basis.

Keywords: *Ips typographus*, bark beetle outbreaks, drought, solar radiation, thermal data

Declaration

I declare that I have independently written the dissertation on the topic “Analysis and detection of *Ips typographus* L. infestations using remote sensing methods”, with the use of literature and based on consultations and supervisor’s recommendations. I agree to the publication of this dissertation according to Act no. 111/1998 Coll., on schools, as amended, regardless of the outcome of its defence.

Prague, 2025

MSc Aleksandr Karpov

Acknowledgements

I would like to express gratitude to my supervisor, Rastislav Jakuš, for his guidance, constructive feedback, and continuous support throughout my Ph.D. research.

I would like to thank Dr Pavel Mezei, Dr Maria Potterf, Dr Milan Koreň and Dr Miroslav Blaženec for their co-authorship of several publications and their invaluable help in preparing the manuscripts.

I would also like to express gratitude to my wife, Nana Pirtskhalava-Karpova, who participated as a member of my Ph.D. team and provided critical reviews and encouragement at every stage.

This work was carried out as part of the EXTEMIT-K project and was further supported by grants from IGA and NAZVA.

Finally, I appreciate the contributions of all colleagues and collaborators whose discussions and advice have helped to shape this dissertation.

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List of original publications

- I. **Karpov, A.**, Pirtskhalava-Karpova, N., Trubin, A., Surovy, P., & Jakuš, R. (2025). Analysis of solar radiation and thermography data using tree crowns parameters for Norway spruce. In *Forest Ecology and Management* (Vol. 582, p. 122557). Elsevier BV. <https://doi.org/10.1016/j.foreco.2025.122557>
- II. **Karpov, A.**, Pirtskhalava-Karpova, N., Singh, V., Trubin, A., Korolyova, N., Modlinger, R., Jakuš, R. (2025). Response of mature Norway spruce to experimental thermal and drought stress in relation to *Ips typographus* attack: Crown temperatures and sap flow. Manuscript.
- III. **Karpov, A.**, Pirtskhalava-Karpova, N., Trubin, A., Mezei, P., Potterf, M., & Jakuš, R. (2024). Infestation patterns of two bark beetle species in multi-species coniferous forests on Kunashir Island in North Pacific Ocean region. In *Forest Ecology and Management* (Vol. 558, p. 121774). Elsevier BV. <https://doi.org/10.1016/j.foreco.2024.121774>
- IV. Pirtskhalava-Karpova, N., **Karpov, A.**, Trubin, A., Koreň, M., Blaženec, M., Holuša, J., & Jakuš, R. (2024). Spruce bark beetle phenological modelling and drought risk within framework of TANABBO II model. In *Ecological Modelling* (Vol. 496, p. 110814). Elsevier BV. <https://doi.org/10.1016/j.ecolmodel.2024.110814>

1. Introduction and literature analysis

Spruce bark beetle (*Ips typographus* L.) outbreaks pose a serious threat to spruce forests. The global distribution of the spruce bark beetle ranges from Europe to Asia (EPPO, 2020). The species therefore poses a significant threat to European forests, and outbreaks also occur in Asia (Karpov et al., 2024). The Czech Republic exemplifies this ongoing crisis in Central Europe. The extreme drought of 2018 intensified bark beetle proliferation to unprecedented levels (Hlásny et al., 2021). Climate change is leading to higher temperatures, more frequent heatwaves and longer droughts, which are affecting the sustainability of spruce forests (Seidl et al., 2016; Marini et al., 2017).

1.1 Drivers of spruce bark beetle outbreaks

1.1.1 Drought driver

In recent decades, an increase in bark beetle outbreaks in Central Europe, particularly in the Czech Republic, has been closely linked to drought stress (Hlásny et al., 2021). A historical perspective suggests that wind disturbances were once the primary trigger of bark beetle outbreaks (Stadelmann et al., 2014). However, more recent massive spruce bark beetle outbreaks were driven primarily by extreme drought (Marini et al., 2017). Massive bark beetle damage was recorded in the Czech Republic following a severe drought year in 2018, culminating in the most devastating spruce dieback observed in two centuries (Hlásny et al., 2021; Pirtskhalava-Karpova et al., 2024). While wind disturbance remains a significant trigger for new outbreaks, prolonged drought related to climate change is drastically exacerbating damage to Norway spruce (*Picea abies* (L.) Karst.) forests.

Drought-induced bark beetle outbreaks have consequently devastated spruce stands across Central Europe, intensifying salvage logging operations and leading to widespread mortality that continues to affect local forest economies (Hýsek et al., 2021; Kutnar et al., 2022; Šimůnek et al., 2024). Deficient precipitation reduces the defensive capacity of Norway spruce, while warm early spring and higher temperatures during the spring–autumn period create ideal breeding conditions for bark beetles (Potterf et al., 2025). Marini et al. (2017) argue that drought, exacerbated by climate change, can increase beetle populations even in the absence of windthrow events, thereby increasing forest damage, particularly in the southern border of the distribution of natural spruce stands. Kärvement et al. (2023) also highlight that forest characteristics such as spruce age and stand height, soil moisture deficits and the presence of neighbouring infestations are important in determining the severity of drought-

induced outbreaks. The authors suggest that the interplay between climatic factors and local stand conditions shapes the dynamics of each outbreak, determining both the likelihood and magnitude of future epidemics.

1.1.2 Effect of drought on spruce stands

Tree carbohydrate allocation, resin flow and phenolic production can be noticeably altered under drought conditions (Netherer et al., 2015). While mild water deficits can stimulate certain defence mechanisms and temporarily enhance chemical defences, prolonged or acute drought can deplete vital energy reserves and ultimately reduce a tree's resistance to mass attacks. Spruce's resin defence mechanisms are progressively reduced during water stress, increasing the chance of successful colonisation by bark beetles (Netherer et al., 2014). Drought stress not only impairs a tree's ability to synthesise and transport resinous compounds, but also alters the volatile organic compounds (VOCs) profile (Šamajová et al., 2024), thereby increasing host attractiveness to beetles. Netherer et al. (2024) found that reduced resin flow and lower mono- and diterpene production increased host selection by spruce bark beetles, but chemical defence did not decrease significantly under moderate, prolonged drought stress. However, large-scale beetle infestations and fungal lesions may deplete the defences of spruce trees. Collectively, these results align with those of Basile et al. (2024), demonstrating that short-term water deficits can alter spruce physiology to the extent that defences against attacks by bark beetles are significantly decreased.

1.1.3 The effect of solar radiation on the infestation of spruce bark beetles

Solar radiation is identified as an important environmental factor in spruce bark beetle infestation (Jakuš et al., 2011; Mezei et al., 2012; Kautz et al., 2013; Mezei et al., 2019; Akıncı et al., 2021; Fernández-Carrillo et al., 2024). Studies in Central Slovakia and the Artvin region of Turkey showed a positive relationship between increased solar radiation and beetle activity, suggesting that increased solar radiation facilitates bark beetle colonisation of spruce stands (Mezei et al., 2012; Akıncı et al., 2021). These results suggest that the attractiveness of potential host trees can be increased under higher solar radiation, possibly because solar energy promotes microclimatic conditions suitable for beetle infestation and development throughout the season (Öhrn, 2012).

Further landscape-scale investigations in Central Slovakia confirmed solar radiation as a driver of bark beetle infestation in spruce forests. At the peak and decline phases of the outbreak, Mezei et al. (2019) recorded intensified infestations in areas with greater solar

radiation. Higher daytime temperatures and drier microclimate conditions affect the physiological defences of trees and make spruce stands more susceptible to bark beetle infestation (Singh et al., 2025). Alongside solar radiation, spruce physiological parameters such as age, height, diameter, and the ratio of tree height to trunk diameter are considered to be the predominant factors for infestation (Mezei et al., 2014a, 2014b). Nevertheless, solar radiation exerted a particularly pronounced effect during the epidemic stage of bark beetle development, which influenced both spruce defences and presumably increased reproduction and development of the bark beetle in warmer conditions (Wermelinger and Seifert, 1998; Wermelinger et al., 1999).

Research by Hroško et al. (2020) found that cumulative under-canopy solar radiation was a highly significant factor in spruce bark beetles colonising and infesting windthrown and uprooted trees. This study revealed that higher solar irradiation, along with factors such as trunk diameter, significantly increased the probability of bark beetle infestation of downed trees. Windthrown and uprooted trees after windfall create favourable conditions for increasing bark beetle populations to epidemic levels, allowing bark beetles to attack relatively healthy stands (Økland et al. 2016; Mezei et al., 2017).

1.1.4 The forest edge effect and thermal stress

Forest edges and gaps typically experience higher solar radiation and temperatures than trees in the forest interior. Sun-exposed edges often become focal points for beetle infestation. Investigating infested patches where sanitary logging had created new edges, Kautz et al. (2013) discovered a pronounced predisposition of recently formed south-facing edges to bark beetle attack. In contrast, permanent forest edges proved less attractive to the bark beetle, although still more susceptible than interior forest canopies.

In a gap-creation experiment, Stříbrská et al. (2022) recorded 2°C higher bark temperatures at the forest edges, a twofold increase in the concentration of VOCs such as monoterpenes near the bark of edge trees at the early season (May and early June), and a sixfold increase in this concentration during the season (until August). A previous study by Marešová et al. (2020) confirmed these edge-effect patterns. They also found that, just two months after the formation of the gap, the canopy temperature of spruce trees increased slightly and their sap flow rate doubled. Šamajová et al. (2024) extended these observations by showing that monoterpene concentrations remained elevated by 1.6– to 4.4–fold for at least 14 months after gap formation. The emission of volatile monoterpenes from spruce

stands serves to enhance the olfactory signals used by the beetles to find suitable host trees (Jirošová et al., 2022).

These observations of spruce stands under thermal stress, similar to the results published earlier by Kautz et al. (2013), suggest that the microclimatic changes caused by the formation of new forest edges are contributing to bark beetle infestations. However, drought stress, rather than thermal stress at lower elevations, appears to be a key factor in the susceptibility of spruce to bark beetle attack (Netherer et al., 2015). The main abiotic stress affecting monoterpene production that correlates with seasonal dynamics is drought (Šamajová et al., 2024).

1.1.5 Effect of spruce stands and landscape factors on stress conditions

In addition to climatic factors, stand composition, density and site characteristics profoundly affect a tree's response to drought. Sap flow rate is a physiological indicator of water stress and is strongly influenced by environmental variables such as air temperature, soil moisture, topography, vapour pressure deficit and solar radiation (Ježík et al., 2014; Marešová et al., 2022; Özçelik et al., 2022; Mikita et al., 2023; Zavadilová et al., 2023). Marešová et al. (2022) found a significant positive correlation between sap flow rate and terpene concentrations in airborne samples collected near the bark. In addition, site-specific variables such as elevation, slope and soil texture significantly affect tree transpiration rates. Tree characteristics, including trunk angle, internal trunk temperature, leaf biomass and stand density were also highlighted as important variables affecting sap flow (Zabihi et al., 2023; Singh et al., 2025; Zabihi et al., 2025). Low-density spruce stands can have higher transpiration rates than their denser counterparts because they receive increased levels of solar radiation (Singh et al., 2025).

1.1.6 Thermal response of trees under drought conditions

Increasing canopy temperatures can serve as sensitive markers of physiological stress in vegetation (Sack et al., 2006; Costa et al., 2013; Still et al., 2019). Under optimal non-stress conditions, stomatal opening provides transpiration to cool the canopy, reducing canopy temperature (Roelfsema and Hedrich, 2005; Daley and Phillips, 2006). However, under drought stress, stomatal aperture decreases in accordance with a water conservation strategy. This reduces evaporative cooling and increases leaf temperature (Kimball and Bernacchi, 2006; Prashar and Jones, 2014). In cases of bark beetle infestation, the feeding of phloem bark beetles disrupts physiological functions, which exacerbates canopy temperature increases

(Majdák et al., 2021). Moreover, once trees are infested, needle discoloration and partial defoliation reduce chlorophyll content and photosynthetic capacity, which impairs overall transpiration and intensifies heat accumulation in canopy layers (Zakrzewska and Kopeć, 2022). Spruce crowns at the edge of the forest under thermal stress have a higher crown temperature due to a higher transpiration rate than spruce crowns in the forest interior (Marešová et al., 2022). Additionally, low relative humidity, high vapour pressure deficit, and strong winds can further prompt more pronounced stomatal closure, which restricts transpirational cooling (Costa et al., 2013).

1.2 Remote sensing

1.2.1 Optical and infrared spectral range in multispectral and hyperspectral imagery

Remote sensing (RS) has become an effective technology for assessing the health of forest canopies, allowing early detection of vegetation stress caused by both biotic and abiotic factors (Lawley et al., 2016). Many studies have successfully used RS data to identify drought-induced tree mortality, fire-affected areas, soil salinity effects and grazing. For forest ecosystems, canopy temperature estimates derived from RS imagery have proven especially valuable for monitoring vegetation stress (Huo et al., 2021; Trubin et al., 2024; Pivovar et al., 2025). Multispectral aerial and satellite imagery is used to map forest health, disturbance, and insect outbreaks (Migas-Mazur et al., 2021; Junttila et al., 2022; Kovalev et al., 2024; Bozzini et al., 2025). In addition to the use of optical and infrared bands, research has also explored the use of radar data to detect insect infestations in forests (Ortiz et al., 2013; Hollaus and Vreugdenhil, 2019). Such approaches can also be integrated for forest monitoring, combining radar with optical and infrared imagery (König et al., 2023).

The selection of remote sensing data depends on the type of task and the size of the identified object. The spatial resolution should be half to three-quarters of the size of the target object (Woodcock and Strahler, 1987). Given that individual conifer crowns measure approximately 5–6 m in diameter (Ortiz et al., 2013), spatial resolutions of 4 m or finer are recommended (Mullen, 2016). Coarser resolutions risk blending target tree signals with background reflections (e.g. shadows, understorey vegetation), thus undermining reliable discrimination between healthy and infested crowns (Zabihi et al., 2021).

A variety of optical ranges including the visible, red edge, near infrared (NIR) and shortwave infrared (SWIR) have been found to be useful for detecting subtle physiological changes in conifer foliage. Research demonstrates that trees attacked by bark beetles often

exhibit changes in chlorophyll pigment concentration and water content (Ortiz et al., 2013; Zabihi et al., 2021). Foliage under severe stress typically reflects more visible and red-edge light while reducing absorption in NIR and SWIR bands due to changes in mesophyll structure and increased needle desiccation (Mullen et al., 2018; Trubin et al., 2023).

A recent airborne hyperspectral study by Pivovar et al. (2025) demonstrated that sub-metre VNIR–SWIR imagery covering 380–2500 nm can distinguish drought-stressed and acutely thermally stressed Norway spruce stands from healthy ones. Statistically significant differences were found primarily in the blue (450–500 nm) and red-edge region (640–720 nm) and in the SWIR windows (1500–1800 nm and 1950–2250 nm), which respectively track pigment degradation and canopy water status. These findings corroborate previous work and reinforce evidence that shifts in the green and red-edge bands provide an early warning signal of the bark beetle green-attack phase (Huo et al., 2021, 2023; Trubin et al., 2023).

1.2.2 Thermography technology

Thermography, using sensors in the thermal infrared (TIR) range of 8–14 μm , has emerged as a valuable tool for assessing plant physiological responses to environmental stressors (Zakrzewska and Kopeć, 2022; Smigaj et al., 2023). By measuring the energy emitted by the canopy, TIR images can provide estimates of surface temperature. Canopy temperature is then correlated with stomatal behaviour. Transpiration rates reflect vegetation health, making thermal data particularly useful for monitoring tree health and detecting early changes before visible symptoms appear (Zakrzewska and Kopeć, 2022). A growing research interest highlights the capability of thermal data to reveal spatial and temporal variability in tree stress. Airborne thermography has been used to successfully detect drought stress and pathogen-induced disease in diverse tree species by identifying warmer canopies, which are characteristic of reduced transpiration (Leuzinger et al., 2007; Junttila et al., 2016; Smigaj et al., 2015; Smigaj et al., 2023).

Thermal remote sensing has shown particular promise in distinguishing spruce trees infested by *Ips typographus* from healthy trees. For instance, canopy temperature from Landsat 8 TIR bands allowed identification of early-stage infestations, which often preceded visible needle yellowing (Abdullah et al., 2019). Airborne thermal surveys similarly distinguished healthy spruce tree crowns (mean canopy temperature of approximately 27.7 °C) from those in "poor condition" (28.6 °C) and "dead" (30.2 °C) (Zakrzewska and Kopeć, 2022). Handheld thermal cameras have also been investigated for detecting infested Norway

spruce, particularly at trunk level (Majdák et al., 2021). Infested spruce trunks generally register higher daily temperatures than healthy trunks, especially along forest edges exposed to direct sunlight. Thermal sensors can detect temperature increases in the canopy and trunk. Therefore, thermal imaging can improve early detection of tree infestations and stress.

1.2.3 LiDAR technology

Various remote sensing techniques are currently employed to assess forest cover. These range from satellite and drone images in the optical and infrared spectrum to LiDAR scanning (Smigaj et al., 2023). LiDAR scanning, for instance, is widely used in forestry to measure tree height, stand volume, and canopy structure (Sačkov, 2022). A point cloud acquired from LiDAR data can provide detailed information on canopy structure and individual tree metrics. LiDAR and multispectral data are often used together to achieve higher classification accuracy, because LiDAR data provide structural information that can be used to delineate individual crowns and define canopy metrics, and multispectral data contain spectral information that is sensitive to canopy physical changes such as water stress and infestation (Cessna et al., 2021; Zakrzewska and Kopeć, 2022).

1.2.4 Solar radiation modelling

Quantifying the amount of solar radiation received by tree stands and how much sunlight penetrates the forest canopy is central to understanding tree physiology, microclimate, drought stress and ultimately the risk of bark beetle infestation. Earlier work relied on indirect proxies to approximate solar irradiance within the canopy. These proxies included leaf area index (LAI), vertical foliage profiles, gap fraction photography, long-term field placement of photodiodes or quantum sensors, and hemispherical imaging (Niinemets, 1996; Welles and Cohen, 1996; Niinemets et al., 2004; Weiss et al., 2004; Gonsamo et al., 2010). These techniques suffer from low spatial or temporal resolution and are sensitive to solar angle, instrument calibration and operator bias.

Airborne LiDAR has largely overcome these limitations. High-density point clouds capture the three-dimensional structure of individual crowns, making it possible to develop solar radiation models that extend below the canopy — an area that is almost inaccessible to optical sensors alone. For the calculation of solar radiation, different LiDAR-based strategies can be used. Metric-based LiDAR approaches (e.g. laser penetration index, canopy height or density percentiles) correlate simple point cloud statistics with measured photosynthetically active radiation under the canopy (Witzmann et al., 2024). Voxel approaches divide the point

cloud into cubic volume elements whose occupancy represents foliage density. Radiation is traced through this 3D grid and attenuates each time a ray intersects a voxel (Pružinec and Ďuračiová, 2022).

2. Methods

2.1 Study area and sites

2.1.1 The School Forest Enterprise

The School Forest Enterprise (ŠLP) is located near Kostelec nad Černými lesy in the Central Bohemian Region of the Czech Republic. ŠLP is managed by the Czech University of Life Sciences in Prague and covers an area of 5,700 hectares. Elevations range from approximately 300–527 metres above sea level (a.s.l.). Climatically, the region experiences relatively warm and dry summers, with an average annual temperature of 7.5°C and total annual precipitation of nearly 600 mm (Tolasz et al., 2007). Droughts have intensified in recent years, creating favourable conditions for bark beetle outbreaks. Norway spruce dominates the forest composition, although Scots pine (*Pinus sylvestris*) and European beech (*Fagus sylvatica*) with oak species (*genus Quercus*) are also common (Pirtskhalava-Karpova et al., 2024).

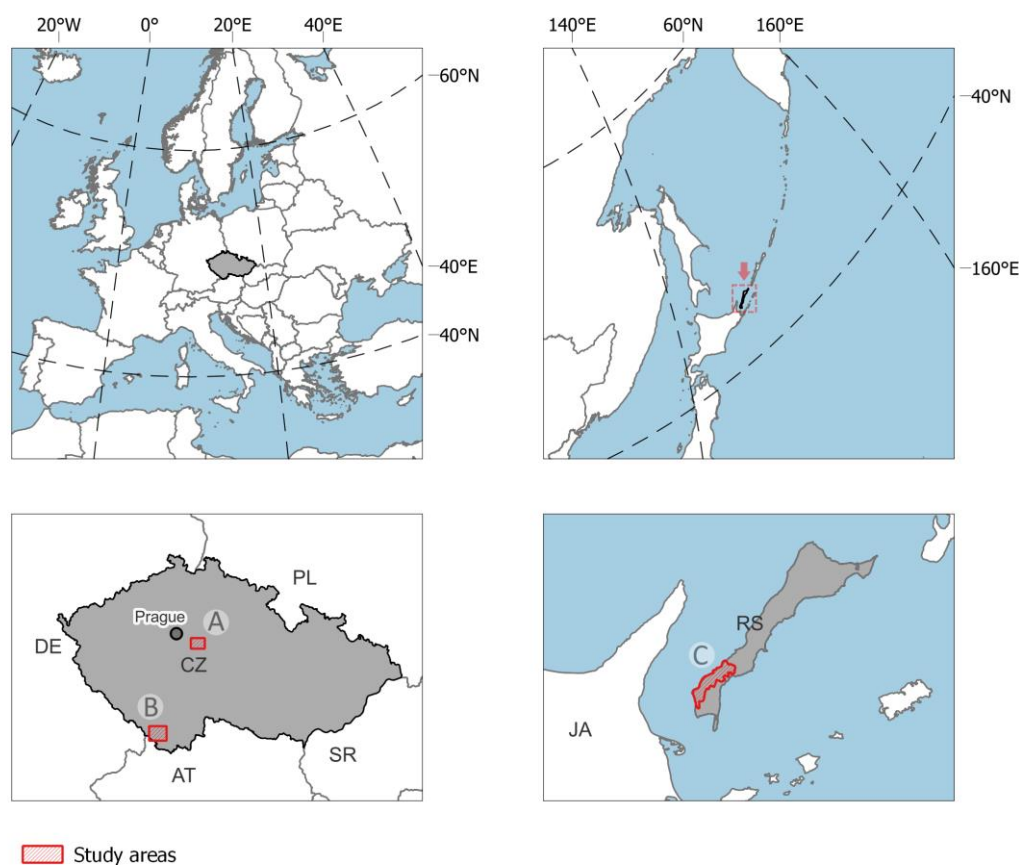


Figure 1 - Map of the study areas covered by this thesis: A – study area in the ŠLP; B – study area in the Horní Planá region; C – study area on Kunashir Island.

Experimental plots were established in 2018 as part of the EXTEMIT-K project (<http://extemit.fld.czu.cz>). Plots numbered 1, 2, 5, 7 and 8 (Figs. 1 and 2) constitute the study area of Article 2. Each plot consisted of four subplots designated A, B, C and D, which received different treatments. Each subplot has eight to ten Norway spruce trees monitored for sap flow and bark-surface temperature and soil temperature. Subplots referred to as 'Edge' (1B, 2A, 5A, 7A, 8A) were established to study thermal stress in spruce at the edge of forest stands resulting from clear cutting. Another treatment, 'Roof' (1A, 2B, 5B, 7B, 8B) was designed to study drought stress in spruce trees in the forest interior. For this purpose, a polycarbonate roof was installed over a wooden frame beneath the canopy to divert precipitation away from the roots. 'Control' subplots (C and D) were left to develop naturally in the interior of the forest (Pivovar et al., 2025; Singh et al., 2025).

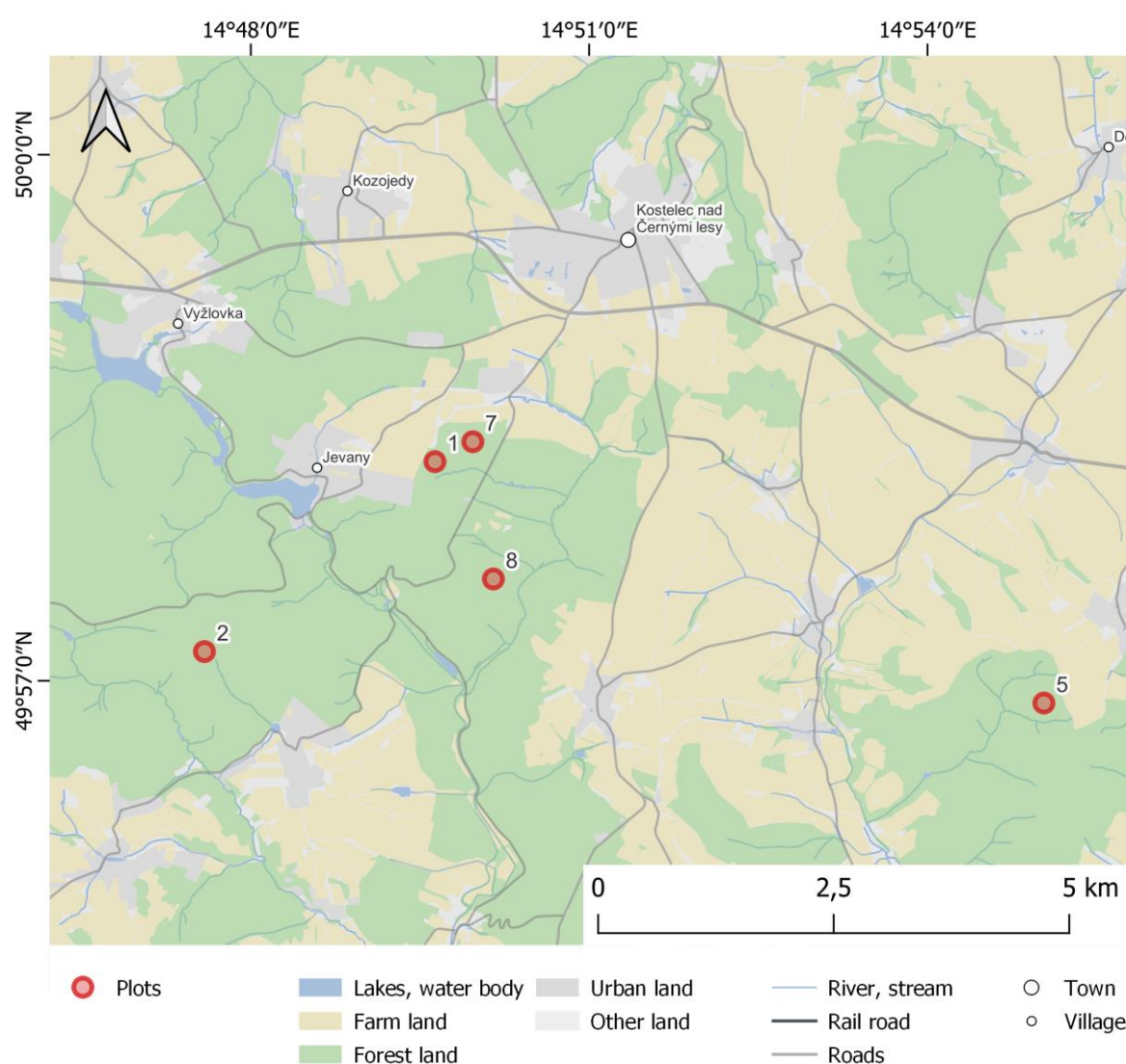


Figure 2 - Map of the trial plots in the ŠLP study area.

The study area of Article 1 is located around plot 1, with the centre of this area at longitude 14.827054° E, latitude 49.970676° N, and an elevation of 450 metres a.s.l. The research area is 230 metres long and 150 metres wide, situated in forest management units dominated by Norway spruce (45–100%) ranging in age from 50 to 110 years (Fig. 2).

2.1.2 Kunashir Island

Kunashir Island is situated in the southernmost section of the Great Kuril Chain, characterised by a predominantly volcanic landscape formed by three mountain ranges and four active volcanoes (Tyatya, Rurui, Mendeleev and Golovnin). The climate is moderately humid and marine, influenced by both the Sea of Okhotsk and the Pacific Ocean. The island's wind regime has an average speed of 4.9 m/s, with record gusts reaching up to 60 m/s during typhoons. The island receives a substantial annual precipitation of 1300–1500 mm. Average temperatures vary from -5.6°C in the coldest month to +15.5°C in the warmest month (August). Overall, the average annual temperature is +5.1°C, with a relative humidity of around 80.2% (Ganzei et al., 2008; Igarashi, 2016; Korznikov et al., 2019).

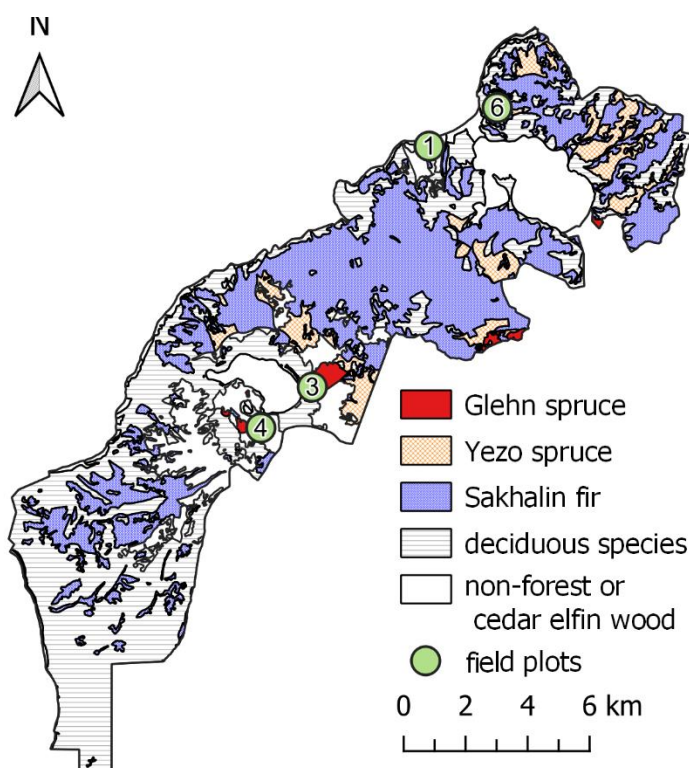


Figure 3 – Map of the study area on Kunashir Island.

The study area of Article 3 is situated in the southern part of the Kurilskiy Nature Reserve and covers 15,317 hectares (Figs. 1 and 3). The highest elevation point in this area is

Golovnin volcano at 543 m, and the mean elevation of our study area is 117 m. The study area features a hilly relief. The forest area is 13,831 ha (90.2%), with coniferous trees covering 6,555 ha (47.4%). Sakhalin fir (*Abies sachalinensis*) dominates (82% of the coniferous cover), together with Yezo spruce (*Picea jezoensis*, 15%) and Glehn spruce (*Picea glehnii*, 3%). No large-scale bark beetle outbreaks have been documented, although minor infestations and diseases have been observed sporadically (FID, 2007).

2.1.3 Study area in Horní Planá region

The Horní Planá region is located in the southern part of the Czech Republic and is managed by the state enterprise Military Forests and Farms of the Czech Republic (Figs. 1 and 4; study area of Article 4). This enterprise is responsible for managing a total land area of 19,960 ha, which includes 16,569 ha of forests area. The landscape of this area is gently hilly, with elevation differences of about 100–150 metres. Most of the study area is situated between 600 and 800 metres a.s.l.

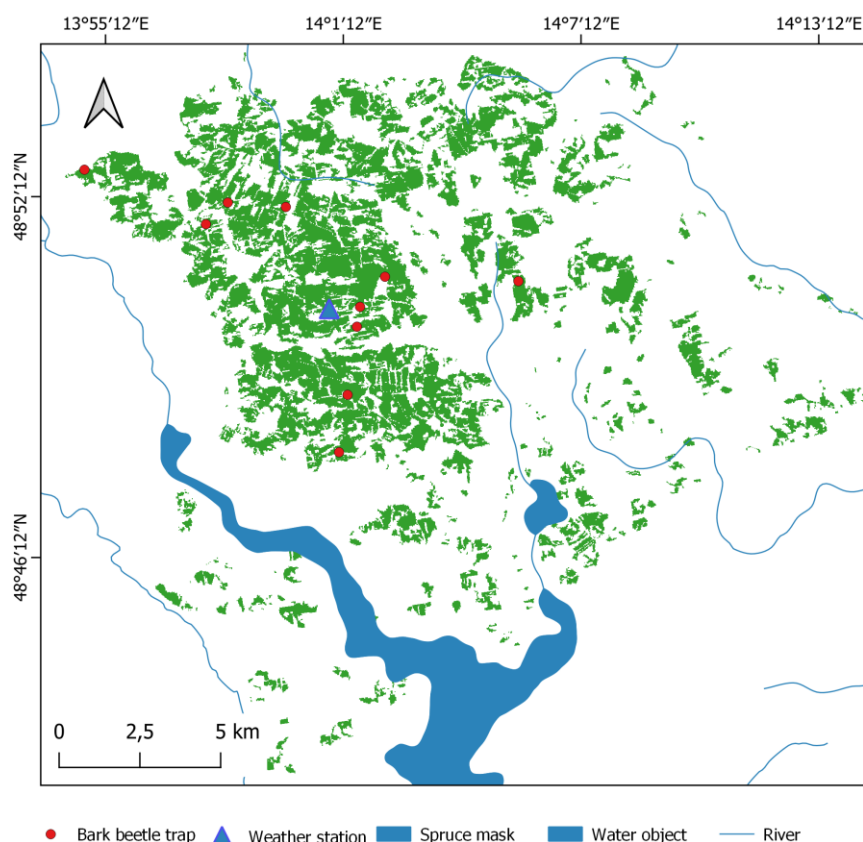


Figure 4 – Map of the study area in the Horní Planá region.

The climatic conditions are characterised by an average annual temperature of 5 to 7 °C and annual rainfall of 700 to 800 mm. Norway spruce represents 69% of the total forest cover,

accompanied by 6% silver fir (*Abies alba*) and 5% European beech. Scots pine is present at lower altitudes and accounts for 12% of the tree composition. Stands younger than 40 years occupy around 23.5% of the region, while those exceeding 100 years account for approximately 32% (Culek et al., 2013).

2.2 Remote sensing data acquisition and processing

A multi-source remote sensing framework was implemented to capture stress conditions of spruce stands and monitor bark beetle-related disturbances. Datasets include satellite imagery, airborne thermal and hyperspectral data, and LiDAR point clouds. This integrated approach enabled analysis at both the canopy and landscape levels.

2.2.1 Global Forest Change

The Global Forest Change (GFC) dataset (Hansen et al., 2013) provides spatial data on forest cover loss. The dataset is based on Landsat imagery with a spatial resolution of 30 m. It is organised in $10^\circ \times 10^\circ$ tiles and covers forest loss over the period 2000-2023. The pixel value of this layer reflects the year of forest cover loss. This layer was used to produce a windfall area in the period 2015-2016 (Article 3).

2.2.2 Satellite images and data

Sentinel-2 satellite imagery has a high spatial resolution of 10 metres and was used to detect standing tree mortality caused by bark beetle infestation (Article 3). Coniferous forest mortality induced by bark beetles was classified using k-means clustering and performed in Google Earth Engine (Gorelick et al., 2017). The validation dataset was created using high-resolution Google Earth imagery.

The Shuttle Radar Topography Mission (SRTM) Digital Elevation Model (DEM) (NASA, 2013) with a resolution of 90 m was used in Article 3, and the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global DEM (NASA, 2024) with a spatial resolution of 30 m was used in Article 4.

2.2.3 Thermographic and hyperspectral surveys

Thermographic data collection focused on forest canopy temperature as a potential indicator of tree stress. The DigiTHERM thermal sensor with a spectral range of 7.5–14 μm was mounted on an SDO 50 V2 VTOL drone to acquire high resolution thermal imagery with a spatial resolution of 0.1 m in the Article 1 study area. The thermal survey was carried out on 7 August 2020.

Surface temperature data were provided by the TASI-600 sensor for the Article 2 study area. The spatial resolution of this thermal data is 1.25 metres. This thermographic sensor was mounted on a Cessna 208B Grand Caravan with hyperspectral sensors and the survey was performed on 11 August 2023. Both surveys were conducted at times of peak midday solar radiation to maximise temperature contrasts between stressed and unstressed trees.

Hyperspectral data were acquired using two sensors: CASI-1500, operating in the visible and near infrared (VNIR), and SASI-600 in the shortwave infrared (SWIR) spectrum. This survey was conducted alongside thermal data acquisition on 11 August 2023. The spatial resolution of hyperspectral data ranged from 0.5 m (CASI-1500) to 1.25 m (SASI-600). The acquired images were compiled into a mosaic and then vegetation spectral indices were calculated to analyse the spruce stand condition.

2.2.4 LiDAR data

Airborne LiDAR surveys provided structural information on the forest canopy and a cloud point for solar radiation calculation. In the study area in Article 1, LiDAR data were acquired using a Leica ALS70-CM sensor on board a Cessna 206. In a separate LiDAR campaign for the study area of Article 2, a Riegl LMS Q-780 scanner was used on a Cessna 208B Grand Caravan in August 2022. These LiDAR surveys captured the forest canopy to complement the hyperspectral and thermographic survey.

The point clouds were processed through noise filtering, ground classification, Canopy Height Model (CHM) generation, and canopy density index calculation (Kane et al., 2010; Khosravipour et al., 2014). CHM was used for crown delineation. Structural attributes derived from the LiDAR data, such as canopy height and canopy density index, were then integrated with other data in the analysis.

LiDAR point clouds were processed using LasTools (ver. 220926; LasTools, 2022) in Article 1, while in Article 2, they were processed in RStudio (v. 4.3.3, RStudio Team, 2023) using the lidR package (Roussel et al., 2020). The delineation of the crowns was performed in RStudio using the ForestTools library (Plowright, 2023).

2.2.5 Solar radiation modelling

Solar radiation was modelled at both tree canopy and landscape scales. At the canopy level in Articles 1 and 2, the Point Cloud Solar Radiation Tool (PCSRT; Pružinec and Ďuračiová, 2022) and LiDAR data were used to calculate the direct and diffuse solar radiation

components according to the voxel-based approach. At the landscape level in Articles 3 and 4, potential solar radiation was modelled using the SRTM DEM with the “Area Solar Radiation” toolbox in ArcGIS 10.6.1 (Esri, 2011), and the ASTER Global DEM in GRASS GIS 7.8 (GRASS Development Team, 2020) and the TANABBO II tool (Pirtskhalava-Karpova et al., 2024).

2.3 Field surveys, forestry, climate and sensor data

2.3.1 Sap flow and additional physiological measurements

The sap flow of spruce trees was measured continuously at 10-minute intervals using EMS81 sensors manufactured by EMS Brno in the Czech Republic. The sensor is installed at breast height (Fig. 5) and measured sap flow in kilograms per second per centimetre ($\text{kg s}^{-1} \text{cm}^{-1}$) using trunk heat balance principle (Čermák et al., 2004). The sap flow data were recorded at 10-minute intervals using a GreyBox N2N 3P data logger connected to a cloud system for real-time data delivery and storage. Prior to subsequent analysis, raw sap flow values were preprocessed in the manufacturer's Mini 32 software (Singh et al., 2025).

In addition to sap flow measurements, bark temperature was recorded on the north and south sides. Soil temperature and soil water potential were measured using 2–5 soil sensors per subplot (Stříbrská et al., 2022). Sap flow, bark and soil temperature, and soil water potential were extracted on 11 August 2023 to align with the aerial survey activities. Spruce trees in the study plots were visually inspected for signs of bark beetle attack in August and September 2023.

2.3.2 Field, forest inventory, bark beetle trapping and climate data

Field test plots were established on Kunashir Island in the southern part of the Kurilskiy Nature Reserve, particularly in the Golovnin Volcano Caldera and the Danilovskiy Field (Article 3). Ten circular plots with a 20-metre radius were initially established in 2019, followed by an additional four plots in 2021. Each standing tree in the test plots was measured for height, DBH and age. The health status of conifers was classified as green (healthy), red or grey based on visual inspection. In addition, the presence of beetles under the bark of deadwood was examined at breast height.

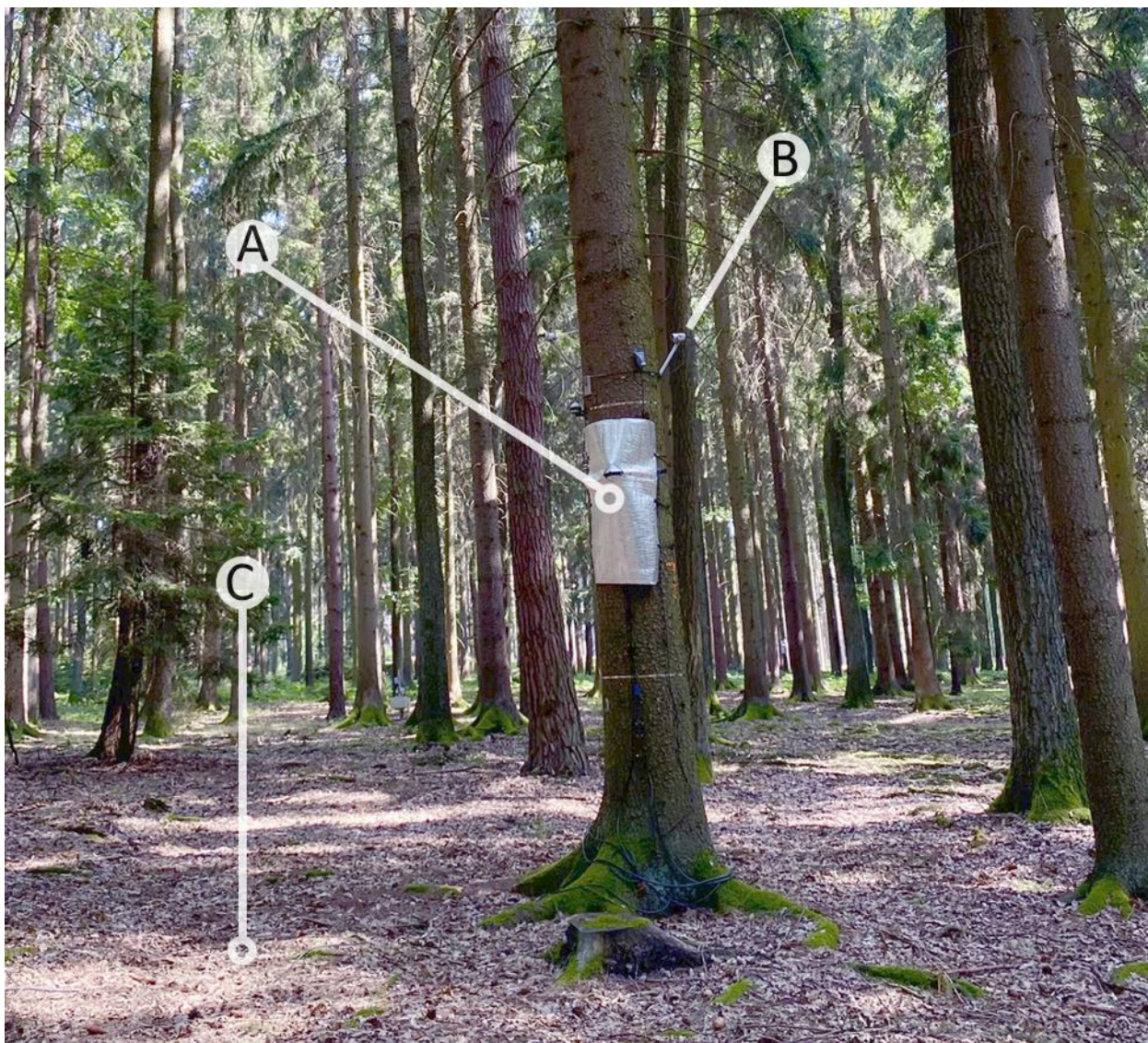


Figure 5 – Control plot in the ŠLP study area. Sensors installed on a spruce tree: A – sap flow sensor; B – bark temperature sensor; C – soil water potential sensor (photo: Nana Pirtskhalava-Karpova).

Field data on bark beetles caught in pheromone traps were collected at several sites during the 2014 and 2015 growing seasons in Horní Planá study area (Article 4). The number of bark beetles caught in pheromone traps was included in our datasets, together with specific characteristics of the forest management unit, such as the percentage of spruce and the age of the forest, extracted for each trap location based on the forest management plan. Meteorological parameters, including average and maximum temperatures, precipitation and solar radiation, were collected from a weather station located at approximately 1100 m a.s.l. in the study area.

2.4 Statistical analysis

Statistical analyses for Articles 1–3 were conducted using R software (version 4.3.3; R Core Development Team, 2023) within RStudio, while Article 4 was analysed in Python (version 3.11.1; Rossum & Drake, 2010) using Visual Studio Code (version 1.73.1). The datasets were checked for missing values and outliers. Checks for autocorrelation and collinearity were also performed on the variables in the datasets. Statistical tests were used to compare groups, while modelling approaches provided insights into more complex relationships and identified influencing factors.

The assumption of normality was tested using the Shapiro-Wilk test, and homogeneity of variance was assessed using Levene's test. Non-parametric Kruskal-Wallis and parametric ANOVA tests were then used to detect significant differences between groups in the datasets. Pairwise comparisons were carried out using Dunn's and Tukey's post hoc tests. Boosted Regression Tree (BRT) models were used to calculate the contribution of each explanatory variable in the datasets to the predicted variable. The relative contribution of each predictor was scaled so that all variables summed to 100%. The optimal BRT model was selected based on the highest mean cross-validation correlation and training data correlation. This modelling approach was used to identify drivers of canopy temperature and disturbance severity in Articles 1 and 3.

In Articles 2 and 4, Linear Regression (LR) and Generalised Additive Models (GAMs) were applied. Both studies used an information-theoretic (I-T) approach to model selection. Candidate models were ranked using the Akaike Information Criterion (AIC). Models with a ΔAIC less than 2 were considered the best fit. Those with a ΔAIC between 2 and 7 were considered plausible alternatives. Akaike weights measured the relative likelihood of each model. The best model performance was measured by the adjusted R-squared and Root Mean Square Error (RMSE) criteria. In Article 2, the significance of the GAM predictors was assessed using F-statistics and effective degrees of freedom (EDF).

Analyses in Articles 1–3 made use of R packages including *dismo* and *gbm* for BRT (Ridgeway, 2007; Elith and Leathwick, 2011; Hijmans et al., 2023), *mgcv* for GAMs (Wood, 2017), *corrplot* (Taiyun & Simko, 2021), and *dunn.test* for non-parametric post hoc comparisons (Dinno, 2024). The Python workflow in Article 4 used *pandas* (1.5.0) for data manipulation, *numpy* for numerical operations, *scikit-learn* (1.3.0) for regression and cross-validation, *statsmodels* (0.15.0) for statistical tests, and *pyGAM* (0.5.5) for GAM fitting.

3. Results

This thesis combines high-resolution remote sensing and field data to elucidate how crown structure, microclimate and drought stress determine the vulnerability of spruce to bark beetles. At the stand scale, thermal data and spectral indices linked stand characteristics and canopy architecture to physiological stress, while landscape-scale analyses showed how species composition and landscape characteristics determined outbreak spread. Finally, the incorporation of phenological modelling with drought indices proved effective in predicting spruce bark beetle swarming periods at a fine spatial scale and mapping potential risk areas.

3.1 Analysis of solar radiation and thermography data using tree crowns parameters for Norway spruce

Published as: Karpov, A., Pirtskhalava-Karpova, N., Trubin, A., Surovy, P., & Jakuš, R. (2025). Analysis of solar radiation and thermography data using tree crowns parameters for Norway spruce. In *Forest Ecology and Management* (Vol. 582, p. 122557). Elsevier BV. <https://doi.org/10.1016/j.foreco.2025.122557>

The main objectives of this study were to quantitatively compare the relative effects of crown and canopy characteristics on spruce crown temperature and solar radiation, and to investigate the relationship between solar radiation and crown temperature.

This study identified four factors: area of forest gaps, LiDAR canopy density index, tree height and standard deviation of crown height using BRT approach. These predictors have significant and broadly comparable influences on crown temperature and retain their importance for predicting solar radiation. However, tree height was found to be the strongest determinant of insolation. Higher crown temperatures and solar radiation were associated with increases in gap area, tree height and southern crown openness.



Analysis of solar radiation and thermography data using tree crowns parameters for Norway spruce

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ARTICLE INFO

Keywords:

Norway spruce
Thermography
LiDAR
Solar radiation modelling
Voxel

ABSTRACT

This study investigates how tree crown and forest canopy characteristics affect crown temperature and solar radiation in Norway spruce (*Picea abies*) stands, providing insights into forest health and the potential impacts of climate change. The research was conducted at the School Forest Enterprise near Kostelec nad Černými Lesy in the Czech Republic. Using a dataset from LiDAR and thermographic surveys, our research utilises the Point Cloud Solar Radiation Tool to model solar radiation. The voxel method was applied to the LiDAR data to calculate solar radiation. In addition, LiDAR data were used for crown segmentation and to assess individual tree parameters such as height, variability in crown height, crown area, canopy density index, the openness of the crown to gaps from south direction, area of forest gaps surrounding the tree. The findings indicate that the average crown temperature is significantly influenced by gaps area, the crown density, tree height, crown area, and crown openness to the south. For solar radiation, factors such as height of trees, crown density, and gaps area were found to be important. This research provides valuable insights for the development of effective forest management strategies, particularly for adapting to and mitigating the effects of climate change under the threat of bark beetle outbreaks.

1. Introduction

Forests cover a significant proportion of Earth's surface, and they play an integral role in regulating global energy balance and biodiversity. Canopy temperature can serve as an indicator of the physiological condition of trees, acting as early warning signs of potential issues. The impact of climate change on forests is a pressing issue. Rising global temperatures have forced us to seek new approaches to forest management in order to reduce the impact on the distribution and behaviour of insect pests, which has led to increased forest damage (Solomon et al., 2007; Seidl et al., 2008; Allen et al., 2010). Current forest management practices utilise a variety of tools for measuring and analysing forest environments, including structure, biomass, and temperature. These tools employ advanced techniques such as 3D LiDAR mapping (Morsdorf et al., 2006; Solberg et al., 2009). This context sets the stage for a comprehensive examination of forest canopy temperatures and solar radiation amount and their implications for forest health and management.

Leaf temperature deviations in plants are indicative of physiological changes and serve as an early indicator of disruption to plant functioning. These deviations are closely linked to stomatal activities, which facilitate photosynthetic gas exchange and transpiration under optimal conditions, leading to cooler canopy temperatures due to effective transpirational cooling (Roelfsema and Hedrich, 2005; Daley and Phillips, 2006). In contrast, canopies under stress exhibit higher temperatures, which are often attributed to disrupted transpirational processes. In the case bark beetle infestation, the feeding of the beetles and their larvae on floem disrupts the hydration function of the tree (Wermelinger, 2004). The hydration level of plants is crucial in determining stomatal behaviour, which in turn affects the canopy temperature (Costa et al., 2013). Understanding the relationship between hydration, stomatal function, and canopy temperature is crucial for assessing plant stress and health.

Previous studies have demonstrated that older forest stands with higher biomass and closed canopies generally exhibit lower temperatures than younger forest stands. These studies have established a

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<https://doi.org/10.1016/j.foreco.2025.122557>

Received 6 January 2025; Received in revised form 9 February 2025; Accepted 10 February 2025

Available online 19 February 2025

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correlation between canopy closure and thermal data, with denser canopies correlating with lower temperatures. Furthermore, there have been findings of higher canopy temperatures in pine trees experiencing moisture stress and bark beetle infestation (Weber, 1971; Olson, 1972). Recent research by Zakrzewska and Kopeć (2022) supports these findings by demonstrating that thermal infrared survey combined with laser scanning can effectively identify healthy, stressed and dead Norway spruce trees based on canopy temperature. Also, self-shading conditions have been found to be an important factor associated with tree survival during bark beetle outbreaks, highlighting its importance in the context of forest health and resilience (Jakuš et al., 2011; Korolyova et al., 2022a, 2022b). Forest canopy temperature can be measured effectively using thermal sensors in the thermal infrared spectrum at both regional and local levels. These sensors are highly effective in the 8–14 µm range, which is commonly used in remote sensing due to its minimal interference from reflected sunlight (Smigaj et al., 2023).

The thermal infrared region of the electromagnetic spectrum is extensively used in remote sensing, with applications ranging from climatology to ecology. Thermography is an essential tool in forestry research. At the regional level, studies utilising thermal infrared data, primarily from sensors such as MODIS, NOAA-AVHRR, and the Landsat constellation, have been instrumental in identifying areas that are vulnerable to forest fires and drought stress (Leblon, 2005; Manzo-Delgado et al., 2009; Fernandes et al., 2022). Increases in canopy temperature have proven to be more effective than standard vegetation indices in detecting defoliation caused by insect outbreaks using this technology (Abdullah et al., 2019). At a local level, the use of thermal cameras mounted on Unmanned Aerial Vehicles (UAVs) or aircraft has revealed that trees experiencing biotic stress, such as insect and disease outbreaks, exhibit higher canopy temperatures, indicating higher levels of stress (Smigaj et al., 2023; Zakrzewska and Kopeć, 2022). UAVs have become increasingly significant in recent years, providing the ability to obtain high-resolution data from mounted sensors for detecting stress in individual trees.

Currently, various remote sensing techniques are employed to assess forest cover, ranging from satellite and drone images in the optical and infrared range to LiDAR scanning and thermographic surveys of forest canopy (Smigaj et al., 2023). LiDAR data can provide detailed information on crown structure, while thermographic data can reflect physiological stress within the stand. LiDAR data can form the basis for generating a 3D model with which to compute solar radiation. This article presents an evaluation and comparison with thermographic survey of a novel approach using a voxel-based model for solar radiation modelling. This method enhances understanding of the forest canopy environment, which could lead to more effective strategies for managing forests comprised predominantly of Norway spruce (*Picea abies*) and controlling spruce bark beetle (*Ips typographus*) infestations.

The study analysed data from a thermographic and LiDAR survey of the forest canopy, and modelled the amount of solar radiation at the tree crown level. The research methodology involves the use of the Point Cloud Solar Radiation Tool (PCSRT; Pružinec and Ďuračiová, 2022) to model solar radiation in 3D space, particularly in complex environments such as those with vegetation. PCSRT employs the European Solar Radiation Atlas model to calculate direct and diffuse solar radiation components. The software converts point clouds into 3D voxel grids and computes insolation for designated time frames. LasTools software (LasTools, 2022) was used to process LiDAR data and to construct the Canopy Height Model (CHM), and the Forest Tools library in RStudio was used for crown delineation. Data on the structure and parameters of each tree crown were prepared based on LiDAR data. A dataset was collected for further analysis, and it contained data on crown structure and parameters, solar radiation, and crown temperature. The Boosted Regression Trees (BRT) model was used in our study to analyse the various factors that influence crown amount of solar radiation and temperature, with a specific focus on the role of solar radiation.

The objectives of this study included the following: quantitative

comparison of the relative effects of tree crowns and forest canopy characteristics on spruce crown temperature and solar radiation; investigation of the relationship between solar radiation and crown temperature.

2. Material and methods

2.1. Study area

The study area is located in the area of the School Forest Enterprise (ŠLP) around the town of Kostelec nad Černými Lesy in the Central Bohemian region of the Czech Republic. The research area is 230 m long, 150 m wide, and it is located in forest management units that are dominated by Norway spruce (45–100 %) ranging in age from 50 to 110 years (Fig. 1). The centre of this area is at longitude 14.827054°E, latitude 49.970676°N, and an elevation of 450 m above sea level (a.s.l.). The ŠLP area experienced a spruce bark beetle outbreak, which peaked in 2020. Sanitary felling was carried out to prevent the spread of the spruce bark beetle (Trubin et al., 2023; Pirtskhalava-Karpova et al., 2024).

The soil across the ŠLP is granodiorite covered with Luvisol (Singh et al., 2024). The climate is characterised by drier and warmer summers, with an average annual temperature of 7.5°C and annual rainfall of 600 mm (Tolasz et al., 2007). More detailed recent climate data from the Ondřejov weather station (id P3ONDR01, Český hydrometeorologický ústav (CHMÚ), n.d), located approximately 8 km from the study area and at an elevation of 491 m a.s.l., indicated that in August 2020 the maximum temperature reached 25.3°C with an average temperature of 19.2°C. During the summer months from June to August, total precipitation was recorded at 248.8 mm, with July recording the minimum monthly precipitation of 33.4 mm.

2.2. Preprocessing LiDAR dataset

For the ŠLP area, a LiDAR data survey was carried out in 2022. The characteristics of the LiDAR sensor, the acquired data for the study area, and the date of the survey are summarised in Table 1. The LiDAR dataset was processed using LasTools (ver. 220926; LasTools, 2022). Noise removal, ground point classification, and additional processing were applied to the point clouds to produce the Canopy Height Model (CHM; Khosravipour et al., 2014), calculating the canopy density index (Canopy; Kane et al., 2010) based on the ratio of first returns that are 3 m above ground to all returns. This is performed step's description in the following order using LasTools:

1. Noise removal (lasNoise): A step size of 1 m was used in the x, y, and z directions to identify and remove noisy points (points with significant deviation from surrounding points) that were isolated within a 5-unit neighbourhood.
2. Ground point classification (lasGround): This was used to classify ground and non-ground points. The "hyper_fine" parameter allowed detailed ground surface extraction, and the "replace_z" option recalculated the vertical coordinates of each point by measuring the height from the ground surface.
3. CHM construction (las2dem): CHM layers were constructed by filtering out points based on height, specifically excluding points below 0.1 m and above 2 m, below 2 m and above 5 m, and continuing in 5 m increments up to 45 m elevation. The maximum values of these layers were integrated into a pit-free CHM layer using the QGIS v. 3.22.11 raster calculator tool. A 'pit-free' CHM is a refined representation that is cleared of inaccuracies caused by laser beams hitting lower obstacles. This ensures a smoother and more accurate representation of the canopy (Khosravipour et al., 2014; QGIS.org, 2022). The CHM layers have a horizontal resolution of 0.3 m.

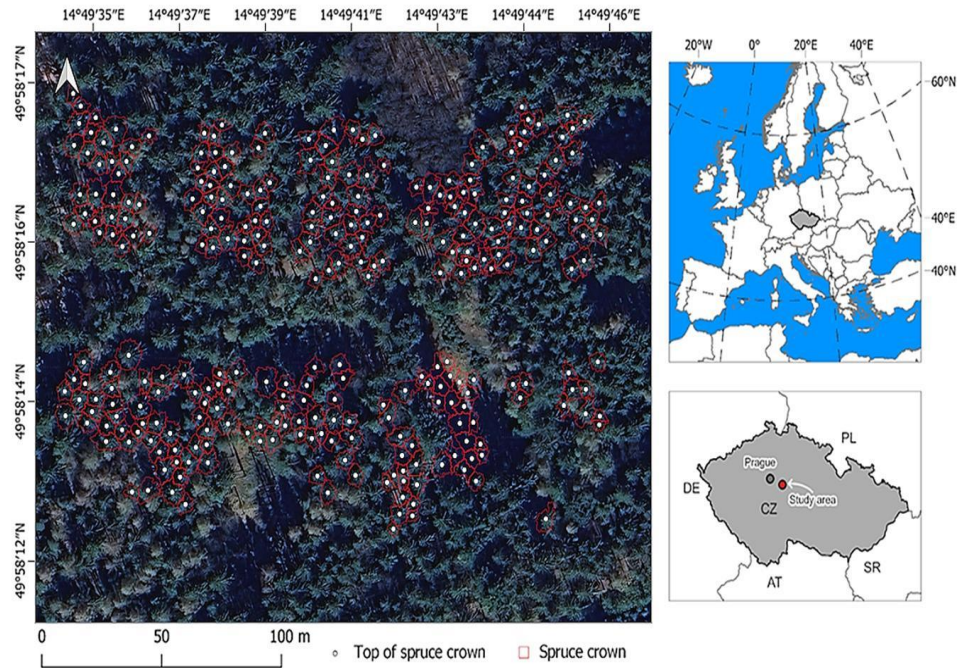


Fig. 1. Map of study area.

Table 1

Name of sensors, airplane, drone and characteristics of LiDAR and thermal data.

	LiDAR	Thermal data
Sensor	Leica ALS70-CM	DigiTHERM
Airplane/drone	Cessna 206	SDO 50 V2 VTOL
GPS/INS	SPAN3.911/CR56	Novatel OEMV1
Characteristic of data	Point density: all returns	Spatial resolution: approx.
	24.96 last only 12.76 sq. m	10 cm Size of image: approx.
	Spacing: all returns 0.20 last only 0.28 sq. m	40x60 m
Time and date	17.07.2020	11:27 – 11:33 a.m. 07.08.2020

4. Canopy calculation (lasgrid): Two raster layers were generated. The first layer included all LiDAR returns, and the second layer included only the first return above 3 m. The Canopy was calculated in the QGIS raster calculator as the ratio of the first returns above 3 m to all returns (Kane et al., 2010).

2.3. Crown delineation

The Forest Tools library in RStudio v. 4.3.1 (RStudio Team, 2022) was utilised for crown delineation based on the pit-free CHM raster layer. Tree crowns with a minimum height of 20 m were identified and then polygons were created around these crowns, also using the 20 m minimum height criterion. A linear function $x \times 0.05 + 0.6$ was used for delineation (Plowright, 2023). The delineated spruce crowns were manually selected using high-resolution drone imagery and Google Earth images. The quality of the crown delineation was then evaluated visually, and any crowns that were incorrectly delineated were excluded from the subsequent analysis.

2.4. Solar radiation

Solar radiation for each LiDAR point was determined using PCSRT method, which calculates the direct and diffuse solar radiation

components and insolation time using a voxel approach (Pružinec and Đuračiová, 2022). Parameters included geographical coordinates of the centre of the study area and elevation, a time frame from 11:00 to 11:30 am (10-minute intervals) on 7 August 2020. This time corresponded to the thermal image acquisition period (Table 2). The Link turbidity factor was set to 3.8 based on data from the SoDa service site (SoDa Service, 2023). This is a factor that is used to evaluate water clarity and pollution levels. Higher values indicate greater turbidity. The noise-removed LiDAR dataset was used to calculate solar radiation. The PCSRT automatically fitted the voxel size, which was found to be 1.03 m, or an average of 3.7 LiDAR points were used for each voxel. Direct solar radiation values from cloud points were rasterised using CloudCompare v. 2.13 (CloudCompare, 2023) with a spatial resolution of 1 m, averaging values per pixel.

2.5. Preprocessing thermal images

A drone thermographic survey was carried out for the study area in 2020. The characteristics of the thermal sensor, the data acquired, and the date of the survey are summarised in Table 1. The thermal sensor

Table 2

Names and descriptions of variables.

Variable	Unit	Description
H	m	Height of tree
H_SD	m	Standard deviation of crown height based on Canopy Height Model
Crown_area	m ²	Crown area
Distance	m	Distance crown from centre of thermal image
Gaps_area	m ²	Sum area of forest gaps, which touches the crown
Canopy	-	Lidar canopy density index, which represents ratio of first returns above ground 3 m to all returns
Tmean	°C	Average temperature of crown
SolRad	W/m ²	Average solar radiation of crown
S_percent	%	Openness of the crown to the forest gaps on the South side

DiGiTHERM is designed with a spectral range of 7.5–14 μm and is equipped with an automated internal temperature calibration system, which takes dark images at 30 s intervals to facilitate self-calibration. Thermal image files were converted from irb to tiff format for subsequent data processing using IRBIS software v. 3 (InfraTec, 2023). The thermal imagery was then georeferenced in QGIS using the tree top and crown boundaries generated by the Forest Tools library in R. The spatial resolution of the georeferenced thermal images was 0.1 m.

2.6. Data preprocessing and cleaning

Height and crown area of each tree (variables H, Crown_area, Table 2) were measured using the Forest Tools library in Rstudio after the crown delineation procedure. Average of crown temperature, solar radiation, Canopy per crown, and standard deviation of tree height (variables Tmean, SolRad, Canopy, H_SD, Table 2) were calculated using the zonal statistics tool in QGIS based on CHM, solar radiation and Canopy rasters. Distances from the centre of each georeferenced thermal image to the top of the tree crowns were determined using the “Distance matrix” tool in QGIS. This tool is used to calculate the shortest distance to an object (variable Distance, Table 2).

Furthermore, a forest gap layer was produced by subtracting the spatial layer of delineated tree crowns from the polygon layer with georeferenced thermal image boundaries. The resulting polygon layer was split into separate forest gap polygons. The area of each gap was then determined using the Field Calculator in QGIS. The area of forest gaps touching tree crowns was attached to the attributes of the tree crown spatial layer using the “Join Attributes by Location” tool in QGIS. The areas of all forest gaps touching a crown were also added together, based on added attribute data (variable Gaps_area, Table 2).

To determine the intersection length of each crown with a forest gap, the aforementioned polygon layers were converted into linear layers. The intersections between these linear layers were identified and length in metres was calculated for each tree crown. The percentage of intersection by different crown directions such as North, West, East, and South was calculated by dividing the length of forest gaps intersected by the crown by the total perimeter of that crown segment direction. The analysis was conducted using only the values of crown openness from the South (variable S_percent, Table 2), as this is the direction from which the largest amount of is received at midday. Prior to analysis, the variables were tested for correlation. The correlation matrix of variables is shown in Table S1. Additionally, the distribution of each variable and scatter plots with linear regressions are presented in Fig. S3.

The LiDAR and thermal imagery data were acquired at different times. As a result, several of the trees that were visible in the thermal imagery had already been felled. These tree crowns were excluded from subsequent analyses. Spruce crowns were validated by visual analysis of high-resolution drone imagery with a spatial resolution of 0.1 m. The dataset includes 297 spruce crowns. Only spruce tree crowns that were entirely within the boundaries of the thermal images were used for further analyses.

2.7. BRT analysis

The primary determinants of average canopy temperature and solar radiation of spruce crown were investigated using the Boosted Regression Trees (BRT) machine learning approach. We used the entire dataset for both training and evaluation through cross-validation, as implemented in the “gbm.step” function of the “dismo” library in Rstudio (Hijmans et al., 2023). This approach is robust and widely accepted for model evaluation, as detailed in Elith et al. (2008). The “gbm.step” function performs k-fold cross-validation, with 10 folds by default. The data are divided into k subsets, and the model is trained on k-1 subsets while being validated on the remaining subset. This process is repeated k times, allowing the model to be assessed for its ability to generalise and avoiding overfitting by evaluating the average performance across all

folds.

The optimal set of parameters for tuning the models of the methods was identified through a process of enumeration, whereby all the most important parameters of the model were considered. For each case, 45 BRT models were evaluated using different parameters: bag fractions of 0.5, 0.75, 1; tree complexities of 1–5; and learning rates of 0.1, 0.01, 0.001. The evaluation of several models was carried out through a comparative analysis to identify the optimal model, based on specific parameters:

1. Correlation with Training Data. A higher correlation value indicates a better fit to the data than other models.
2. Mean cross-validation (CV) correlation. A mean CV correlation that is similar to the correlation of the training data indicates an effective generalisation ability of the model and avoids overfitting.
3. Reduction in mean residual deviance. The extent to which the mean residual deviance is reduced relative to the mean total deviance is an indication of the fit of a model. A significant reduction suggests that the model is effectively capturing the underlying patterns in the data.
4. Estimated mean CV deviation. A lower value indicates that the model is likely to perform well on new data.

3. Results

The optimal BRT model of average crown temperature used a tree complexity of 4, a learning rate of 0.01, and a bag fraction of 0.5. This model produced a mean total deviance of 0.62 and a mean residual deviance of 0.32. The training data correlation was 0.75 and a CV correlation of 0.31 (standard error = 0.066) with the estimated CV deviance was 0.555 (standard error 0.055). This demonstrated the highest correlation with the training data and no sizable differences in other statistical parameters such as mean residual deviance, mean total deviance, and estimated mean CV deviance when compared to other models. This suggests that the model was an adequate fit for the data, and that the model parameters conformed to our established model estimation rules. The predictors impacting this model, in order of influence, are Gaps_area, Canopy, H, H_SD, Crown_area, S_percent (Fig. 2; Table 3). The crown temperature increased simultaneously with increases in the values for Gaps_area, H and S_percent. The canopy influence function shows an initial decrease followed by a sharp increase at values around 0.55 (Fig. 2). This may be related to a few cases of extremely high crown temperatures with high canopy density values (see Fig. S2). The predictor Crown_area is difficult to interpret based on its influence function on crown temperature, as the function has several sections of both increasing and decreasing influence on crown temperature.

A BRT model with the same parameters was used to estimate average crown temperature, but a variables for SolRad and Distance were also included in the dataset for analysis. This model produced a mean total deviance of 0.62 and a mean residual deviance of 0.20. The training data correlation was 0.87 and a CV correlation of 0.36 (standard error = 0.072) with the estimated CV deviance was 0.54 (standard error 0.059). The SolRad variable has the greatest effect on crown temperature after Gaps_area (Fig. S2; Table 3), and increasing solar radiation increase crown temperature. Increasing the Distance variable also has an effect on the increase in canopy temperature, especially at a distance of 25 m from the centre of the thermal image to the centre of the spruce crown. The other variables have the same pattern as in the first model (Fig. S1).

The optimal BRT model of average solar radiation had the following parameters: tree complexities: 4, learning rate: 0.1, and bag fraction: 0.5. This model produced a mean total deviance of 29013.12 and a mean residual deviance of 13875.65. The training data correlation was 0.74, a CV correlation was 0.49 (standard error = 0.024), and the estimated CV deviance was 23102.41 (standard error 2472.12). This suggests that the model was an adequate fit for the data, and the parameters of the model are consistent with our model estimation rules. The results indicated that an increase in the values of H, Canopy, Gaps_area and S_percent was

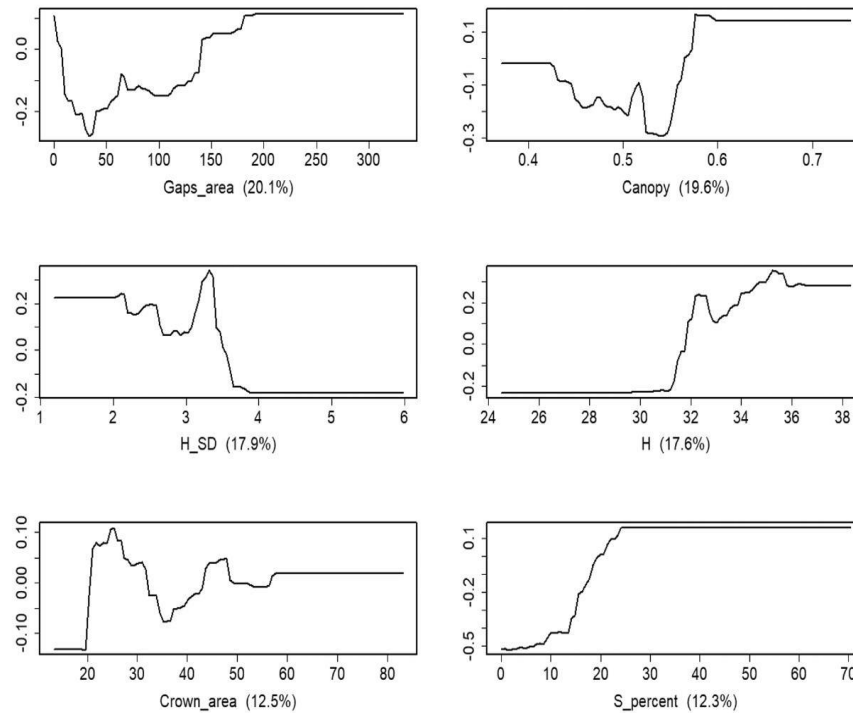


Fig. 2. The function of the influence of each predictor on average temperature crown BRT modelling.

Table 3

Influence of predictors on average temperature and solar radiation of spruce crown.

Predictor	Average temperature of spruce crown, %	Average temperature of spruce crown, % (with SolRad and Distance)	Average solar radiation of the spruce crown, %
SolRad	-	15.2	-
Canopy	19.6	14.1	17.9
H	17.6	10.5	34.4
Crown_area	12.5	10.0	11.2
Gaps_area	20.1	15.6	17.9
Distance	-	12.3	-
H_SD	17.8	13.3	11.5
S_percent	12.3	8.7	3.9
R ²	0.48	0.69	

associated with an increase in crown solar radiation, while a decrease in the values of H_SD and Crown area was linked to a reduction in solar radiation (Fig. 3; Table 3). This pattern was observed to be similar to that observed in the model estimation of crown temperature (Fig. 2).

4. Discussion

In this study, we used a BRT approach to quantitatively assess the interactions between crown temperature and solar radiation and crown characteristics. The analysis identified key variables such as the area of forest gaps (Gaps_area), LiDAR canopy density index (Canopy), tree height (H) and standard deviation of crown height (H_SD) as significant influences on crown temperature, each with comparable effects. These variables also played a significant role in modelling solar radiation, with tree height (H) showing a particularly strong influence compared to the others. The dynamics between these variables revealed a clear pattern: increases in the area of forest gaps (Gaps_Area), the height of the tree (H) and the openness of the crown on the south side (S_percent) led to

increased crown temperature and solar radiation values, whereas decreases in the standard deviation of the crown height (H_SD) led to lower values. The effect of the canopy density index (Canopy) was complex; while increasing Canopy values increased solar radiation, crown temperature initially decreased to a value of 0.55 and then increased sharply.

4.1. Effect of height of tree stand and canopy density on crown temperature

Foliage that is fully exposed to the sun in the upper canopy will typically experience higher temperatures, due to greater exposure to the sunlight. These leaves also have higher transpirational cooling rates compared with the rates in the lower, partially shaded parts of the crown (Sack et al., 2006; Reinert et al., 2012). Our research indicates that tree height is a significant factor in determining the average temperature of the crown (H - 17.6 %), along with the LiDAR index of stand density (Canopy - 19.6 %) and spruce crown area (Crown area - 12.5 %). The crown area and tree height are significantly related parameters, and their percentages of influence may overlap. Nevertheless, these variables were not highly correlated in our dataset (Table S1).

In a separate analysis, Webster et al. (2018) contribute to this discussion by examining the vertical temperature gradients of trees. The research of those authors demonstrates that in standalone trees, such as Norway spruce, temperature gradients tend to decrease with increasing height. Conversely, dense tree stands exhibit positive temperature gradients due to self-shading, that protects the lower canopy from direct solar radiation. These findings highlight the cooler temperatures in the lower canopy of dense forests, as opposed to standalone trees that receive uniform sun exposure along their vertical profile.

In contrast, Junttila et al. (2016) found a robust negative linear correlation between canopy height and relative surface temperature, suggesting that taller, mature trees tend to have cooler canopies than younger trees. The study of those authors focused on sample plots with a

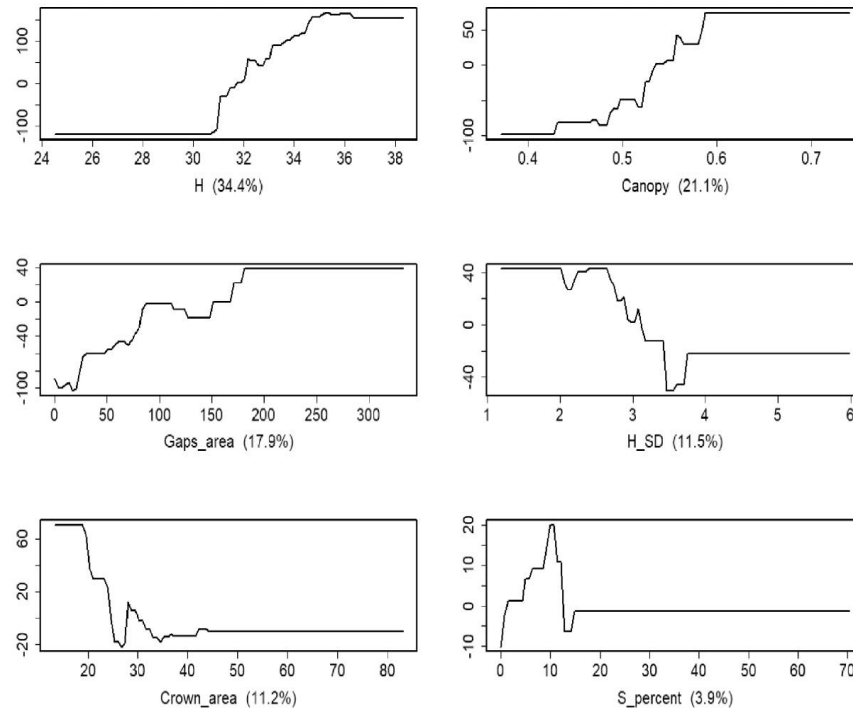


Fig. 3. Function of the influence of each predictor on solar radiation BRT modelling.

radius of 9 m, rather than on individual Norway spruce crowns. These findings may have been influenced by colder and more humid Finland's weather conditions than the conditions noted in other studies. The thermal imagery was acquired at a low temperature of around 3 °C, causing the stomata of trees to nearly close, and resulting in a transpiration rate close to zero (Hällgren et al., 1982; Schwarz et al., 1997). Additionally, Junttila et al. (2016) found that the impact of structural crown factors on surface temperature was greater than the impact of crown defoliation. As the percentage of defoliated trees increased, there was a corresponding increase in relative surface temperature.

A higher density of healthy crown foliage can effectively reduce canopy temperature by increasing transpiration if the tree is not under water stress (Roelfsema and Hedrich, 2005; Costa et al., 2013). In other hand, canopy architectural traits, such as leaf density, branching pattern, and the vertical distribution of leaves, are crucial in temperature regulation through convective heat exchange (Leuzinger and Körner, 2007). Trees with compact canopies and high leaf density tended to dissipate heat more slowly, resulting in warmer temperatures, whereas trees with more open canopies often had temperatures that were equal to, or lower than, the ambient air temperature (Leuzinger and Körner, 2007; Scherrer et al., 2011).

In the present study, while we did not directly measure the degree of crown defoliation, we used canopy density index (Canopy) to analyse crown temperature. A decrease in this index correlates with a decrease in crown temperature up to Canopy value of 0.55 and increases sharply after this value. Our results may also be influenced by several factors, including an increase in foliage cover within the spruce stand, which affects transpiration rates and subsequently reduces canopy temperature. In addition, variations in crown architecture and features of the dataset, which includes several crowns with higher temperatures associated with high Canopy index values (Fig. S2), also contribute to the results.

4.2. Effect of forest structure and other factors on crown temperature

The crown structure, including leaf density, branching patterns, and vertical canopy distribution, is essential for heat exchange. The principles discussed in part 4.1 of this paper are applicable, not only to thermal exchange for a single tree, but also to the forest canopy as a whole, which includes forest gaps, edges, and patches with denser and less dense stands (Leuzinger and Körner, 2007). Forest gaps and edges can increase the potential for heat exchange, but gaps in the forest from the south also increase the amount of sunlight reaching tree stands on the edge of the forest. In this context, our thermographic survey, conducted at noon on a cloudless day with direct solar radiation coming from the south, showed that south-facing openness (S_percent - 9.0 %) substantially influenced crown temperature, with increases in openness correlating with higher temperatures. Moreover, the area of forest gaps (Gaps_area - 20.1 %) had a more pronounced effect on crown temperature, due to reduced shading from neighbouring stands and consequently increased solar radiation falling on trees at the edge of the forest. In addition, the distance between the thermography sensor and the point of measurement is critical in measuring canopy temperatures (Aubrecht et al., 2016; Kim et al., 2018). The distance of the tree crown from the centre of the thermal image accounted for 12.8 % of the variance in crown temperature values in our study. When the Distance variable exceeds 25 m, it significantly affects the recorded crown temperature.

Atmospheric factors have a significant influence on the acquisition of thermography data. Thermal measurement can be affected by relative humidity and air temperature. Low relative humidity and a high vapour pressure deficit, together with wind, can induce stomatal closure. Conversely, high relative humidity can impede transpirational cooling by reducing evaporation. Stomatal closure occurs in high light irradiance, especially during peak sunlight, to prevent photo-oxidative stress. This can lead to a decrease in photosynthesis and stomatal gas exchange (Zhang and Gao, 1999; Guo et al., 2023), as well as a reduction in transpirational cooling of the canopy. High temperatures also promote

stomatal opening, facilitating transpiration and reducing heat stress. However, stomatal closure in Norway spruce can occur at temperatures above 25 °C, especially when combined with water stress (Urban et al., 2017). The importance of timing in thermographic surveys was emphasised by Smigaj et al. (2015), who found that a strong correlation between canopy temperature and disease level occurred during the period of highest solar radiation.

4.3. Influence of solar radiation on canopy temperature

We observed that the effect of different factors on the prediction of average crown temperature varied in terms of percentage and pattern when compared to solar radiation. The height of the tree has a greater impact on solar radiation (H - 34.4 %) than on crown temperature (17.6 %). Gap area has practically the same effect on canopy temperature (Gaps_area - 20.1 %) as solar radiation (17.9 %). Similar, crown area has a comparable impact on temperature (Crown_area - 11.2 %) and solar radiation (12.5 %). No clear pattern emerges for crown temperature regarding crown area changes. There is an inverse relationship between gaps area and crown temperature. Crown density also has a nearly identical effect on canopy temperature (Canopy - 19.6 %) and solar radiation (21.1 %), but the influence of canopy density index on these models has a different pattern. The present study examined the impact of south-facing openness of the crown. The findings indicated that increased openness primarily elevates crown temperature (S.percent - 12.3 %), while also exerting a relatively minor influence on solar radiation (3.9 %).

We did not find a significant linear relationship between the average crown temperature and the solar radiation falling on the crown. Therefore, we constructed a BRT model to estimate the effect of solar radiation on crown temperature, including other relevant factors. This analysis identified that solar radiation is the significant factor affecting crown temperature prediction, with an estimated influence of 15.6 %. The weak linear correlation between these two variables may be attributed to various factors that affect crown temperature, such as crown structure, defoliation, timing of the survey, weather conditions, water stress, and the physiological state of the tree. Crown temperature can also be influenced by the openness of the crown to forest gaps, and the density of the stand surrounding this tree crown.

4.4. Study limitations

The main issue is the considerable impact of the distance between the thermography camera and the measurement point. This factor becomes particularly relevant when the distance from the centre of the thermal image to the centre of the crown exceeds 25 m. This affects the accuracy and quality of thermal imagery, especially near image edges. Challenges of using thermal infrared data in forest environments have been highlighted by Smigaj et al. (2023). Retrieving surface temperature can be complicated by factors such as the small size of thermography cameras used on UAVs, atmospheric conditions, and canopy characteristics. Miniature cameras can be highly sensitive to rapid changes in body temperature, particularly from external heat, which can influence temperature measurement.

In addition, discrepancy between the timing of the LiDAR and thermal imaging campaigns, which were conducted one month apart. There was also a tree removal activity during this period, but all removed and nearest trees were deleted from the analysed dataset. However, a difference of one month does not result in significant changes in rest canopy cover in the study area. The mismatch in spatial resolution between the 1 m solar radiation and the 10 cm thermal raster layer could pose challenges. However, this study addresses these differences by focusing on averaged rather than pixel-specific data, thus accommodating the resolution disparity within our analytical framework.

4.5. Practical implementation

The methodology of comparing canopy temperature with solar radiation holds is promising for the identification of water-stressed trees and for the detection of bark beetle infestation. This approach requires an understanding of various factors, including crown structure and openness, and their impact on solar energy modelling and crown temperature. High temperature zones indicating water stress can be delineated by comparing thermographic survey data with solar radiation models. Implementing this method could enhance forest management by identifying areas that are vulnerable to bark beetle attacks, and aiding in forest protection strategies. The validation of the solar radiation model against thermal data can have implications for atmospheric, hydrological, and ecological modelling. It offers a broad range of applications for effective thermal measurements of remote environmental landscapes.

In addition, the Distance variable - the distance of a given crown from the centre of the thermal image - is used in the analysis of thermal data. The effect of distance was significant at 25 m from the centre of the images, highlighting its importance in thermal scanning. This variable is essential to improve thermal image overlap parameters when processing thermal mosaics and to reduce errors in thermal measurements.

We recommend further research, in accordance with what has been emphasised by Smigaj et al. (2023). The development and testing of methods for thermal data analysis across different tree species, and under various climatic conditions, are crucial to establish how thermography can supplement existing forest health monitoring approaches.

5. Conclusion

This study contributes to a detailed understanding of the factors influencing crown temperature and solar radiation in Norway spruce stands, with a focus on the impact of tree crown parameters, canopy structure, and forest gaps. Our research shows that the height, forest gaps area and canopy density of the spruce crown has a significant effect on the microclimate around the crown, particularly on temperature and solar radiation. This study emphasises the significance of gaps area in forest canopy; southern gaps have a significant impact on crown temperature. The relationship between solar radiation and crown temperature was found to be non-linear, indicating the presence of complex interplay factors within forest ecosystems. These insights are valuable for forest management strategies, especially in adapting to climatic variations and addressing challenges posed by bark beetle infestations.

CRedit authorship contribution statement

Karpov Aleksandr: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation. **Pirtskhalava-Karpova Nana:** Writing – review & editing, Writing – original draft, Formal analysis. **Trubin Aleksei:** Writing – review & editing, Writing – original draft. **Surovy Peter:** Writing – review & editing, Writing – original draft. **Jakuš Rastislav:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

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.

Acknowledgements

This research was funded by: Development of integrated modern and innovative diagnostic and protection methods of spruce stands with the use of semiochemicals and methods of molecular biology. NAZV –

Ministry of Agriculture – Czech Republic QK1910480. Grant no. CZ.02.1.01/0.0/0.0/15.003/0000433, “EXTEMIT-K” financed by the Operational Program Research, Development and Education (OP RDE). Grant no. 43950/1312/3165 “The study of relationship between spruce stand insolation and bark beetle attack with the use of LIDAR data” financed by Internal Grant Agency FFWS CULS in Prague. Grant no. 43150/1312/3129 “Integrating climate data and forest dynamics to predict and manage spruce bark beetle outbreaks” financed by Internal Grant Agency FFWS CULS in Prague. Grant no. VEGA - 2/0155/22 “Norway spruce (*Picea abies*) resistance to bark beetle attack in condition of changing climate”, funded by the Scientific Grant Agency of the Ministry of Education, Science, Research, and Sport of the Slovak Republic and the Slovak Academy of Sciences. The authors express their thanks to Filip Pruzinec, developer of the Point Cloud Solar Radiation Tool, for his valuable assistance with this software.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2025.122557](https://doi.org/10.1016/j.foreco.2025.122557).

Data availability

Data will be made available on request.

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3.2 Response of mature Norway spruce to experimental thermal and drought stress in relation to *Ips typographus* attack: Crown temperatures and sap flow

Published as: Karpov, A., Pirtskhalava-Karpova, N., Singh, V., Trubin, A., Korolyova, N., Modlinger, R., Jakuš, R. (2025). Response of mature Norway spruce to experimental thermal and drought stress in relation to *Ips typographus* attack: Crown temperatures and sap flow. Manuscript.

This article investigates how trees subjected to experimental thermal and drought stresses differ from undisturbed trees in stand interiors, particularly with regard to their physiological responses and remotely sensed characteristics, with a particular focus on thermal remote sensing. The primary objective of this work is to study the relationship between sap flow measurements and spectral indices, thermography data sensitive to canopy water content under drought conditions. Sap flow measurements serve as an indicator of drought stress. A second aim is to assess the sensitivity of thermal data and spectral indices to sap flow rate in spruce stands, thereby identifying the most effective factors influencing both sap flow and crown temperature.

The study comprised the integration of remote sensing data and direct measurements of sap flow, together with spectral and LiDAR indices, simulated solar radiation, and tree and landscape parameters. This article shows that significant differences in sap flow, crown temperature and spectral indices occur between trees located at forest edges, under artificial roofing and within the forest interior, reflecting variations in shade and water availability. Moreover, Generalised Additive Models (GAMs) of sap flow and crown temperature provided a quantitative assessment of the influence of each predictor on these response variables. This highlighted crown temperature as one of the top four variables with the highest influence on sap flow, alongside tree trunk diameter, soil water potential and solar irradiation. Additionally, tree canopy density and canopy density within a 10 metre buffer around the crown were identified as variables exerting a strong influence on crown temperature.

1 **Response of mature Norway spruce to experimental thermal and drought**
2 **stress in relation to *Ips typographus* attack: Crown temperatures and sap flow**

3

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12

13

14 **Abstract**

15 The effects of climate change are exacerbating the impact of drought and heat stress on forest
16 ecosystems, affecting forests worldwide. This study investigates the physiological responses of
17 mature Norway spruce (*Picea abies*) to drought and thermal stress, focusing on sap flow and crown
18 temperature. Three trial plots were established in Kostelec nad Černými Lesy, Czech Republic,
19 under different environmental conditions: forest edge, under rain-excluding roofs (simulating
20 drought), and forest interior. A combination of remote sensing techniques, including spectral
21 indices, LiDAR, and direct sap flow measurements, was used to assess the tree response. Sap flow
22 sensors, aerial hyperspectral, and thermal imaging were employed to measure sap flow and crown
23 temperature, while LiDAR was used to assess canopy structure. Our results revealed significant
24 differences in sap flow, crown temperature, and spectral indices between the groups, influenced
25 by factors such as trunk diameter, canopy temperature, soil moisture, and canopy density. Trees
26 with larger canopies and adequate soil moisture exhibited higher sap flow rates. The results suggest
27 that mature Norway spruce trees are sensitive to thermal and drought stress, increasing their
28 vulnerability to bark beetle infestations. This study highlights the importance of understanding
29 these responses for developing forest management strategies to mitigate the effects of climate
30 change and pest outbreaks.

31 **Keywords:** drought stress, thermal stress, crown temperature, forest edge, Norway spruce, Sap
32 flow, remote sensing, thermal imaging

33 1. Introduction

34 Forests cover approximately 30% of the Earth's terrestrial surface, playing a critical role
35 in local and global climate regulation, biogeochemical cycles, and biodiversity support (Právělie,
36 2018). Over recent decades, climate-change anomalies have adversely affected forest ecosystems
37 worldwide, increasing their susceptibility to drought and pest infestations. For instance, European
38 boreal forests experienced unprecedented mortality following the severe drought in 2018 (Singh
39 et al., 2024; Pirtskhalava-Karpova et al., 2024b). The primary biotic factor contributing to spruce
40 stand mortality is the spruce bark beetle, *Ips typographus* L. In mountainous forests, intense solar
41 radiation can predispose spruce to beetle infestation by causing thermal stress at newly formed
42 forest edges (Kautz et al., 2013; Karpov et al., 2024). This condition often arises at forest edges
43 created by wind damage, where spruce trees are adjacent to trees that have been defoliated by prior
44 infestations, or along edges established through harvesting activities. In lower elevation spruce
45 stands, drought stress appears to be a key factor contributing to the susceptibility of spruce to bark
46 beetle attack (Netherer et al., 2015).

47 The analysis of forest canopy temperature using remote sensing technologies may provide
48 vital insights into forest ecosystem functions. Techniques such as thermal imaging are key in
49 assessing energy flux, evapotranspiration rates, and plant stress at various spatial resolutions.
50 These technologies facilitate a deeper understanding of the interactions between forest structure
51 and environmental factors, essential for effective forest management and conservation strategies
52 (Morsdorf et al., 2006; Erdody & Moskal, 2010). Thermal sensors operating in the thermal infrared
53 (TIR) region (8–14 μm) measure the radiation emitted from tree crowns. This wavelength range
54 is optimal for remote sensing applications as it minimizes contamination from reflected sunlight,
55 and requires fewer atmospheric corrections (Smigaj, 2023). By integrating TIR remote sensing
56 with spectral data, researchers can obtain a detailed assessment of crown temperatures, a critical
57 indicator of water stress.

58 Recent studies suggest that increases in canopy temperature can be more sensitive
59 indicators of insect-related defoliation than conventional vegetation indices. For example,
60 Abdullah et al. (2019) demonstrated that Landsat thermal and spectral data outperformed standard
61 vegetation indices in detecting insect-induced defoliation, while Smigaj et al. (2023) reviewed
62 research showing that thermal cameras mounted on UAVs or aircraft can detect canopy
63 temperature rises in biotically stressed trees. Several studies have specifically explored the
64 relationship between canopy temperature and stress in spruce and pine forests, often focusing on
65 visible signs such as canopy discoloration and defoliation (Smigaj et al., 2015; Junttila et al., 2016;
66 Smigaj et al., 2019; Zakrzewska & Kopeć, 2022). Simultaneously, other research has examined

the effects of tree, site, and environmental characteristics on sap flow velocity—an important physiological indicator of water stress (Zabihi et al., 2023; Singh et al., 2025). Zabihi et al. (2023) provides a comprehensive overview of the influence of various environmental factors on sap flow, identifying key drivers such as air temperature, soil water potential, solar radiation and vapor pressure deficit. In addition, site-specific variables such as elevation, slope, and soil texture affect considerably tree transpiration rates. Tree characteristics, including trunk angle, internal trunk temperature and leaf biomass, were also highlighted as important variables influencing sap flow. Previous studies have investigated the impacts of forest structure, stand density, site characteristics such as elevation, tree characteristics such as tree diameter and bark temperature on sap flow (Zabihi et al., 2023; Singh et al., 2025). However, while these studies have considered various tree and site related factors, they have not integrated remote sensing-based approaches to access water stress using sap flow measures.

This research aims to enhance the understanding of two primary types of stress that predispose spruce trees to bark beetle infestation. To investigate these stresses, we implemented tree cutting to establish fresh forest edges, thereby inducing thermal stress, and utilized roofing techniques to create conditions for drought stress. Through high-resolution remote sensing, including LiDAR and hyperspectral imaging, combined with direct physiological measurements of sap flow, crown temperature, and soil temperature, this study offers a comprehensive view of the environmental and physiological factors that influence forest health. We utilized vegetation indices, which, in the context of bark beetle-related disturbances, demonstrate greater sensitivity compared to the analysis of spectral signatures (Klouček et al., 2024).

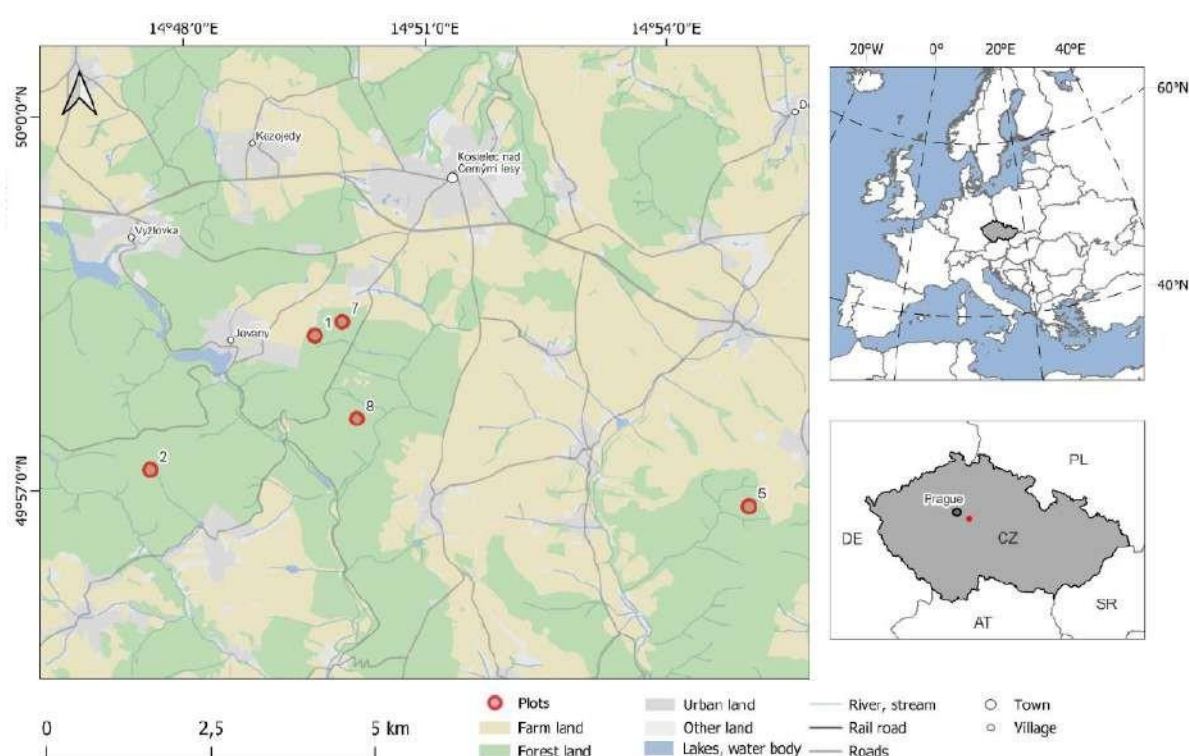
The primary objective is to investigate how trees subjected to thermal and drought stresses differ from undisturbed trees in stand interiors, especially in terms of their physiology and remotely sensed parameters, with an emphasis on thermal remote sensing. On this basis, we propose two specific aims:

1. Study of the relationship between sap flow measurement as an indicator of drought stress and spectral indices sensitive to canopy water content under drought stress.
2. Assessment of the sensitivity of thermal data and spectral indices to sap flow rate in spruce stands, identifying the most effective factors influencing both sap flow and canopy temperature in this research.

2. Materials and Methods

99 2.1. Study area

100 The study area is located near Kostelec nad Černými lesy in the Central Bohemian Region
 101 of the Czech Republic. The area is characterized by Norway spruce-dominated forests with an
 102 admixture of fir and beech (Trubin et al., 2023, 2024; Pirtskhalava-Karpova et al., 2024a). The
 103 soil across the study area is granodiorite covered with Luvisol. The climate tends to be drier and
 104 warmer in summer, with a mean annual temperature of 7.5 °C and 600 mm of precipitation (Tolasz
 105 et al., 2007). The study plots were established in 2018 under the EXTEMIT-K project
 106 (<http://extemit.fld.czu.cz>). Each plot consisted of four subplots (viz., A, B, C, and D), each having
 107 8-10 Norway spruce trees monitored for sap flow and bark surface temperature (Zabihi et al., 2023,
 108 Singh et al., 2025).



109 **Fig.1.** The study area with five experimental plots near Kostelec nad Černými lesy in the Central
 110 Bohemian Region, Czech Republic.

111

112 Subplots 1B, 2A, 5A, 7A, 8A, referred to as ‘Edge’, were established to study thermal
 113 stress in spruce trees at the edges of forest stands, resulting from clear cuttings conducted in April
 114 2022. Subplots 1A, 2B, 5B, 7B, 8B, referred to as ‘roof’, were designed to study drought stress in
 115 spruce trees in the forest interior. For this purpose, a roof constructed from polycarbonate and
 116 fiberglass over a wooden frame was installed beneath the canopy to divert precipitation away from
 117 the roots. With the exception of Plot 8 (where installation occurred in spring 2022), the roofs were

118 installed in spring 2021. During the winter, the roof plots were moderately irrigated to mitigate
119 extreme drought stress, thereby preventing potential tree mortality. Subplots C and D, collectively
120 referred to as ‘Control’ were also located in the interior of the forest, and were left to develop
121 naturally.

122

123 *2.2 Sap flow and other sensors, data acquisition*

124 Sap flow was measured continuously at 10-minute intervals using EMS81 sensors
125 manufactured by EMS Brno, Czech Republic. The sensors were installed at diameter at breast
126 height (DBH) at the onset of vegetation season, considering the physical attributes of trees. The
127 EMS81 sensors work on the trunk heat balance (THB) principle and consist of four electrodes, of
128 which three are electrically heated while the fourth serves as a reference. The temperature between
129 the heated and the reference electrode was set to 1K, and the heat balance of the heated space was
130 calculated using the following equation (Čermák et al., 2004):

$$131 \quad Q = \frac{P}{C_w} \times d \times \Delta T - \frac{Z}{C_w} \quad (1)$$

132 The THB method measures sap flow rate (Q) in kilograms per second per centimeter, where
133 P is the power of heat input (W), ΔT is the temperature difference at the measuring points (K), C_w
134 is the specific heat of water (J kg⁻¹ K⁻¹), d is the circumferential distance, and Z/ C_w is the heat
135 loss. The method calculates sap flow in kilograms. To determine the total water consumption of
136 the tree, the measured sap flow rate (Q) is multiplied by the xylem circumference at the installation
137 height. The sap flow data were collected from the field at 10-minute intervals using a single data
138 logger (GreyBox N2N 3P) connected to a cloud system, allowing real-time data delivery and
139 storage. The measured sap flow was pre-processed in Mini 32 by setting a baseline to remove
140 nighttime fluxes as per the manufacturer’s recommendation (EMS, Brno, CZ). The sap flow data
141 were then extracted on August 11 2023 to align with the aerial survey. In addition, visual
142 symptoms of bark beetle attack were assessed for all trees in all study plots during the week
143 beginning August 11 2023, and subsequently in September and later.

144

145 *2.3 Spectral and LiDAR data acquisition and preprocessing*

146 A Cessna 208B Grand Caravan photogrammetric aircraft with installed sensors was used
147 for the survey of the study area. On 11 August 2023, hyperspectral data were obtained using three
148 sensors: CASI-1500, SASI-600, and TASI-600, alongside an RGB sensor (Sony Alpha 7 III) and

LiDAR scanners (Tables 1 and 2). The acquisition process occurred between 12:40 and 13:10 local time, under a solar elevation angle of $\sim 50^\circ$ and a flight azimuth of 180° . Atmospheric conditions were favorable, with minimal cumulus clouds near the flight altitude, ~ 88 km visibility, and only partial shadowing observed on Plots 1 and 7. Radiometric corrections (including scattered light correction, Frame Shift Smear Correction, Second Order Light Correction, Bad Pixel Interpolation), georeferencing, atmospheric corrections, and mosaic composition were performed. LiDAR data were acquired from a separate survey on August 4 2022.

Table 1. Description of hyperspectral sensors.

Sensor	Spectral region	Spectral range [nm]	Number of spectral bands	Number of spatial pixels	Max. spectral resolution [nm]	Viewing angle [$^\circ$]	Spatial resolution at an altitude
CASI-1500	VNIR	380-1050	48	1500	3.2	40	0.5
SASI-600	SWIR	950 - 2450	100	600	15	40	1.25
TASI-600	LWIR	8 000 - 11 500	32	600	110	40	1.25

Note: VNIR - Visible Near Infrared, SWIR - Short Wave Infrared, LWIR - Long Wave Infrared - (Long Wave Infrared, Thermal)

Table 2. Description of LiDAR scanner.

Sensor	Riegl LMS Q-780
Maximum range [m]	up to 5800
Wavelength [nm]	1064
Laser pulse frequency [kHz]	up to 400
Laser beam divergence [mrad]	0.25

161

162 *2.4 Data processing*163 *2.4.1 Lidar data Processing*

164 LiDAR data were processed using the lidR library (Roussel et al., 2020) in RStudio (v.
 165 4.3.1, RStudio Team, 2023) to create a pit-free Canopy Height Model (CHM). Points were filtered
 166 based on height in 5 m increments up to 45 m elevation, excluding returns below 0.1 m and above
 167 2 m, then 2 m to 5 m, and so forth. The maximum values from these layers were integrated into a
 168 pit-free CHM, reducing errors from laser beams hitting lower obstacles (Khosravipour et al.,
 169 2014). The horizontal resolution of each CHM layer was 1 m.

170 The Forest Tools library (Plowright, 2023) was used for crown delineation from the pit-
 171 free CHM raster. Polygons were created around tree crowns that reached a minimum height of 20
 172 m, and these polygon layers were used in georeferencing the hyperspectral and thermal images
 173 with the CHM.

174 To calculate the LiDAR-derived canopy density (Canopy), two raster layers were
 175 generated: one including all LiDAR returns and another including only the first returns above 3
 176 m. The Canopy index was computed as the ratio of first returns above 3 m to all returns, at a 1 m
 177 spatial resolution (Kane et al., 2010). The Canopy_10 index was derived similarly but
 178 encompassed the average canopy density within a 10 m buffer around the crown center.

179 *2.4.2 Calculation of spectral indices and surface temperature*

180 Based on hyperspectral mosaics accrued during aerial survey and sensor CASI-1500,
 181 spectral indices were calculated: Enhanced Vegetation Index (EVI; Huete et al., 2002), Red Edge
 182 Normalized Difference Vegetation Index (RENDVI; Gitelson & Merzlyak, 1994; Sims & Gamon,
 183 2002), Modified Red Edge Normalized Difference Vegetation Index (MRENDVI; Datt, 1999;
 184 Sims & Gamon, 2002) with spatial resolution 0.5m. Additionally, based on the hyperspectral
 185 mosaic of sensors CASI-1500 and SASI-600 spectral indices were calculated: Disease-Water
 186 Stress Index (DWSI; Galvao et al., 2005) and Normalized Difference Water Index (NDWI; Gao,
 187 1995; Jackson et al., 2004) with spatial resolution of 1.25 m. Formulas for these indices are shown
 188 in Table S1. One spectral band from the TASI-600 mosaic provided surface temperature in Kelvin.

189 *2.4.3 Calculation of solar radiation*

190 Solar radiation for each LiDAR point was determined using the PCSRT method, which
191 calculates the direct and diffuse solar radiation components and insolation time using a voxel
192 approach (Pružinec & Ďuračiová, 2022). Parameters included geographical coordinates of the
193 center of the study area and elevation, a time frame from 12:40 to 13:10 (10-minute intervals) on
194 August 11 2023. This time corresponded to the thermal image acquisition period (Table 2). The
195 Link turbidity factor was set to 3.8 based on data from the SoDa service site (SoDa Service, 2023).
196 This is a factor that is used to evaluate water clarity and pollution levels. The PCSRT automatically
197 fitted the voxel size, which was found from 1.18 to 1.25 m for five LiDAR datasets covering the
198 study area, or an average of 3.7-3.8 LiDAR points were used for each voxel. Direct solar radiation
199 values from cloud points were rasterized using CloudCompare v. 2.13 (CloudCompare, 2023) with
200 a spatial resolution of 1 m, averaging values per pixel.

201 *2.4.4 Preparing the dataset for analyses*

202 The dataset comprises various measurements from sap flow sensors and temperatures from
203 the northern and southern sides of the bark, soil temperature, and soil water potential. The average
204 soil water potential was calculated for each subplot, as only 2-5 sensors were installed per subplot
205 and these measurements could not be associated with a specific tree. Average crown temperature
206 data, derived from thermal mosaics, were also included. Additionally, the dataset included
207 calculated values such as solar radiation, canopy density index for each crown, a canopy density
208 index with a 10-meter buffer from the center of each crown, and the standard deviation of tree
209 height, along with spectral indices (Table 3). These calculations were performed using the Zonal
210 Statistics tool in QGIS (QGIS, 2023) based on values from prepared raster layers. Following the
211 exclusion of tree crowns that were challenging to identify from high-resolution drone imagery, the
212 dataset now contains 180 observations. The data containing sap flow values are 107 observations,
213 including data from Edge (25 observations), Control (58 observations), and Roof subplots (24
214 observations).

215 *2.5 Statistical analyses*

216 Data normality and homogeneity of variance among the three groups (Edge, Roof, and
217 Control) were assessed using the Shapiro–Wilk test and Levene’s test, respectively. Only three
218 variables satisfied normality, and approximately half exhibited homogeneity of variance.
219 Consequently, non-parametric methods were deemed more appropriate. Kruskal–Wallis tests were
220 conducted to detect significant differences in the variables (Table 3), followed by Dunn’s post hoc
221 tests to elucidate pairwise differences among Edge, Roof, and Control.

222 A correlation matrix (Fig. S1) was generated to examine relationships among the variables.
223 High correlation (0.8 to 0.98) was found among certain spectral indices, whereas MRENDVI
224 exhibited a moderate correlation (0.4) with sap flow. To prevent autocorrelation, only MRENDVI
225 was used in subsequent models. Sap flow data were square-root transformed to better approximate
226 a normal distribution.

227 Both Linear Regression (LR) and Generalized Additive Models (GAMs) were explored to
228 analyze the relationship between sap flow, temperature, and the explanatory variables. An
229 Information-Theoretic (I-T) approach was employed to evaluate models and select the best-fitting
230 model based on the Akaike information criterion (AIC) for small samples. Delta AIC (ΔAIC)
231 indicates the difference between each model and the top model. Models with $\Delta AIC < 2$ can be
232 considered as good as the best, while models in the ΔAIC range of 2–7 are also plausible. Akaike
233 weights were used to rank the relative likelihood of each model, providing a probability estimate
234 of each model's suitability (Burnham et al., 2011).

235 The importance of each predictor in the GAM models was determined by its F-value and
236 the complexity of its relationship with the response variable, represented by the effective degrees
237 of freedom (EDF; see Table S3; Wood, 2017). Higher F-values indicate a stronger effect of the
238 predictor on the predicted variable, while the EDF described the complexity of the relationship.
239 Predictors with lower EDF values show linear effects, suggesting a straightforward influence,
240 whereas higher EDF values reflect non-linear relationships, suggesting more complex interactions
241 between predictor and predictor variable.

242 For statistical analyses and visualization, we used R software (version 4.3.3, R Core
243 Development Team, 2013) and RStudio (version 2023.12.1, RStudio Team, 2023), employing
244 libraries such as `dunn.test` (Dinno, 2024), `corplot` (Wei & Simko, 2021), `GGally` (Schloerke et al.,
245 2024), `Metrics` (Hamner & Frasco, 2018), and `mgcv` (Wood, 2017).

246 **Table 3.** Names and descriptions of variables.

Variable	Unit	Description	Number of measurements
Location	-	Edge – Forest edge, Roof – trees on the roof plot and Control – forest interior	-
Tavg	°C	Average temperature of crown	180
Sap flow	kg/h	Amount of sap flow measured by sensor	107
Height	m	Height of tree	180
Hstdev	m	Standard deviation of crown height based on Canopy Height Model	180
DBH	cm	Diameter at breast height	180
Canopy	-	Average LiDAR-derived canopy density index for each spruce crown, calculated as the ratio of first LiDAR returns above 3 meters to all LiDAR returns. This index represents the canopy density of the spruce crown	180
Canopy_10	-	Average LiDAR-derived canopy density index within a 10-meter buffer around the center of each spruce crown, calculated as the ratio of first LiDAR returns above 3 meters for all LiDAR returns. This index represents the canopy density of the site with a buffer of 10 meters.	180
Solar	Watt	Average solar radiation of crown	180
EVI	-	Enhanced Vegetation Index	180
RENDVI	-	Red Edge Normalized Difference Vegetation Index	180
MRENDVI	-	Modified Red Edge Normalized Difference Vegetation Index	180
DWSI	-	Average Disease-Water Stress Index of crown	180
NDWI	-	Normalized Difference Water Index	180
Bark_N	°C	Bark temperature from Northern site of tree trunk	83
Bark_S	°C	Bark temperature from Southern site of tree trunk	82
Soil	°C	Temperature of soil	95
SWP	kPa	Soil water potential	91
SWP_avg	kPa	Average soil water potential for subplot	-

247

248 3. Results

249 No visual signs of bark beetle attack were identified during the week following August 11 2023.
250 However, later in the season, beginning in September, bark beetle attacks were detected on 17
251 out of 47 trees in the Roof subplots. Specifically, 2 trees in plot 2, 8 trees in plot 4, 3 trees in plot
252 7, and 4 trees in plot 8 exhibited symptoms of infestation.

253 3.1 Statistical test-based comparison of Edge, Roof, Control groups

254 The Kruskal–Wallis test showed significant differences in sap flow, average crown
255 temperature (Tavg), canopy density (Canopy_10), MRENDVI, and various environmental
256 parameters (e.g., soil temperature, soil water potential, bark temperature) among the Edge, Roof,
257 and Control subplots (Table S2). Subsequent pairwise comparisons using Dunn’s post hoc test
258 revealed significant differences at $p < 0.05$, denoted by “+” in Table 4 (Table S3).

Sap flow was significantly lower in Roof plots (mean = 1.7 kg/h) compared with both Edge (3.5 kg/h) and Control (3.8 kg/h). Crown temperature was highest in the Edge plots (mean = 301 K) and differed significantly from that of both the Control (297 K) and Roof (298 K). While there was no statistically significant difference in overall crown temperature between the Roof and Control groups, attacked trees within the Roof subplots exhibited significantly higher crown temperatures (mean = 299 K). The MRENDVI index, which is sensitive to water stress, was notably lower at both the Roof (mean = 0.71) and Edge and (0.74) subplots compared with the Control group (0.78), implying drought conditions under the Roof treatments and thermal stress along the forest edges. In addition, the Kruskal-Wallis test indicated that MRENDVI and several other spectral indices were significantly lower in attacked trees compared to non-attacked trees (Table S4), suggesting that non-attacked trees maintain higher MRENDVI values (mean = 0.74), and thus may have less stress than attacked trees (mean = 0.67).

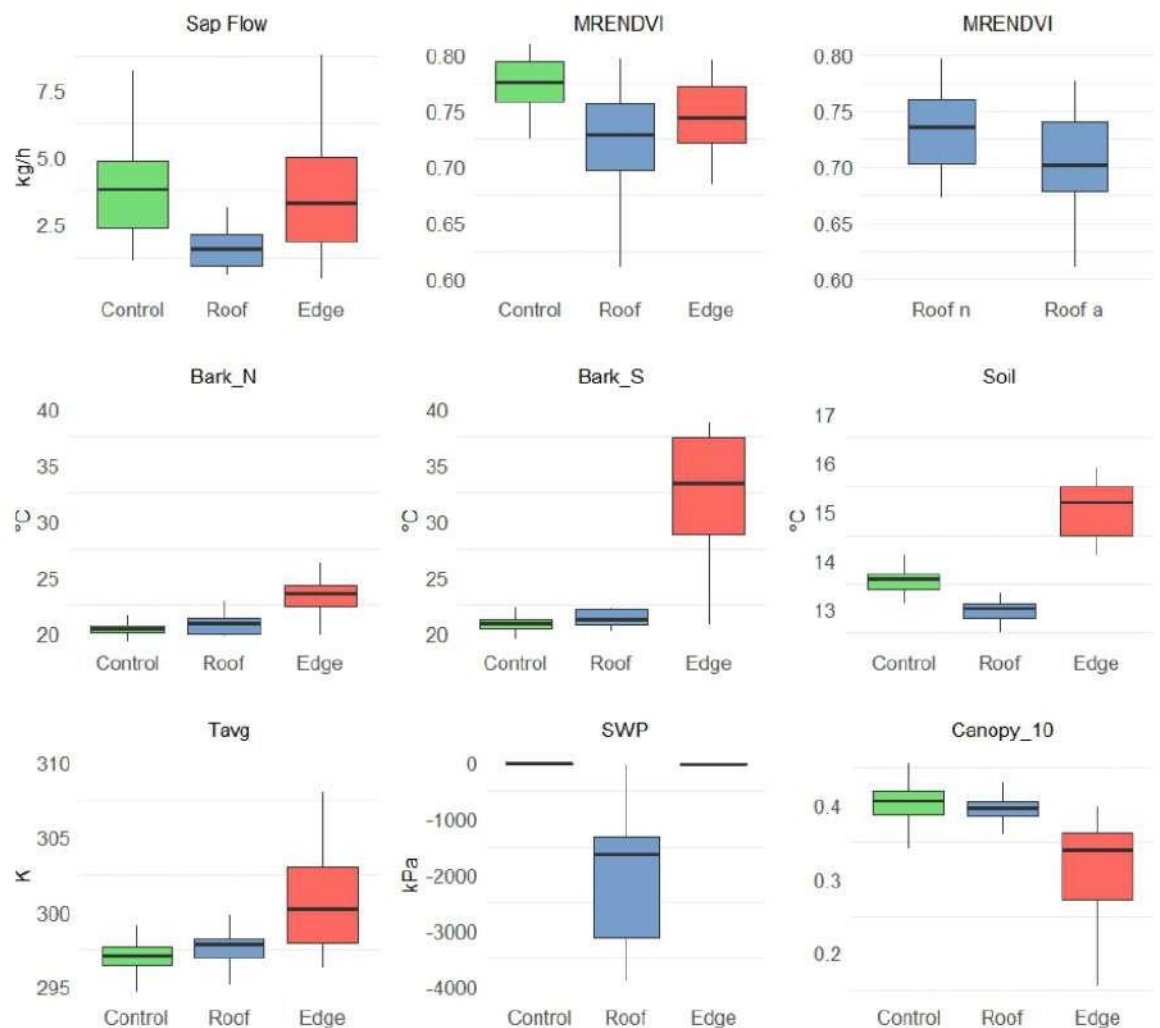
Soil temperature (Soil) and bark temperatures on both the northern (Bark_N) and southern sides (Bark_S) of tree trunks were also higher in the Edge subplots, reflecting higher solar exposure at newly established forest boundaries. In contrast, soil water potential (SWP) was lowest in the Roof subplots, indicating that precipitation exclusion led to water deficits that ultimately reduced soil moisture levels. Figure 2, Table 4, and Table S2 depict variations in these measurements across the Edge, Roof, and Control groups.

Table 4. Differences between groups for variables according to Dunn's post hoc test. Values marked * shows statistical significance ($p < 0.05$).

Variable	Control vs. Edge	Roof vs. Edge	Roof vs. Control
Sap flow		*	*
Tavg	*	*	
Canopy_10	*	*	
EVI	*		*
RENDVI	*		*
MRENDVI	*		*
DWSI	*		*
NDWI	*		*
Soil	*	*	*
SWP		*	*

Bark_N	*	
Bark_S	*	*

279



280

281 **Fig. 2.** Variations of environmental, tree stand parameters and values of spectral index between
 282 groups Control, Roof, Edge, and Roof n - non-attacked trees, Roof a - attacked trees in group
 283 Roof.

284

285 3.2 Assessment of environmental and stand characteristics influences on sap flow

286 GAM and LR were used to further investigate the relationships between sap flow
 287 measurement and stand tree characteristics, landscape factors, spectral index, and crown
 288 temperature (Table 3). The set of most parsimonious GAM models explains the variation in sap
 289 flow better than the set of LR models based on the highest adjusted R^2 . The a priori set of

competing GAM models sorted by ΔAIC is given in Table 5. More detailed information on these models is given in Table S5, and competing LR models are given in Table S6.

Table 5. Proposed seven best GAM regression models used to study relationship between sap flow and stand tree characteristics, landscape factors, spectral index, crown temperature.

Model	Combination	AIC	ΔAIC	AIC weight
1	$INIT = s(DBH) + s(Tavg) + s(Canopy) + s(SWP_avg) + \epsilon$	106.29	0.00	0.69
2	$INIT = s(Height) + s(DBH) + s(Tavg) + s(SWP_avg) + \epsilon$	110.35	4.06	0.09
3	$INIT = s(DBH) + s(Canopy) + s(Solar) + s(SWP_avg) + \epsilon$	111.95	5.67	0.04
4	$INIT = s(DBH) + s(Tavg) + s(SWP_avg) + \epsilon$	112.66	6.37	0.03
5	$INIT = s(DBH) + s(Tavg) + s(MRENDVI) + s(SWP_avg) + \epsilon$	112.87	6.58	0.03
6	$INIT = s(DBH) + s(Tavg) + s(Solar) + s(SWP_avg) + \epsilon$	113.01	6.72	0.02

Notes: For the explanation of variables used, refer to Table 3. All models include an intercept. ϵ is a random error.

As per the Akaike's information criterion, Model 1 emerged as the most significant (see Tables 5 and 6). Insights extracted from our model, suggest that the trunk diameter, crown temperature, tree canopy density, soil water potential have influence on amount sap flow (Table 5). The most influential predictors in the model are trunk diameter (DBH), soil water potential (SWP_avg), and canopy temperature (Tavg), which has the strongest effect on sap flow. Additionally, canopy temperature (Tavg) has linear relationships with sap flow, indicating a direct and simple influence. Soil water potential (SWP_avg) stands out with both a high impact and a non-linear relationship, suggesting that it has a strong but complex effect. Other predictors, canopy density (Canopy) and trunk diameter (DBH) have less effect and non-linear relationships with sap flow. Higher values of trunk diameter (DBH) correspond to higher sap flow values, whereas higher values of average canopy temperature (Tavg) correspond to lower sap flow values (Fig. 3).

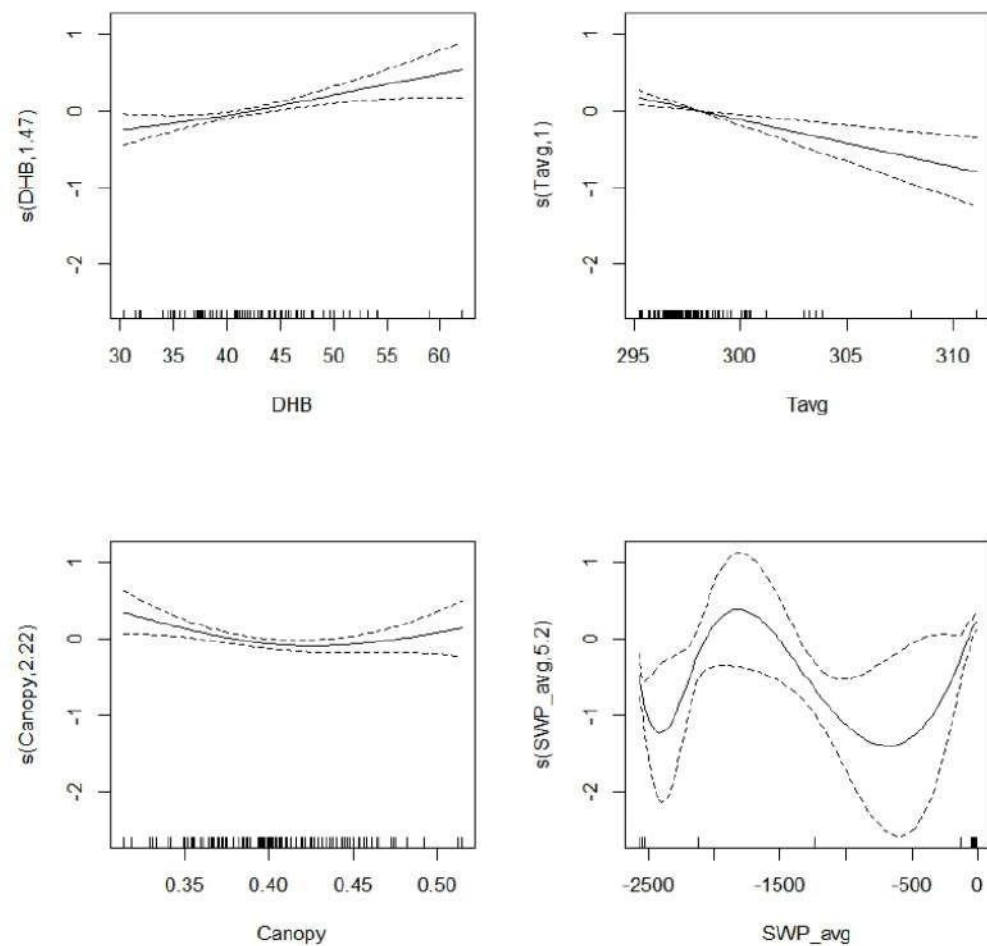
The predictors DBH and SWP_avg are present in all parsimony models, while Tavg is present in five of the six models. The predictors Canopy, Height, Solar, and MRENDVI are present in only one or two models, and have the lower F-values (Table S5). This indicates that DBH, SWP_avg and Tavg have a greater effect on sap flow.

Table 6. GAM model equation estimating the relationship between sap flow and stand tree characteristics, landscape factors, spectral index, crown temperature.

Parameter	Estimate	p-value	F-value	EDF	Model values
-----------	----------	---------	---------	-----	--------------

Intercept	1.73				Adjusted R-squared: 0.48
DBH	0.001	8.6	1.5		Deviance explained: 0.53
Tavg	0.001	12.9	1.0		RMSE: 0.36
Canopy	0.004	2.9	2.2		
SWP_avg	0.001	14.0	5.2		

313



314

315 **Fig. 3.** Partial dependence plots estimating the impact of predictors on sap flow for the most
316 parsimonious GAM model.

317

318 3.3 Assessment of environmental and stand characteristics influences on temperature of crown

319 GAM and LR were used to further investigate the relationships between sap flow

measurement and stand tree characteristics, landscape factors, spectral index and crown temperature (Table 3). The set of most parsimonious GAM models explains the variation in sap flow better than the set of LR models based on the highest adjusted R^2 . The a priori set of competing GAM models sorted by ΔAIC is given in Table 7. More detailed information on these models is given in Table S7, and competing LR models are given in Table S8.

Table 7. Proposed seven best GAM regression models used to study the relationship between crown temperature and stand tree characteristics, landscape factors, spectral index.

Model	Combination	AIC	ΔAIC	AIC weight
1	INIT = s(Sap_flow) + s(Canopy) + s(Canopy_10) + s(Solar) + ϵ	387.94	0.00	0.34
2	INIT = s(Canopy) + s(Canopy_10) + s(Solar) + s(MRENDVI) + ϵ	390.22	2.28	0.11
3	INIT = s(DBH) + s(Canopy) + s(Canopy_10) + s(Solar) + ϵ	390.54	2.60	0.09
4	INIT = s(Height) + s(Canopy) + s(Canopy_10) + s(Solar) + ϵ	390.56	2.62	0.09
5	INIT = s(Hstdev) + s(Canopy) + s(Canopy_10) + s(Solar) + ϵ	390.70	2.77	0.09
6	INIT = s(Canopy) + s(Canopy_10) + s(Solar) + ϵ	390.89	2.95	0.08
7	INIT = s(DBH) + s(Canopy_10) + s(Solar) + s(MRENDVI) + ϵ	393.00	5.06	0.03
8	INIT = s(Canopy) + s(Canopy_10) + s(Solar) + s(SWP_avg) + ϵ	393.03	5.09	0.03
9	INIT = s(Canopy_10) + s(Solar) + s(MRENDVI) + ϵ	394.49	6.56	0.01
10	INIT = s(DBH) + s(Hstdev) + s(Canopy_10) + s(Solar) + ϵ	394.55	6.61	0.01
11	INIT = s(DBH) + s(Canopy_10) + s(Solar) + ϵ	394.67	6.73	0.01

Notes: For the explanation of variables used, refer to Table 3. All models include an intercept. ϵ is a random error.

As per the Akaike information criterion, Model 1 emerged as the most significant (see Tables 7 and 8). Insights extracted from our model suggest that the sap flow, tree canopy density and canopy density with 10 meters buffer, and solar irradiation have an influence on crown temperature (Table 5). The most influential predictors in the model are amount of sap flow (Sap flow), tree canopy density (Canopy), and canopy density with 10 meters buffer (Canopy_10), which has the strongest effect on crown temperature. Additionally, sap flow (Sap flow) and tree canopy density (Canopy) have linear relationships with crown temperature, indicating a direct and simple influence. Canopy density with buffer 10 meters (Canopy) stands out with both a high impact and a non-linear relationship, suggesting that it has a strong but complex effect on temperature. Solar irradiation (Solar) has less effect and non-linear relationships with crown

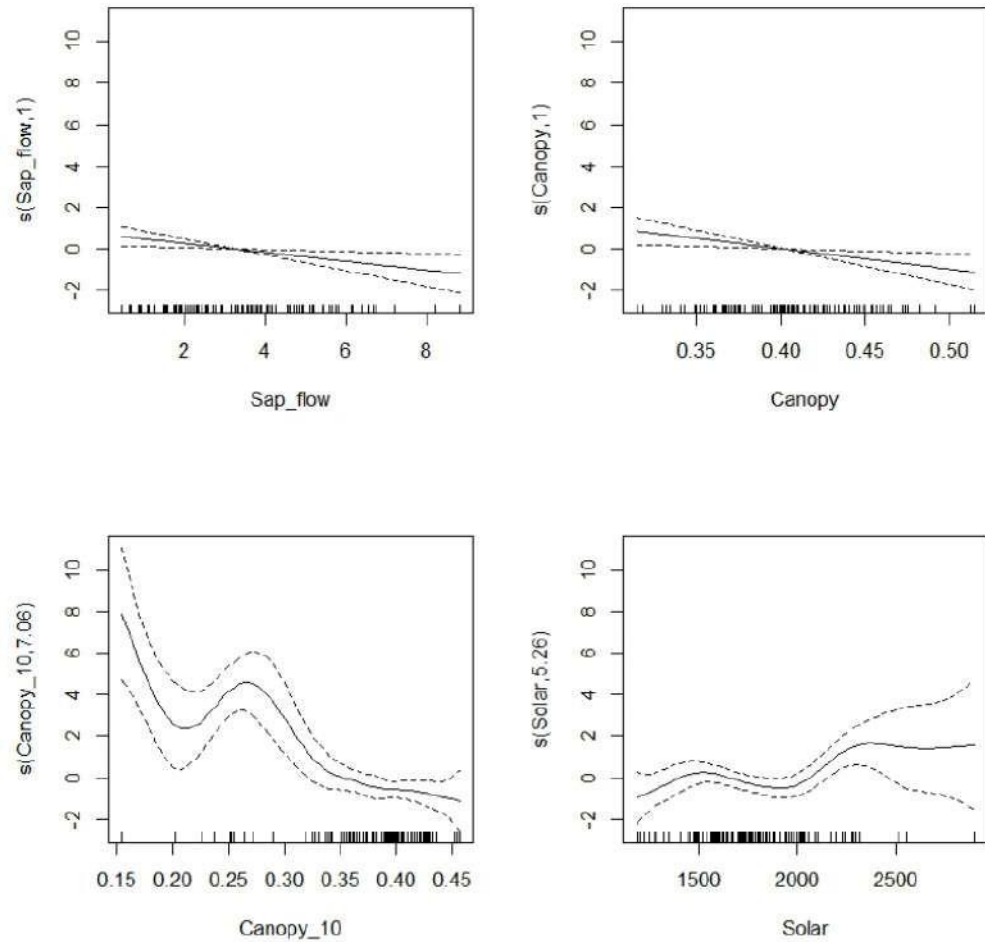
339 temperature. Higher values of sap flow (Sap flow) and tree canopy density (Canopy) and canopy
 340 density with buffer 10 meters (Canopy_10) correspond to lower temperature values, whereas
 341 higher values of solar radiation (Solar) correspond to higher temperature values (Fig. 4).

342 The predictors Canopy_10 and Solar are present in all parsimony models, while Canopy is
 343 present in seven of the eleven models. The predictor Sap flow, Height, DBH, Hstdev, SWP_avg,
 344 and MRENDVI are present in only from one to four and have the lower F-values (Table S7). This
 345 indicates that Canopy_10, Solar and Canopy_10 have a greater effect on temperature.

346 **Table 8.** GAM model equation estimating the relationship between sap flow and stand tree
 347 characteristics, landscape factors, spectral index, crown temperature

Parameter	Estimate	p-value	F-value	EDF	Model values
Intercept	298.06				Adjusted R-squared: 0.65 Deviance explained: 0.70 RMSE: 1.27
Sap flow		0.001	6.6	1.0	
Canopy		0.001	6.7	1.0	
Canopy_10		0.001	9.7	706	
Solar		0.021	2.5	5.26	

348



349

350 **Fig. 4.** Partial dependence plots estimating the impact of predictors on crown temperature for the
 351 most parsimonious GAM model.

352

353 **4 Discussion**

354 We integrated remote sensing data and direct measurements of sap flow to study the
 355 thermal response of Norway spruce crowns under drought and thermal stress. Spectral and LiDAR
 356 indices, tree and landscape parameters were used for investigation of this relationship as additional
 357 variables. The results of the study show significant differences in sap flow, crown temperature,
 358 and spectral indices between trees located at forest edges, under artificial roofing, and within the
 359 forest interior, representing different shade and water availability conditions. Furthermore, the
 360 GAM models of sap flow and crown temperature provided a quantitative assessment of the
 361 influence of each predictor on these prediction variables. This highlighted crown temperature as

one of the top three variables with the highest influence on sap flow, along with tree trunk diameter, soil water potential, and solar irradiation. Additionally, tree canopy density and canopy density around the crown with a buffer of 10 meters were identified as variables with high influence on crown temperature.

4.1 Differences among trees exposed to thermal and drought stresses compared to undisturbed trees in the stand interior.

The results of this study provide critical insights into the physiological and environmental responses of spruce trees subjected to distinct stress treatments: Edge, Roof, and Control. Spruce trees in the Edge plots exhibited significant thermal stress, as evidenced by elevated soil and bark temperatures, consistent with previous findings that forest edges experience higher temperatures due to increased solar radiation and reduced canopy cover (Chen et al., 1999). The sparse canopy in Edge plots, reflected by the lowest Canopy_10 values, aligns with the notion that edge environments often undergo structural alterations that exacerbate thermal conditions (Murcia, 1995). Our observations of forest edges correspond with previous experiments (Marešová et al., 2020; Majdák et al., 2021; Stříbrská et al., 2022; Özçelik et al., 2022); however, unlike reports from mountainous spruce forests (Kautz et al., 2013; Majdák et al., 2021), no bark beetle attacks were observed in the Edge plots. This aligns with findings from Stříbrská et al. (2022) and Özçelik et al. (2022), who conducted similar studies within the same forest enterprise under comparable conditions and also reported no bark beetle infestations. Özçelik et al. (2022) suggest that in low-elevation spruce forests, edge formation reduces the likelihood of sudden bark beetle outbreaks when trees are healthy, and soil moisture is sufficient to mitigate the impacts of new micro-meteorological conditions. The slightly increased sap flow rates observed in Edge plots indicate a degree of physiological resilience to edge-induced stress, potentially reflecting the species' adaptability to variable environmental conditions.

Another possible explanation for the absence of bark beetle attacks on trees at the forest edge is the elevated temperature of these trees. *I. typographus*, has an upper flight activity threshold of 30 °C (Lobinger, 1994). Annila (1969) reported that the bark surface temperature of sun-exposed sections of trees can exceed the ambient air temperature by up to 20 °C. Consequently, bark temperatures ranging from 40 to 50 °C can result in *I. typographus* mortality. Annila (1969) also observed that swarming *I. typographus* avoid establishing galleries on portions of logs that are directly exposed to sunlight for extended periods. In our experiment, the maximum bark temperatures recorded on the southern sections of trees at the forest edge reached 40 °C (Fig. 2).

395 In contrast, the Roof treatment was characterized by severe drought stress, driven by the
396 exclusion of precipitation from the soil. This treatment resulted in the lowest sap flow rates and
397 significantly reduced SWP values, indicative of impaired water transport and limited soil
398 moisture availability. The reduced MRENDVI values in Roof plots further confirm heightened
399 water deficiency, emphasizing the sensitivity of spruce trees to drought conditions. Notably, only
400 spruce trees on the Roof subplots were naturally attacked by spruce bark beetles, and the
401 attacked trees had lower MRENDVI values than their non-attacked trees. These findings are
402 consistent with the literature documenting the critical role of soil water availability in
403 maintaining tree physiological functions, particularly in species adapted to mesic environments
404 (Anderegg et al., 2015). The pronounced drought stress in Roof plots also highlights the potential
405 impacts of climate-induced changes, such as prolonged dry periods, on forest ecosystems.

406 Moreover, while there was no statistically significant difference in overall crown
407 temperature between the Roof and Control groups, attacked trees within the Roof subplots
408 exhibited significantly higher crown temperatures. These results provide a better understanding
409 of the processes occurring in spruce stands at lower elevations in Central Europe. In our study,
410 the *I. typographus* attack occurred in relatively compact stands (unfragmented and without forest
411 edges), where trees exhibited higher surface temperatures due to water shortages. The preference
412 of *I. typographus* for attacking trees with higher surface temperatures has also been
413 demonstrated by Kozhoridze et al. (2024) in mountainous conditions. However, in low-elevation
414 forests, the conditions at sun-exposed stand edges are excessively warm.

415 Our results align with previous roofing experiments in spruce stands, which demonstrated
416 increased susceptibility of drought-stressed spruces to *I. typographus* attack (Netherer et al.,
417 2014, 2024; Basile et al., 2024). Notably, the study by Basile et al. (2024) was conducted on one
418 of the research plots included in our study, one year prior to our investigation. However, unlike
419 previous studies, we observed natural bark beetle infestation in the roofed plots during the course
420 of our study.

421 Control plots, serving as a baseline, exhibited stable conditions with the highest sap flow
422 rates and minimal stress indicators. These plots demonstrated dense canopy cover and optimal
423 MRENDVI values, reflecting favorable water and thermal conditions. The stability of these plots
424 underscores the importance of maintaining intact forest structures for sustaining tree health and
425 resilience (Singh et al., 2024, 2025). This finding aligns with the work of Lindenmayer et al.
426 (2012), which emphasizes the role of undisturbed forest stands in mitigating environmental
427 stresses and promoting ecological stability.

428 Comparing the Edge and Roof treatments reveals contrasting stress dynamics. While the
429 Edge treatment primarily highlights the impacts of thermal stress due to increased exposure, the
430 Roof treatment underscores the consequences of water limitation. These findings resonate with
431 research demonstrating that edge effects and drought stress are among the most significant
432 drivers of tree physiological changes in managed and natural forests (Brunet et al., 2010; Allen et
433 al., 2015). The differences observed between these treatments also underscore the need for
434 integrated forest management strategies that address both thermal and hydrological stressors to
435 enhance forest resilience.

436 From an ecological perspective, the observed responses provide valuable insights into the
437 adaptive mechanisms of spruce trees under varying environmental pressures. The moderate sap
438 flow rates in Edge plots, despite significant thermal stress, suggest potential acclimation to edge
439 environments. Similarly, the reduced sap flow and spectral indices in Roof plots highlight the
440 limitations of spruce trees in coping with prolonged drought conditions, suggesting thresholds
441 beyond which physiological functions are impaired.

442 *4.2 Factors affecting sap flow*

443 *4.2.1 Diameter at Breast Height*

444 Trunk diameter (DBH) is a crucial variable affecting tree water dynamics and sap flow. The larger
445 the diameter of a spruce tree, the more extensive its canopy, which consequently increases its water
446 demand. In this study, DBH emerged as the most significant variable, included in all parsimony
447 models with the highest F-value and an EDF of 1, indicating a strong, linear relationship and
448 affecting sap flow values. These findings align with the findings of Hassler et al. (2018), who
449 identified a combination of tree- and site-specific factors, including tree species, diameter, and site
450 geology, as the primary drivers of sap velocity. The pronounced influence of DBH suggests that
451 larger trees, which typically exhibit a greater basal area, and volume of crown foliage have
452 increased sap flow. However, research by Zabihi et al. (2023) indicates DBH as only the fifth
453 variable from the top after elevation, tree density, and bark temperature, with an influence of
454 18.8%. It should be taken into account that although the studies have a similar study area, they
455 have different methodologies and sets of variables. The relationship between DBH and sap flow
456 is positive in our study and in the study by Zabihi et al. (2023).

457 *4.2.2 Spectral index*

458 The spectral index MRENDVI is identified as not a very effective indicator of water stress in this
459 study according to GAM parsimony models. This index presents only one of the six parsimony
460 models and has a low F-value, indicating that this effect on sap flow is relatively insignificant. On

the other side, the results of the statistical tests and the average value of the index indicated a positive correlation between higher MRENDVI values and higher sap flow rates. The index demonstrates a statistically significant difference between different environmental conditions, including forest edges, artificial roofing, and forest interior. An important point is that this index serves as a reliable predictor of natural bark beetle attacks. This differentiation aligns with observations by Trubin et al. (2023, 2024) and Huo et al. (2021), who noted spectral differences between healthy and stressed trees prior to bark beetle infestations. These findings underscore the potential of MRENDVI as a proactive tool in forest health monitoring, enabling early detection of water stress before visible symptoms appear, thus aiding in timely management interventions.

Additionally, as Singh et al. (2025) note, a reduction in living foliage volume can significantly decrease transpiration and photosynthetic rates, further impairing the trees' ability to mount a resource-intensive defense against pests like bark beetles. Our analysis suggests that while higher MRENDVI values are associated with increased sap flow, indicating healthier trees, lower values might reflect crown defoliation. However, there remains some level of uncertainty in these interpretations, due to the absence of direct information about crown defoliation from trees on our trial plots.

4.2.3 Crown temperature

Crown temperature is a key indicator of a tree's thermal environment, and its interplay with physiological processes. In this study, crown temperature emerged as one of the primary variables influencing sap flow, which was present in five out of six parsimony models and exhibited high F-values in models that indicated the significance of this predictor. This finding is consistent with the observed trends that higher crown temperatures were prevalent at forest edges, as opposed to the more moderated temperatures within the forest interior. The elevated crown temperatures at forest edges suggest increased exposure to sunlight and potentially higher transpirational demands. This observation aligns with findings by Smigaj (2023), who noted that fully-exposed sunlit leaves in the upper canopy typically exhibit higher temperatures and greater transpirational cooling rates compared to those that are partially shaded. This observation aligns with findings by Marešová et al. (2020), Majdák et al (2021) and Smigaj (2023). Smigaj (2023) noted that fully-exposed sunlit leaves in the upper canopy typically exhibit higher temperatures and greater transpirational cooling rates compared to leaves that are partially shaded. Additionally, Webster (2018) highlighted that vertical temperature gradients in trees were markedly influenced by stand density, with standalone trees showing higher temperature gradients due to decreased shading.

The increased temperatures can lead to accelerated water loss and may contribute to heightened water stress if not balanced by adequate soil moisture availability. For instance,

495 Zakrzewska & Kopeć (2022) reported that spruce trees under drought stress and bark beetle attack
496 exhibited higher canopy temperatures than healthy trees in similar climatic conditions. This
497 finding aligns with our observations where trees in trial plots under roof, were likely to experience
498 similar stresses, and displayed higher temperatures compared to trees in forest interior plots.
499 Specifically, spruce trees under roof exhibited higher crown temperatures and lower sap flow
500 velocity as a consequence of reduced soil water availability, indicating water stress in these trial
501 plots.

502 *4.3 Factors affecting crown temperature*

503 A consistent finding across coniferous forest research is that stressed trees often exhibit higher
504 crown temperatures (Olson, 1972). Recent research by Zakrzewska & Kopeć (2022) demonstrates
505 that thermal surveys can differentiate healthy, stressed, and dead Norway spruce trees based on
506 canopy temperature.

507 In the present research, the most influential factors affecting crown temperature were found
508 to be the density of the focal tree's crown and the canopy density within a 10 m buffer, followed
509 by solar irradiation. These predictors recur in eleven of the most parsimonious models,
510 emphasizing their high explanatory power in modulating canopy temperature. Notably, canopy
511 density of the crown itself exhibited a linear relationship with crown temperature. Numerous
512 studies support the mechanism behind this correlation: dense, healthy foliage can reduce crown
513 temperature by facilitating greater transpiration (Costa et al., 2013), provided the tree is not
514 experiencing severe water stress. Meanwhile, canopy density within a 10 m buffer emerged as
515 having the maximum effect on crown temperature based on F-values in the top model. This finding
516 aligns with work by Leuzinger & Körner (2007) and Jakuš et al. (2011), which showed that denser
517 stands generally create more shading, thereby mitigating solar heating of the canopy.

518 Sap flow also proved to be closely linked with crown temperature. As the hydration status
519 of a tree directly affects stomatal behavior (Costa et al., 2013), reduced sap flow and water stress
520 can prompt stomata to close, diminishing transpirational cooling and thereby contributing to higher
521 canopy temperatures. Conversely, well-hydrated spruce trees with robust sap flow velocities can
522 maintain lower crown temperatures, reflecting a balance between water availability, stomatal
523 regulation, and solar irradiation. Overall, these results underscore the multifaceted interplay of
524 stand structure, water status, and physiological processes in shaping canopy temperature—a vital
525 parameter in assessing forest health and vulnerability to bark beetle infestation.

526 *4.4 Limitations of the study*

A notable limitation is the lack of crown defoliation data in our analysis. Crown defoliation, which involves the loss of leaves or needles from the canopy, can significantly affect sap flow dynamics and overall physiological responses of the tree. Inclusion of crown defoliation data could provide a more comprehensive understanding of stressors affecting Norway spruce, particularly in relation to spruce bark beetle infestation and environmental stressors. On the other hand, the variable “Canopy” – a LiDAR-derived canopy density index for each spruce crown – can be regarded as a proxy for defoliation (Solberg et al., 2006). Another limitation is the lack of time series data. The study was conducted using a single snapshot approach, which is effective for initial assessments, but does not capture seasonal variations and longitudinal trends in tree responses to environmental change. Time series data could increase the robustness of the research by allowing analysis of trends over time, thereby improving the predictive power and applicability of the results. In addition, there was a discrepancy between the timing of the LiDAR and thermal imaging campaigns, which were conducted one year apart. However, a difference of one year does not result in significant changes in canopy cover on plots in the study area.

4.5 Practical Implementation

The practical implications of this research are significant for forest management, especially in the context of climate change and increasing environmental pressures. The use of thermography to measure canopy temperatures in Norway spruce provides a viable method for early detection of water stress at the individual tree level. This technique allows rapid assessment of tree health over large areas, facilitating early intervention and management decisions.

The ability to detect water stress through changes in canopy temperature could also play a key role in predicting and managing spruce bark beetle outbreaks. As water-stressed trees are more susceptible to pest attack, early detection can trigger timely management actions to prevent or mitigate outbreaks. This approach is also consistent with sustainable forest management practices.

Conclusion

This study provides valuable insights into the physiological and thermal responses of Norway spruce under varying environmental stress conditions, integrating remote sensing data and direct sap flow measurements. By comparing Edge, Roof, and Control treatments, we demonstrated how differences in shade and water availability significantly influence sap flow, crown temperature, and spectral indices.

The Edge treatment revealed that trees at forest margins experience pronounced thermal stress due to increased exposure to solar radiation and reduced canopy cover. Despite elevated

bark and soil temperatures, sap flow rates indicated a degree of physiological resilience, suggesting potential acclimation to edge environments. The absence of bark beetle attacks at forest edges, despite heightened thermal conditions, aligns with studies indicating that high bark temperatures may deter infestations by exceeding the upper thermal tolerance of *I. typographus*.

In contrast, the Roof treatment exposed trees to severe drought stress by excluding precipitation, resulting in the lowest sap flow rates and significantly reduced soil water potential. This treatment underscored the vulnerability of spruce trees to water limitation, with affected trees exhibiting reduced spectral indices, and a heightened risk of bark beetle infestations. The natural bark beetle attacks observed exclusively in Roof plots reinforce the critical role of soil water availability in mitigating pest outbreaks and maintaining physiological functions.

Control plots provided a baseline for undisturbed conditions, characterized by stable sap flow rates, dense canopy cover, and optimal spectral indices. These plots demonstrated minimal signs of physiological stress, underscoring the importance of intact forest interiors for sustaining tree health and promoting ecological stability.

The findings of this study demonstrate that mature Norway spruce stands present notable physiological responses to experimental thermal and drought stress, as evidenced by variations in sap flow and crown temperatures among the subplots under different environmental conditions. The sap flow was found to be predominantly influenced by the trunk diameter, canopy temperature, and soil water potential, indicating that larger trees with sufficient soil moisture and cooler canopies exhibited higher sap flow rates. The data indicated that elevated canopy temperatures were associated with a reduction in sap flow, canopy density, and solar radiation, with increased sap flow and denser canopies leading to lower crown temperatures. In addition, the spectral indices provided valuable insights into water stress conditions, highlighting their potential utility in monitoring early stages of forest decline. These findings highlight the critical role of environmental conditions and tree characteristics in the physiological responses of Norway spruce under stress, which may impact their susceptibility to *Ips typographus* attack. Understanding these relationships is essential for developing forest management strategies to mitigate the impacts of climate-induced stress and bark beetle infestations.

Acknowledgments

This research was funded by:

591 Grant no. CZ.02.1.01/0.0/0.0/15_003/0000433, “EXTEMIT-K” financed by the Operational
592 Program Research, Development and Education (OP RDE).

593 Grant no. 43140/1312/3113 “Forest health diagnostics: integrating thermography and LiDAR
594 data for comprehensive ecosystem management” financed by Internal Grant Agency FFWS
595 CULS in Prague.

596 Grant no. 43150/1312/3129 “Integrating climate data and forest dynamics to predict and manage
597 spruce bark beetle outbreaks” financed by Internal Grant Agency FFWS CULS in Prague.

598 Grant no. VEGA - 2/0155/22 “Norway spruce (*Picea abies*) resistance to bark beetle attack in
599 condition of changing climate”, funded by the Scientific Grant Agency of the Ministry of
600 Education, Science, Research, and Sport of the Slovak Republic and the Slovak Academy of
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3.3 Infestation patterns of two bark beetle species in multi-species coniferous forests on Kunashir Island in North Pacific Ocean region

Published as: Karpov, A., Pirtskhalava-Karpova, N., Trubin, A., Mezei, P., Potterf, M., & Jakuš, R. (2024). Infestation patterns of two bark beetle species in multi-species coniferous forests on Kunashir Island in North Pacific Ocean region. In *Forest Ecology and Management* (Vol. 558, p. 121774). Elsevier BV. <https://doi.org/10.1016/j.foreco.2024.121774>

The landscape-scale analysis in the southern part of the Kurilskiy Nature Reserve on Kunashir Island showed that conifer mortality reached 620 ha between 2015 and 2021. This represents about four percent of the study area. Almost three quarters of this loss was caused by the 2015 typhoons, while the remaining quarter was caused by subsequent bark beetles outbreak. Glehn spruce forests were the most affected. Eight percent of Glehn spruce total area was affected, and the areas of mortality patches were on average more than three times larger than those recorded in Yezo spruce and Sakhalin fir stands.

Results of BRT models showed that stand composition and age structure outweighed topographic factors. The proportion and age of Yezo spruce primarily explained the transition from colonised windthrows to the first phase of standing infestation. In the second phase, the same drivers remained dominant. Wind damage was mainly determined by elevation and tree height. Wind damage was particularly significant in low, gentle terrain below 150 m above sea level (a.s.l.) and on slopes of less than 10 degrees. Overall, the study shows that species composition determines the spread of the beetle in these mixed maritime coniferous forests.



Contents lists available at ScienceDirect

Forest Ecology and Management

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

Infestation patterns of two bark beetle species in multi-species coniferous forests on Kunashir Island in North Pacific Ocean region

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ARTICLE INFO

Keywords:

Spruce bark beetle
Fir bark beetle
Tree mortality
Boosted Regression Trees
Sentinel 2

ABSTRACT

Bark beetle outbreaks are a significant cause of high tree mortality rates, dramatically impacting the resilience of forests. Understanding the triggers and impacts of these outbreaks is critical for effective forest management strategies. In this context, we studied windfall and bark beetle outbreaks in the period 2015–2021 in the southern part of Kurilskiy Nature Reserve, North Pacific Ocean region. Massive bark beetle outbreaks on Kunashir Island were not previously studied. The dominant tree species are Yezo spruce (*Picea jezoensis*) and Sakhalin fir (*Abies sachalinensis*), which collectively form spruce-fir forests on Kunashir Island. Glehn spruce (*Picea glehnii*), although less common on the island, forms pure spruce forests. Typically, spruce bark beetle (*Ips typographus* L.) attacks Yezo and Glehn spruce, and fir bark beetle (*Polygraphus proximus*) attacks Sakhalin fir. Significant tree mortality was observed in the aftermath of a substantial bark beetle outbreak, induced by gale-force winds. The total disturbance area was 620.5 ha, which is about 4% of the study area, 72% of the windfall area, and 28% of the bark beetle-infested area.

Utilising a forest loss dataset (Global Forest Change dataset) and Sentinel 2 imagery, we identified windfall areas and standing tree mortality through unsupervised classification, accompanied by field sampling. Subsequently, the authors analysed the main drivers of disturbances caused by wind and bark beetle outbreaks using datasets combined with forest inventory data. Field data showed a pattern of tree infestation by both bark beetle species at the tree level, and the potential infestation of Sakhalin fir by the spruce bark beetle.

We used boosted regression tree (BRT) models to analyse the main drivers using the presence and severity of wind damage and bark beetle outbreaks by phases. As predictors, we used a set of forest characteristics (tree species percentage, height, diameter of trunk, age, growth class) and environmental characteristics (slope, elevation, potential solar radiation, soil pH). The bark beetle outbreak was split into two phases: the first phase (2017–2019) involved the transition of bark beetles from colonised downed trees to standing trees, and the second phase (2020–2021) occurred during the spreading of beetles in standing trees.

Stand tree characteristics were of greater significance for the likelihood of a bark beetle outbreak than environmental characteristics, across both phases for the southern part of the reserve. The percentage and the age of Glehn spruce and Yezo spruce were the main influencing factors for the presence and severity of an outbreak.

1. Introduction

Forest ecosystems around the world are exposed to the effects of drought, fires, and windstorms. Climate change increases the frequency of these disturbances and their impact on forests. The rising global average temperature, coupled with the elongation of the bark beetle's breeding period, creates conditions for an increase of bark beetle

population over the endemic level (Maslov, 2008; Allen et al., 2010). Furthermore, climate change has the potential to intensify the frequency of windstorm events, consequently leading to an increased number of windfall areas. Windfall trees resulting from windstorms have weak resistance to bark beetle infestation and are a favourable breeding ground. The bark beetle then spreads to healthy stands, endangering the entire forest ecosystem, including plant and animal species (Seidl et al.,

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<https://doi.org/10.1016/j.foreco.2024.121774>

Received 27 June 2023; Received in revised form 11 February 2024; Accepted 12 February 2024

Available online 23 February 2024

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2009).

In this study, we focus on Yezo spruce (*Picea jezoensis*), Glehn spruce (*Picea glehnii*), and Sakhalin fir (*Abies sachalinensis*). These tree species grow within the territory of Russian Far East, on Hokkaido Island (Japan), and form coniferous forests on Kunashir Island. Spruce bark beetle (*Ips typographus* L.) (Coleoptera: Curculionidae: Scolytinae) and fir bark beetle (*Polygraphus proximus*) (Coleoptera: Curculionidae: Scolytinae) are a natural part of these forests' ecosystems. Spruce bark beetle can successfully infest Yezo and Glehn spruce in this territory (Yamaguchi, 1963a; Yamaguchi et al., 1963b; Krivolutsкая, 1965; Maslov, 2010), while Sakhalin fir is the main host tree species for fir bark beetle in this territory. However, these bark beetle species are able to infest not only primary tree hosts but also other conifer species. Both species are multivoltine, with the potential to produce up to two generations per year in the study area (Bystrov and Antonov, 2019). These bark beetles primarily infest windthrown and weakened trees, but can attack healthy trees when their population reach epidemic level. Surveys from 1965 to 2009 established the presence of spruce and fir bark beetles on the Kuril Islands archipelago (Krivolutsкая, 1965; IKIP, 2002; Mandelstam and Petrov, 2009). Typhoon Dujuan and Typhoon Chi-Wan, which occurred in October 2015, triggered a mass outbreak of bark beetle on Kunashir Island (Korznikov et al., 2019).

Most scientific articles studying mass bark beetle outbreaks describe the attack of one specific bark beetle species on a particular tree species. However, a mass outbreak of two beetle species (spruce bark beetle and fir bark beetle) in coniferous forests on Kunashir Island was responsible for the infestations and the causes of mortality of Yezo, Glehn spruce, and Siberian fir. Thus, our research subject includes two bark beetle species and three species of conifer trees. Specifically, the research aims to unravel spruce and fir bark beetle infestation and spread into mixed-to pure multi-species coniferous forests by examining topographic and stand characteristics variables.

It has become common knowledge that *P. proximus* is the main threat to fir forests in Siberia and Russian Far East. The situation with fir bark beetle there is similar to that of spruce bark beetle in European forests. Mass outbreaks of fir bark beetle have been recorded in southern Siberia during the last twenty years and was the cause significant mortality of Siberian fir (*Abies sibirica* Ledeb.) (Krivets et al., 2015). This beetle was transported on the Trans-Siberian Railway from the Far East to southern Siberia in unpeeled fixing material on flat wagons. The fir bark beetle, native to the Far East of Russia, is adaptable to a variety of conifer species (Krivolutsкая, 1996). The *P. proximus* is able to infest balsam fir (*A. balsamea* (L.) Mill.) and Siberian fir (*A. sibirica* Ledeb.) in the European part of Russia in cultural plantations of introduced trees (Krivets et al., 2015). Single specimens of *P. proximus* have already been found in a park near Moscow and in the seaport of St. Petersburg in Russia. Norway spruce (*Picea abies* (L.)) is noted as a host tree where the fir bark beetle was observed (Mandelstam and Popovichev, 2000; Chikhacheva, 2008). Additionally, existing data suggest that bark beetle infestations may also become a potential threat to European fir forests (de la Peña et al., 2020).

Earlier research works on Kunashir Island consisted of entomological descriptions of bark beetles inhabiting the island and are devoid of information about bark beetle outbreaks (Krivolutsкая, 1965; IKIP, 2002; Mandelstam and Petrov, 2009). The latest research of Japanese authors, devoted to outbreaks of spruce bark beetle on Hokkaido Island, was carried out in the over 20 years ago and, therefore, was technically limited in the analysis of factors influencing bark beetle outbreaks, compared to the possibility of utilising modern remote sensing technology and machine learning algorithms (Furuta, 1989; Furuta et al., 1996). Further, the ability of Glehn spruce to resist a bark beetle outbreak has also not been studied, in contrast to Yezo spruce. Notably, Yezo and Glehn spruce species have biological differences that may affect the ability to resist infestation (Kayama et al., 2011). Most importantly, the existing research does not describe the mechanism of the spread of spruce bark beetle from spruce to fir, although Sakhalin fir

has been identified as a potential host tree (Maslov, 2010; CABI, 2022). The number of studies devoted to bark beetle outbreaks in Russian Far East, Japan, and the Asian region as a whole is much lower than that of European studies. There might be significant gaps in understanding of the ecological dynamics in these areas, potentially leaving them vulnerable to unforeseen environmental challenges or policy missteps. Building on this, the knowledge acquired by European scientists can therefore be used to assess bark beetle outbreaks in other regions.

Furthermore, the majority of European studies focus on the study of spruce bark beetle, as it poses the threat to the Norway spruce, the most economically important European tree species (Faccoli, 2009; Kärvelo et al., 2014; Mezei et al., 2014a, 2014b; Trubin et al., 2022). Only a small number of studies describe outbreaks of two or more bark beetle species, and their interaction. For example, Simard et al. (2011) described outbreaks of multiple beetle species on multiple host species, including pine, spruce, and fir in North America. Groot and Ogris (2019) described spruce and fir bark beetle outbreaks in European forests dominated by spruce and fir. However, it should be noted that these studies do not address the specific bark beetle and tree species investigated in our manuscript, with the exception of the study by Groot and Ogris (2019), which examined the same spruce bark beetle – *I. typographus*.

At present, numerous scientific research works are focused on studying bark beetle outbreaks based on remote sensing data and machine-learning statistical methods. Remote sensing technologies are used for detecting forest areas that are infested by bark beetles. Typically, bark beetle infestation is divided into green (no changes), red (crown discoloration), and grey (deadwood) stages of infestation (Abdullah et al., 2018). Most of the methods for detecting bark beetle attacks are based on optical and infrared spectra bands analyses. The main spectral ranges for the determination of forest health are the red edge, near-infrared, or short-wave infrared (Niemann et al., 2015). Numerous studies have been carried out on the detection of bark beetles using Landsat (Landsat 5/7/8) and Sentinel-2 satellite images (Abdullah et al., 2018; Zabihi et al., 2021). Time series of satellite images are often used for mapping tree mortality caused by bark beetles (Hansen and Loveland, 2012; Havašová et al., 2017; Duraciová et al., 2020).

Modern statistical models are based on machine learning methods such as Boosted Regression Trees (BRT), which provide advantages over traditional statistical methods when analysing an extensive set of environmental data. It combines the strengths of two techniques: boosting, a method for improving model predictions, and regression trees, which predict outcomes based on decision paths (Seidl et al., 2007; Elith et al., 2008). Mezei et al. (2014a, 2014b) and Kärvelo et al. (2014) used the BRT model to analyse windfall and bark beetle outbreak factors, and Albrecht et al. (2012) used BRT to assess storm damage of Norway spruce (*Picea abies*) and Douglas-fir (*Pseudotsuga menziesii*) trees in relation to applied silvicultural practices.

Taking into consideration the existing research gap, in the present work we have studied forest mortality caused by bark beetles on two scales. At the plot level, we focused on single tree infestation and the potential shift of the tree hosts. At the subcompartment level, we combined remote sensing datasets of wind disturbances and beetle infestations with forest inventory datasets. In the Russian forest inventory, the smallest unit, denoting a forest stand with uniform characteristics, typically defined by its irregular shape arising from natural boundaries (Trishkin et al., 2015). As drivers of forest damage due to wind and bark beetle infestation, we considered several topographic (elevation, slope, solar radiation) and stand characteristics (tree height, age, diameter, proportion of tree species) in mixed forest stands. We used a BRT model to analyse the drivers of the wind damage and the bark beetle infestation separately. Moreover, the two disturbance agents were split into presence and severity. We compared the different factors in bark beetle dynamics between three major tree species: Glehn spruce, Yezo spruce, and Sakhalin fir.

This study particularly aims to answer the following questions:

- (1) which topographic and tree species characteristics affect tree mortality due to typhoon;
- (2) which topographic and tree species characteristics drive bark beetle-caused tree mortality in multi-tree species forests;
- (3) what difference exists in the initiation and subsequent spread of bark beetle attacks, in terms of the environmental and stand variables involved.

To our knowledge, our study is one of the first works to examine the dynamics of coniferous forest infestation by bark beetles in the Kurilskiy Nature Reserve, Russian Far East.

2. Methods

2.1. Study area

Kunashir Island is the southernmost, and one of the largest islands in the Great Kuril Chain, with a predominantly volcanic landscape that is formed by three mountain ranges and four active volcanoes: Tyatya, Rurui, Mendelev, and Golovnin. The island's climate is characterised as moderately humid marine, influenced by both the Sea of Okhotsk and the Pacific Ocean. The wind regime of the island is characterised by an average wind speed of 4.9 m/s, with record gusts reaching up to 60 m/s during typhoons; additionally, the island receives a substantial annual precipitation of 1300–1500 mm. The location experiences relatively mild winters and cool summers, with average temperatures of -5.6°C during the coldest month and $+15.5^{\circ}\text{C}$ during the warmest month, which is August on Kunashir Island. The average annual relative humidity is 80.2%, while the average annual air temperature is $+5.1^{\circ}\text{C}$ (Ganzei, 2008; Igarashi, 2016; Korznikov et al., 2019).

Our research was conducted within Kurilskiy Nature Reserve, which covers 65,365 ha and consists of three geographically separated sections. We focused on the reserve's southern part, covering an area of 15,317 ha (Fig. 1). The highest elevation point in this area is Golovnin volcano at 543 m, and the mean elevation of our study area is 117 m. The study area features a hilly relief (IKIP, 2002; FID, 2007; Razjigaeva et al., 2013). In the southern part of Kurilskiy Nature Reserve, forest cover occupies 13,831 ha (90.2%). Coniferous forests cover 6555 ha

(47.4%), and include Sakhalin fir (82%), Yezo spruce (15%), and Glehn spruce (3%) as the main conifer species (IKIP, 2002; FID, 2007). Yezo spruce and Sakhalin fir are the dominant forest-forming species here. Predominantly, these tree species create a mixed composition, including a significant portion of deciduous species. The percentage of Yezo spruce and Sakhalin fir in the forest composition increases with elevation, reaching a dominant share of 60–100% from 200 m above sea level (a.s.l.). In contrast to this, areas dominated by Glehn spruce typically comprise 80% of the forest composition and are primarily found at two elevation ranges: 10–50 m and 180–280 m a.s.l. Logging has not significantly impacted Kunashir Island's forests. Currently, forest management activities are limited to infrastructure building and firewood harvesting outside protected areas. Since the establishment of the Kurilskiy Nature Reserve in 1984, logging within its boundaries has been prohibited. No large-scale bark beetle outbreaks or diseases were discovered during the 2006 forest management field survey (IKIP, 2002; FID, 2007).

Kunashir Island suffered two devastating typhoons, Dujan and Chi-Wan on October 2nd and 9th of 2015, leading to extensive windfall patches within the coniferous forest, primarily affecting Yezo spruce and Sakhalin fir. The windfall area is estimated at 1130 ha, accounting for approximately 0.92% of the island's total forested area. Following the windfall, a widespread bark beetle outbreak occurred on the island, affecting forests across the entire region (Korznikov et al., 2019).

2.2. Pilot field survey (plot level)

The research sites for monitoring tree health were established within the Golovnin Volcano Caldera (Golovnin Caldera) and the Danilovskiy Field (Danilovskiy), characterised by distinct environmental conditions. Ten plots were established in 2019, and an additional four plots were established in 2021. The initial ten plots were re-monitored in 2021. Field survey was conducted from August to September in both years.

In the Golovnin Caldera, five plots were randomly established in a forest that is primarily composed of Glehn spruce, with Sakhalin fir as the secondary component. In contrast, the Danilovskiy featured five plots located in fir-spruce forests, where Sakhalin fir and Glehn spruce were present in nearly equal proportions, with the former being slightly

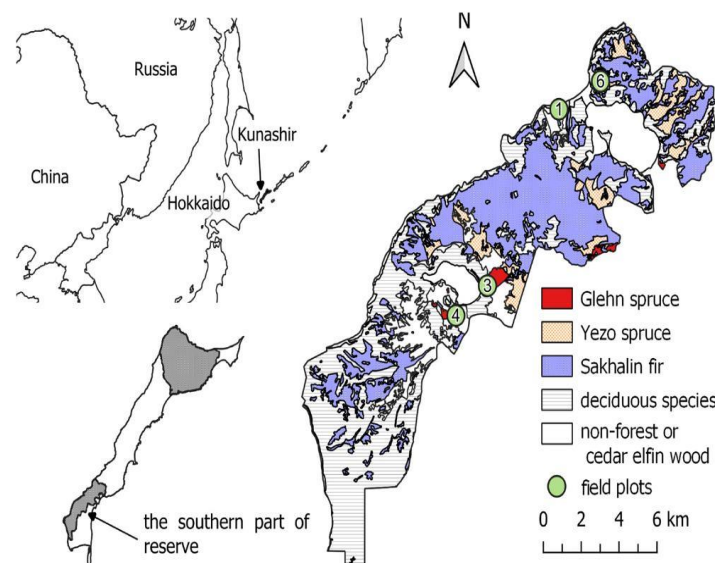


Fig. 1. Location of Kunashir Island, study area, and border of the southern part of the Kurilskiy Nature Reserve. The southern region was used in our analysis. The circled number indicates the number of sample plots in that location. The number of study plots 1, 6 is for the Danilovskiy field, and 4, 3 is for the Golovnin Volcano Caldera field.

more dominant. To capture beetle outbreaks in areas containing Yezo spruce, an additional four sites (two in the Golovnin Caldera and two in the Danilovskiy) were established in 2021.

Every plot had a circular configuration with a 20-meter radius, and only standing trees inside the circle were taken into account. Every tree was identified by species and measured in terms of height, diameter at breast height, and age. The stage of bark beetle infestation (healthy/green, red, or grey stage of attack) was visually determined for every coniferous tree within the test plots, and an investigation for the presence of beetles beneath the bark was conducted at breast height. In total, we surveyed 678 trees.

2.3. Forestry inventory data and environmental predictors

For the analysis of factors influencing windfall and bark beetle outbreaks, we utilised forest inventory data from 2007 (FID, 2007). The data from the forest inventories were referenced in the forest sub-compartments as basic area units. Forest inventory data for this research were supplied by Kurilskiy Nature Reserve.

We used in total 21 environmental and stand variables (see Table 1 for full description). The southern part of Kurilskiy Nature Reserve includes 1945 subcompartments, from which we have selected 896 sub-compartments with coniferous tree species in the top canopy. The average subcompartment size was 9.1 ha, and the range was 1–40 ha.

The forest type is identified in forest inventory data (FID, 2007), and it has been matched with the soil type and pH of the soil (Vorobyev et al., 1985). The growth class variable in our study refers to the forest stand capacity, which has values from 1 to 5 (1–2 – highly productive forest stands; 3–4 – medium productive; 5 – low productive) (FID, 2007).

Initially, the correlation matrix was calculated for all 21 variables. For further analyses, we excluded highly correlated variables (>0.8) of height, diameter, and slenderness ratio per each species (Table S1). The number of variables was reduced to 12. The average age used in the windfall model has been replaced by average stand height, as tree height is directly related to wind load and these variables are usually correlated (Table S1). Also, we did not use the solar radiation variable for the analysis of windfall areas, resulting in a total of 11 variables used for the analysis of wind damage (Table 3).

A Digital Elevation Model (DEM) was derived from the Shuttle Radar

Table 1

List of the variables used in the analyses. Age, height, DBH, and slenderness represent the average value per tree species and per subcompartment. DBH – diameter at breast height; FID – forest inventory data; DEM – digital elevation model.

Variable	Factors	Source	Abbreviation
Species proportion, %	1. Fir	FID, 2007	Fir
	3. Yezo Spruce		Yezo
	5. Glehn Spruce		Glehn
	7. Deciduous		Decid
Age, year	8. Fir	FID, 2007	FirAge
	10. Yezo Spruce		YezoAge
	12. Glehn Spruce		GlehnAge
	13. Fir		FirH
Height, m	15. Yezo Spruce	FID, 2007	YezoH
	17. Glehn Spruce		GlehnH
	18. Fir		FirH
DBH, cm	20. Yezo Spruce	FID, 2007	YezoD
	22. Glehn Spruce		GlehnD
	23. Fir		FirH/D
Slenderness ratio	25. Yezo Spruce	FID, 2007	YezoH/D
	27. Glehn Spruce		GlehnH/D
Growth class	28. Growth class	FID, 2007	Bon
	29. Slope		Slope
pH	30. pH	Vorobyev et al., 1985	pH
Solar radiation, kW h/m ²	31. Solar radiation	DEM	Rad
Elevation, m a.s.l.	32. Elevation	DEM	Elev

Topography Mission (SRTM), at the resolution of 90 m (NASA, 2013). Potential solar radiation was calculated using the toolbox “Area Solar Radiation” in ArcGIS 10.6.1 software (ESRI, 2011). Solar radiation was calculated for one year, and over the entire study area. After this, mean solar radiation and elevation were recalculated for each subcompartment, using the “Zonal Statistic” plugin in QGIS 3.22.5 (QGIS, 2022).

2.4. Identification of windfalls and beetle infestation

Wind-damaged areas were mapped using the forest loss layer from the Global Forest Change dataset, which is based on Landsat data (Hansen et al., 2013). It has a spatial resolution of 30 m and it is sensitive to windfall areas. Forest cover changes in the period 2015–2016 were related only to windstorms, because forest harvesting is prohibited in the reserve and mass drying of trees or forest fires was not observed, according to the reports of Kurilskiy Nature Reserve. High-resolution images in Google Earth confirm this (Fig. S1; Google, 2022). We assume that bark beetles did not cause significant tree mortality in the period following the typhoons. This assumption is consistent with previous research indicating a time lag of 3–4 years between windfall events and subsequent bark beetle outbreaks (Hanewinkel et al., 2008; Modlinger and Novotný, 2015).

The bark beetle-induced standing tree mortality was identified using Sentinel-2 satellite images (Table 2) in two steps: 1) identification of the forest cover, used as a forest mask in the next steps, and 2) proper identification of the bark beetle infestation. Sentinel-2 has resolution of 10 m and is sufficient for the detection of tree mortality by the bark beetle at the landscape level. Image classification was performed using k-means clustering (i.e., unsupervised classification algorithm) (Arthur and Vassilvitskii, 2007). The optimal number of clusters for both steps was determined using a validation dataset, and by overall accuracy estimation.

In the first step, the mask for the coniferous forest was created, using an unsupervised classification based on Sentinel-2 imagery from 6th June 2016 (Table 2). The classification of imagery was performed in the area of the southern part of Kurilskiy Nature Reserve. Bands 2, 3, 4 and 8 were used for the classification. All pixels were divided by visual testing into six clusters. The one cluster corresponds to the mask of the coniferous forest.

The second step was the detection of standing beetle-induced tree mortality areas on the coniferous forest mask. The areas of beetle-attacked forests were classified based on Sentinel-2 images from 19th September 2019, and from 29th August 2021 (Table 2). Also, bands 2, 3, 4 and 8 were used for the classification. Both results of unsupervised classifications divided all pixels into ten clusters.

Satellite images were chosen at the end of the growing season, for the phase of the transition of bark beetles from colonised downed trees to standing trees (Phase I / 2017–2019), and for the phase of spreading of beetles in standing trees (Phase II / 2020–2021). The splitting of the outbreak into two phases took into account the 2015 windfall and a time lag of 3–4 years for spreading spruce bark beetle in the surrounding healthy coniferous trees (Hanewinkel et al., 2008; Modlinger and

Table 2

Sentinel 2 images that were used for the creation of forest masks and to identify the standing tree mortality per specific years. Layers represent the outcome datasets further used in analyses.

Date	Id	Layer
06.06.2016	COPERNICUS/S2/20160606T011115_20160606T043732_T55TCJ	Forest mask
19.09.2019	COPERNICUS/S2/20190919T010651_20190919T010648_T55TCJ	Beetle infestation (Phase I)
29.08.2021	COPERNICUS/S2/20210829T010651_20210829T010954_T55TCJ	Beetle infestation (Phase II)

Table 3

Relative contribution (%) of variables for tree mortality presence and mortality severity for tree mortality due to windfall or bark beetle attack according to the BRT analysis. Phase I - bark beetles transition from colonised downed trees to standing trees (2017–2019), Phase II - spreading of beetles in standing trees (2020–2021).

Variable	Windfall (n = 151)		Phase I of outbreak (n = 390)		Phase II of outbreak (n = 289)	
	Presence	Severity	Presence	Severity	Presence	Severity
Fir %	4.9	6.4	5.5	6.3	4.1	6.9
Yezo %	5.1	7.9	24.2	3.4	25.5	3.7
Glehn %	0.0	0.0	1.7	5.8	3.7	8.3
Decid %	5.5	5.6	5.7	7.7	6.6	6.5
FirAge / FirH*	9.3	6.2	13.3	11.2	9.1	9.1
YezoAge / YezoH*	30.4	21.3	13.6	4.2	18.4	6.3
GlehnAge / GlehnH*	0.0	0.0	0.8	3.7	0.8	4.9
Bon	2.5	4.0	0.9	1.5	1.0	1.8
Slope	4.9	8.7	3.8	3.9	4.6	6.4
pH	1.7	5.8	1.0	0.7	1.0	1.4
Elev	35.4	34.0	16.2	29.7	12.0	25.6
Rad	-	-	13.4	21.7	13.0	19.9
Training data correlation	0.626	0.349	0.957	0.490	0.948	0.635
CV correlation	0.543	0.183	0.832	0.350	0.840	0.523
Se	0.012	0.013	0.012	0.033	0.009	0.034
CV deviance	0.624	0.001	0.313	0.000	0.396	0.000
Se	0.011	0.000	0.022	0.000	0.017	0.000

CV (cross-validation procedure). The variables with the highest influence are in bold type, and the second most important values per model are in italics with bold type. SE – standard error. For the explanation of variables and their units, see Table 1. The high number of related contributions represents the fact that this factor has a high importance in driving tree mortality, and vice versa.

*FirH, YezoH, GlehnH – variables used in analyses of tree mortality by wind. FirAge, YezoAge, GlehnAge – variables used in analyses of tree mortality by infestation of bark beetle.

Novotný, 2015).

The classifications were performed in Google Earth Engine (Gorelick et al., 2017). Three validation datasets were prepared, based on a visual analysis of high-resolution Google satellite images from 2016, 2019, 2021 and forest inventory data. We assessed the accuracy for each classification (forest mask, tree mortality in Phase I and II), where the overall accuracy represents the ratio of correctly classified pixels to the total number of classified pixels (Table S3–S5).

The raster layer of the Global Forest Change dataset was vectorised for calculating windfall areas in the period 2015–2017. Standing tree mortality masks were separately vectorised using the “Raster to Vector” tool in QGIS 3.22.5 (Phase I – mask 2019, Phase II – mask 2021) (QGIS, 2022), and single pixels were removed to reduce noise in the results. Spatial layers, based on classification results, were joined with forest characteristics from forest inventory data.

2.5. Statistical methods

We tested the differences in beetle-killed tree spot areas among different dominant tree species using ANOVA and the posthoc Tukey test for pairwise comparison between the groups. The spot areas were calculated in QGIS 3.22.5 after vectorising the raster layers (QGIS, 2022).

We used the BRT machine learning algorithm to analyse the main drivers of windfall and bark beetle outbreaks. We fitted one model predicting tree mortality for presence and another for severity of each disturbance phase (see below). Variables with high correlation were excluded from subsequent analyses. We set the model-specific variables because for each model we used variables for specific disturbance agent (solar radiation was not considered for wind disturbances and etc.). For each model, we calculated the relative contribution (%) of each predictors to identify tree mortality. The relative significance of each variable is estimated based on how often the variable is selected in the process of building regression trees and the ability of the variable to improve the model. The relative influence of the variables is scaled so that the sum equals 100% (Elith et al., 2008). We cross-validated the BRT models on data from a 0.5 bag fraction, using a tree complexity of 5, and a learning rate of 0.01.

We analysed wind-damaged areas and bark beetle infested areas separately. Both disturbance agents were divided into presence and

severity of tree mortality. The presence of tree mortality was based on the presence (1) or absence (0) of tree mortality in a subcompartments by wind or bark beetles. The severity of beetle infestation represents the ratio of attacked area to total subcompartment area. We separately analysed factors connected with a) wind damage (typhoon), b) factors connected with the transition of bark beetles from colonised downed trees to standing trees (Phase I), and c) factors connected with the spreading of beetles in standing trees (Phase II), i.e. we calculated six BRT models.

All of the models were fitted using R software, version 2.14.1 (Development Core Team, 2013), and R studio version 2022.02.0 (RStudio Team, 2022), with the gbm package, dismo package (Ridge-way, 2007), and an extension developed by Elith and Leathwick (2011). We used the Bernoulli distribution for the presence analysis, and the Gaussian distribution to predict damage severity.

3. Results

3.1. Pilot field survey

The study plots revealed the general pattern of the bark beetle outbreak in a spruce-fir forest dominated by Glehn spruce. By estimating the percentage of changes in tree stand condition by species in the Golovnin Caldera and Danilovskiy, we observed that Glehn spruce was infested first, followed by Sakhalin fir (Fig. 2, Table S2). Additionally, these data indicated that the outbreak in the plots of the Golovnin Caldera field commenced earlier than in the plots of the Danilovskiy.

Four study plots established in 2021 also included field data on the condition of Yezo spruce, which had a high percentage of stand infestation and was in the red stage of the attack, whereas the Glehn spruce had reached the grey stage. Based on this information, we can conclude that the infestation of Yezo spruce occurred after the infestation of Glehn spruce (Fig. 2, Table S2).

Therefore, the field data highlight the following points:

- 1) Infestation of Glehn spruce began in Phase I of the outbreak when the bark beetle transitioned from fallen trees to standing trees.
- 2) Infestation of Yezo spruce and Sakhalin fir corresponds to Phase II of the outbreak when the infestation spreads among standing trees.

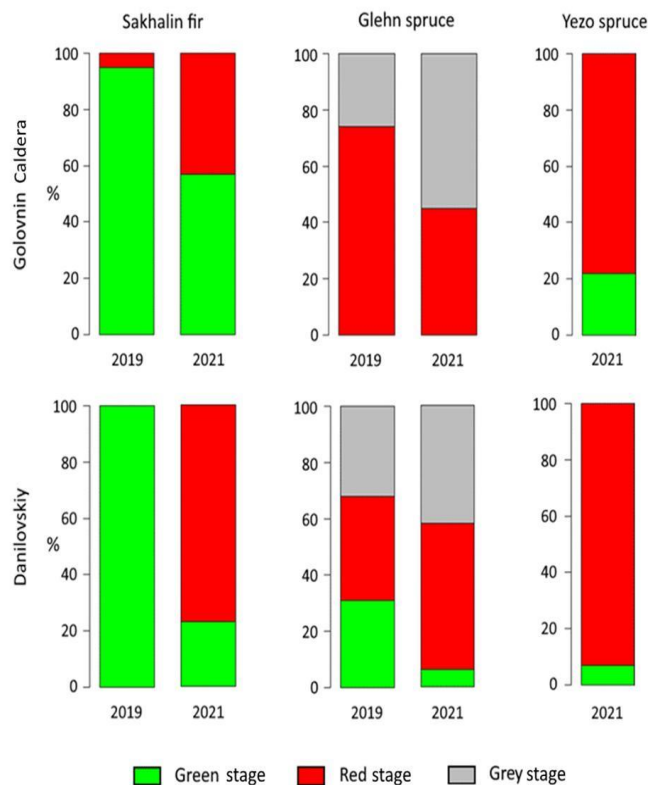


Fig. 2. The proportion of trees at different stages of beetle infestation in two fields.

We recorded that Sakhalin fir was infested by two bark beetle species (spruce and fir bark beetles) in both study locations (Golovnin Caldera and the Danilovskiy). It is noteworthy that the primary host tree species for the fir bark beetle is the Sakhalin fir, and for the spruce bark beetle, it is the Glehn spruce and the Yezo spruce in this region.

3.2. Tree mortality classification: windfall and beetle infestations

The accuracy of the classification is assessed by considering the ratio of correctly classified pixels to the total number of pixels that were classified. In the specific case of the study, the overall accuracy of the forest mask was determined to be 95.5% (Table S3) and the overall accuracies were found to be 96.7% for the standing tree mortality of 2021 and 94.1% for the mask of 2019, as reported (Tables S4, S5). In addition, the errors of omission and commission for each class within the classifications have been determined. As shown in Table S3 for the forest mask, the omission errors for the forest and non-Forest classes in the forest classification were 4.4% and 4.5% respectively, with commission errors of 3.8% and 5.2%. For Phase I bark beetle tree mortality damage classification as outlined in Table S4, the omission errors were noted to be 4.9% for bark beetle damage and 1.9% for forest, while the commission errors were noted to be 2.2% and 4.3%, respectively. Similarly, for the Phase II bark beetle damage classification shown in Table S5, omission errors were found to be 11.8% for bark beetle damage and 10.2% for forest, with a commission error of 0.3% for both classes.

During a six-year period, the forest loss area of coniferous species reached approximately 620.5 ha. Of that amount, an area of 446 ha (72%) was damaged due to severe wind, and an area of 174.5 ha (28%) was damaged due to a bark beetle outbreak. An area of 446 ha of the forest had fallen due to the wind in the period 2015–2016, according to the Global Forest Change dataset (Hansen et al., 2013). An area of

140.4 ha of coniferous forests was affected by bark beetle in the period 2017–2019 (Phase I), and an area of 34.1 ha was affected in the period 2020–2021 (Phase II, Fig. S1). Tree mortality by windfall was recorded in 151 subcompartments, and by bark beetle in 397 compartments (Phase I – 390, Phase II – 289, with repeated infestations in some subcompartments). Subcompartments with dominant deciduous species were taken into account due to the presence of coniferous species.

Fig. 3 shows the tree mortality due to windstorms or bark beetle infestation, by phases and main species of subcompartments. The main species have an equal 50% or more in a tree stand in the subcompartment.

The total percentage of tree damage area for bark beetle outbreak, where Glehn spruce dominates in the subcompartment, is 16.5 ha (8%) of the entire Glehn spruce forest in the southern part of the reserve, Yezo spruce is 23.2 ha (2%), and Sakhalin fir is 126.2 ha (2%). Analyses of area spots show that Glehn spruce has the biggest spots (mean – 0.2 ha, median – 0.041 ha) and Sakhalin Fir and Yezo spruce have smaller spots (mean – 0.06 ha, median – 0.027 ha). The maximum forest spot of bark beetle mortality equals 2.67 ha, and it is located in a coniferous forest that is dominated by Glehn spruce.

The analysis of variance (ANOVA) test showed significant statistical differences between the areas of beetle-killed tree spots, located in the stands dominated by Glehn spruce, Yezo spruce, and Sakhalin fir ($P < 0.05$). Pairwise comparison of these groups using the Tukey test (Honestly-significant-difference, HSD) showed: Yezo spruce and Sakhalin fir have no significant difference $P > 0.05$, but Glehn spruce and Yezo spruce $P < 0.05$, Glehn spruce and Sakhalin fir $P < 0.05$ are significantly different (RStudio Team, 2022).

Results of BRT analysis for windfalls and bark beetle outbreaks, split by presence and severity and phases, are shown in Table 3. The results of the analysis are also divided into tree mortality presence and mortality

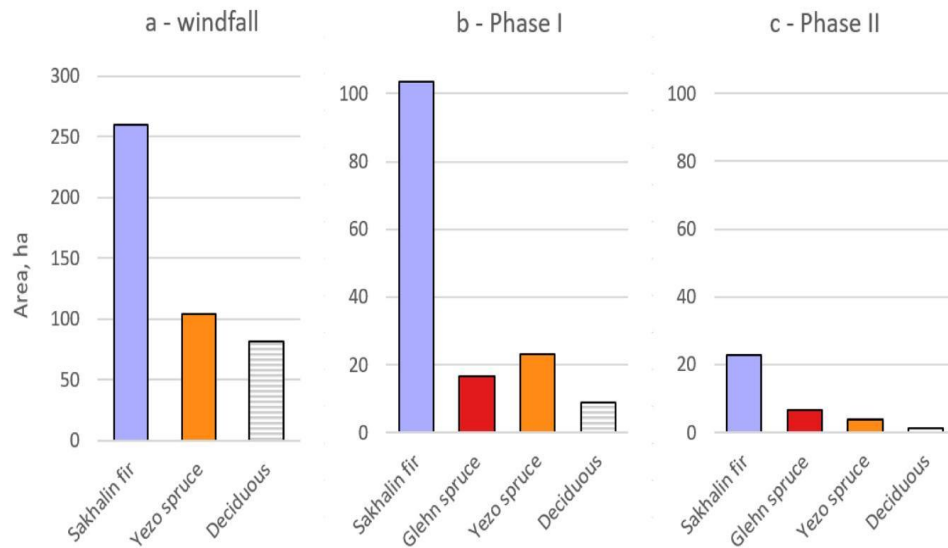


Fig. 3. Areas of tree mortality caused by windfall and bark beetle, divided by dominant tree species.

severity, for trees attacked by bark beetles. In the BRT analysis we reported only the six most important variables in Figs. 4–9. The presence models consider the number of windfall patches or infested areas, whereas the severity of mortality models take into account the size of these areas.

Our results show that the presence of tree mortality by wind is mainly related to elevation, heights of Yezo spruce and Sakhalin fir (Fig. 4). Yezo spruces over 15 m were most damaged (Fig. 4b), whereas most of the fir damage occurred in trees under 15 m (Fig. 4c). The factor of elevation (Fig. 5a) has a high influence (34%) on the severity of mortality damage. However, more windfall-damaged areas were located in subcompartments at elevation levels in the range of 10–100 m. Another factor is that the slope (8.7%; Fig. 5c) had most of the effect of wind damage in the range between 0 and 10 degrees. Therefore, the most damaged forests were on flat terrain and areas lower than 150 m a.s.l. (Fig. 5a).

The main drivers presence in the phase of bark beetles transitioning from colonised downed trees to standing trees (Phase I) were Yezo spruce percentage and its age, the elevation of the site, and solar

radiation (Fig. 6). Yezo spruce forests that were older (approximately over 100 years, as seen in Fig. 6c) were killed by bark beetles, whereas fir forests predominantly occurred in younger stands (under 100 years, depicted in Fig. 6e). In comparison to the presence of tree mortality caused by wind, which was more prevalent at elevations up to 150 m as shown in Fig. 4a, mortality caused by bark beetles was observed at higher elevations, reaching up to 300 m, as depicted in Fig. 6a. Tree mortality caused by bark beetles was initiated at lower elevations (Fig. 6b) and progressively spread to higher elevations with increasing severity (Fig. 7a). The severity of damage in this phase was mainly related to elevation and solar radiation (Fig. 7a, b).

In the second phase of the outbreak (2020–2021), the pattern of tree mortality caused by bark beetles mirrored that of Phase I. Older Yezo spruces continued to be targeted, while younger firs were also affected (as shown in Fig. 8b, e). The influence of deciduous trees on bark beetle-induced mortality of conifers remained consistent throughout the outbreak, with a higher presence of deciduous trees correlating with lower tree mortality of conifers (as seen in Figs. 6d, 8f). Topographic factors and solar radiation exhibited similar patterns in both phases of

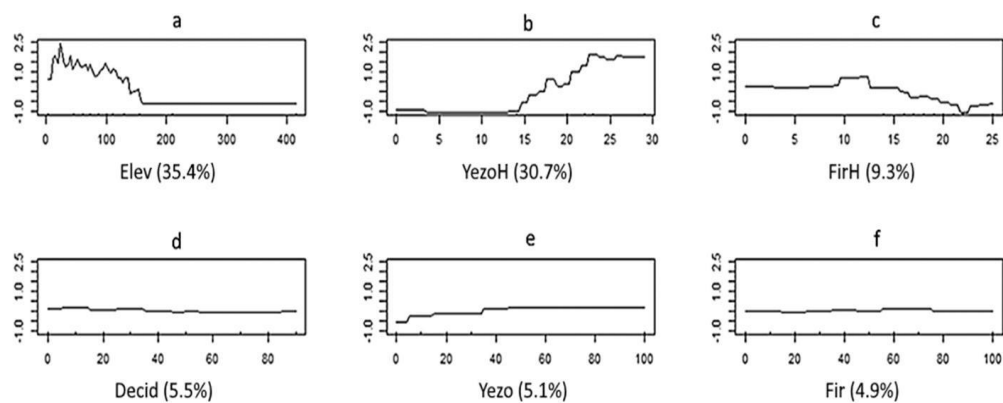


Fig. 4. Partial dependence plots for the six most influential variables in the BRT model for presence of tree mortality by the wind: a) Elev – Stand elevation (m a.s.l.); b) YezoH – average height of Yezo spruce; c) FirH – average height of Sakhalin fir; d) Decid – the percentage of deciduous trees; e) Yezo – percentage of Yezo spruce; f) Fir – percentage of Sakhalin fir. Note: the plots are ordered in decreasing importance of the explanatory variables.

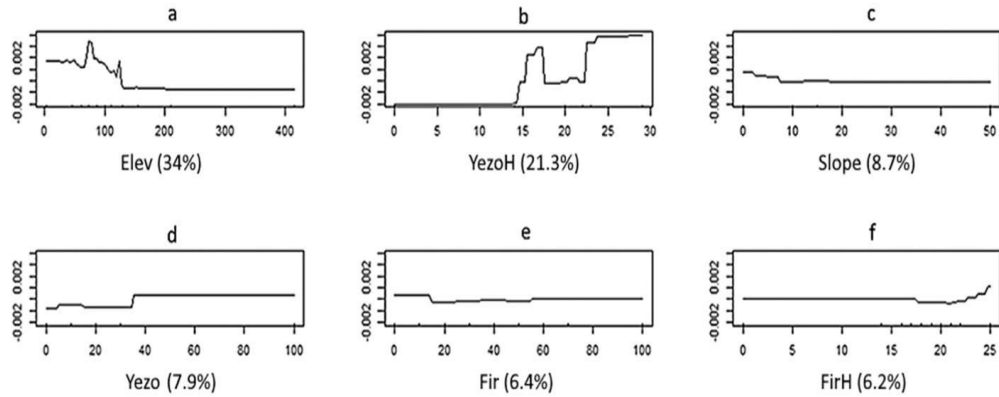


Fig. 5. Partial dependence plots for the six most influential variables in the BRT model for severity of tree mortality by the wind: a) Elev – Stand elevation (m a.s.l.); b) YezoH – average height of Yezo spruce; c) Slope – relief slope; d) Yezo – percentage of Yezo spruce; e) Fir – percentage of Sakhalin fir; f) FirH – the average height of Sakhalin fir.

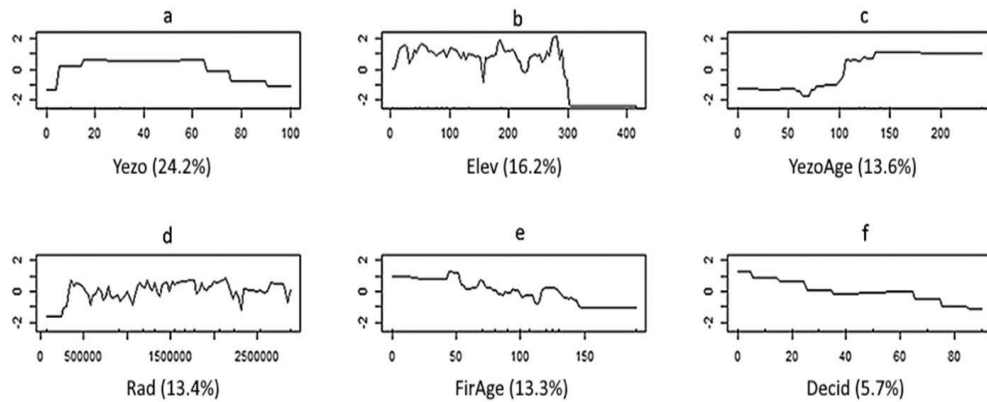


Fig. 6. Partial dependence plots for the six most influential variables in the BRT model for presence of bark beetle-caused tree mortality in the phase of bark beetles transition from colonised downed trees to standing trees (2017–2019): a) Yezo – percentage of Yezo spruce; b) Elev – stand elevation (m a.s.l.); c) YezoAge – average age of Yezo spruce; d) Rad – solar radiation; e) FirAge – average age of Sakhalin fir; f) Decid – percentage of deciduous species.

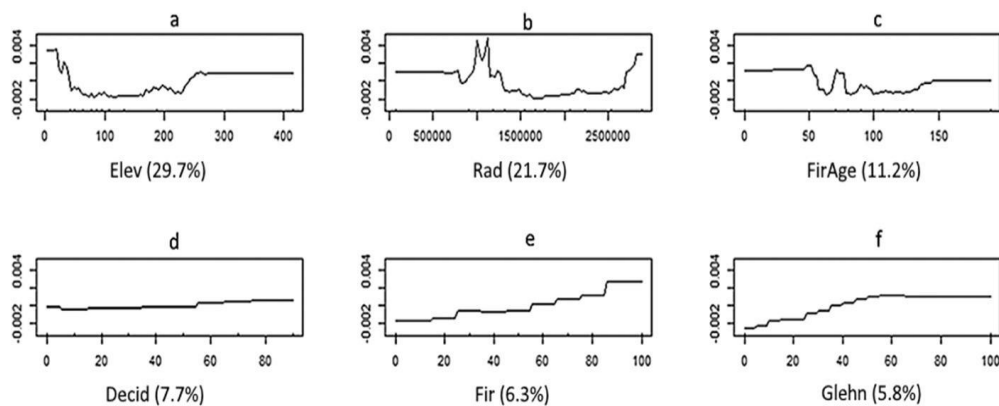


Fig. 7. Partial dependence plots for the six most influential variables in the BRT model for the severity of bark beetle-caused tree mortality in the phase of bark beetles transition from colonised downed trees to standing trees (2017–2019): a) Elev – Stand elevation (m a.s.l.); b) Rad – solar radiation; c) FirAge – average age of Sakhalin fir; d) Decid – percentage of deciduous species; e) Fir – percentage of Sakhalin fir; f) Glehn – percentage of Glehn spruce.

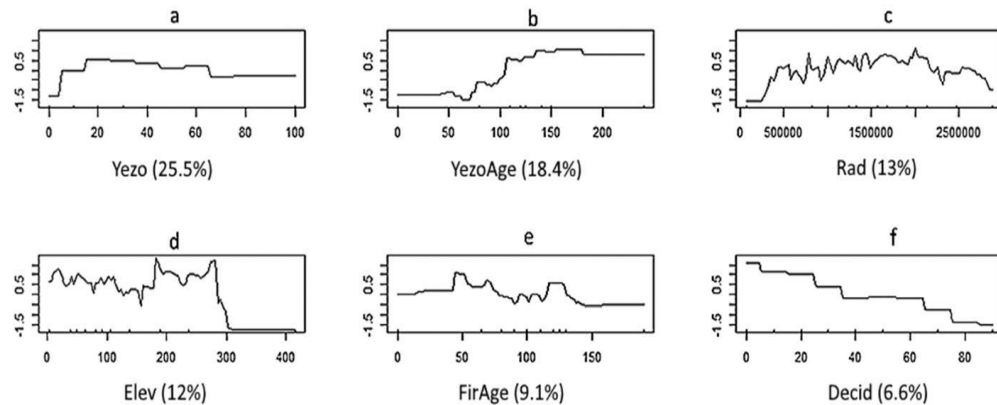


Fig. 8. Partial dependence plots for the six variables in the BRT model that are most influential over presence of bark beetle-caused tree mortality in the phase of spreading of beetles in standing trees (2020–2021): a) Yezo – percentage of Yezo spruce; b) YezoAge – average age of Yezo spruce; c) Rad – solar radiation; d) Elev – stand elevation (m a.s.l.); e) FirAge – average age of Sakhalin fir; f) Decid – percentage of deciduous species.

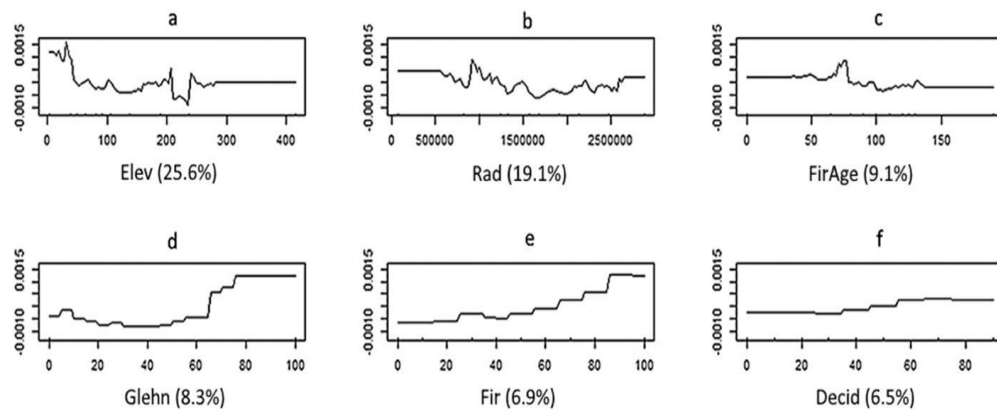


Fig. 9. Partial dependence plots for the six most influential variables in the BRT model for the severity of bark beetle-caused tree mortality in phase II of spreading of beetles in standing trees (2020–2021): a) Elev – Stand elevation (m a.s.l.); b) Rad – solar radiation; c) FirAge – average age of Sakhalin fir; d) Glehn – percentage of Glehn spruce; e) Fir – percentage of Sakhalin fir; f) Decid – percentage of deciduous species.

the outbreak (Figs. 6–9), although their relationship with standing tree attacks was not clearly established.

4. Discussion

The primary objectives of our study were to investigate the key factors influencing the mortality of Yezo spruce, Glehn spruce, and Sakhalin fir due to wind damage and infestations by spruce and fir bark beetles. We aimed to ascertain which factors exerted a greater impact during Phase I of the outbreak in the period 2017–2019 (when infestations spread from fallen to standing trees), and Phase II in the period 2019–2021 (when infestations spread among standing trees). Additional objectives included determining the factors influencing the occurrence of windfalls, as they have been identified as a significant trigger for bark beetle outbreaks in Europe (Potter et al., 2019) and on Hokkaido Island (Furuta, 1989; Furuta et al., 1996). The study was conducted at the tree level during fieldwork in 2019 and 2021, and at the landscape level using satellite imagery and forest inventory data. The landscape-level study enabled the identification of the main factors affecting conifer mortality. Field studies offered insights into the general pattern of outbreaks in mixed-conifer forests, especially regarding the mechanism of outbreaks, and potential host shifts of spruce bark beetle to Sakhalin fir.

4.1. Factors influencing wind-caused tree mortality

In our research of factors influencing the occurrence of windfalls, an important factor is the height of Yezo spruce and Sakhalin fir trees. A significant correlation was observed between a high degree of windfall damage and tree heights exceeding 20 m for Sakhalin fir and 15 m for Yezo spruce (Fig. 4b, c and Fig. 5b, f, respectively). This finding may be attributed to differences in root system types, with Yezo spruce having a shallow root system, and Sakhalin fir having a tap-root system (Ushvatkina et al., 2010). Similarly, Korznikov et al. (2019) did not find a significant correlation between windfall areas distribution and elevation above sea level, and slope gradient in their study on Kunashir Island; however, this depends more on stand characteristics and tree species.

4.2. Initialisation of bark beetle outbreak

Bark beetles use wind-fallen conifer trees as breeding material and can increase their population to the epidemic phase in windfall areas (Furuta, 1989; Yamaguchi, 1963a). Therefore, wind-blown Yezo spruce trees can be suitable breeding material for the spruce bark beetle and fallen Sakhalin fir trees for the fir bark beetle. This corresponds to the importance of windfalls in triggering the transition to a beetle infestation of standing trees and indicates the wider host range for bark beetles.

Lawson et al. (1995) studied the breeding ability of *I. typographus* on logs of Yezo spruce and Norway spruce, finding that beetles produced longer egg galleries and had higher larval survival rates on Yezo spruce logs.

A massive bark beetle outbreak starts after a windfall with a delay of 3–4 years in European forests where Norway spruce is the dominant species (Modlinger and Novotný, 2015). Uprooted trees can maintain constitutive defence for up to seven months, and spruce bark beetle can successfully develop on 17-month-old uprooted trees. Research shows that bark beetles can attack uprooted trees after three years (Hroššo et al., 2020). These studies were undertaken in regions where spruce bark beetles are bivoltine. Therefore, the conclusions drawn are applicable to the area of Kunashir Island, where the spruce bark beetle has more than one generation. A windstorm creates gaps in the forest, thus changing the lighting conditions under the forest canopy, and consequently creating new forest edges, and decreasing the collective shading of trees in the forest. This can create conditions for the occurrence of increased water stress level in trees and provide favourable opportunities for beetle infestation (Vanderhoof et al., 2014).

4.3. Factors influencing bark beetle-caused tree mortality

In this study, while topographical factors such as elevation and slope, along with solar radiation, showed significant relative importance in the models predicting bark beetle-driven tree mortality their precise relationship to the presence and severity of tree mortality remains nuanced and not definitively understood (Figs. 6–9). Specifically, elevation, despite its prominence in the models, exhibited complex or unexpected interactions that might not align straightforwardly with previous literature or initial expectations. However, research by Mezei et al. (2014a, b) shows significant factors of elevation and solar radiation in different phases of the outbreak. Perhaps this is due to the topographic features of the study areas, as the southern part of Kurilskiy Nature Reserve has a lower elevation, and the infested coniferous forest is situated within an elevation range of 10–300 m in comparison with the 970–1670 m a.s.l. in the above mentioned studies. Our study area was not located in mountainous conditions, as are many studies in Central Europe or the Alps (Logan and Powell, 2001; Jakuš et al., 2011 a, Jakuš et al., 2011b; Mezei et al., 2014 a, b); hence, the role of solar radiation and elevation can be different. Kunashir Island has a marine climate, a significant amount of precipitation, and high air humidity values in the vegetation season. These factors might reduce the effect of solar radiation, as high air humidity reduces the transpiration losses and the value of water stress (Kamata, 2002). Moreover, the effect of solar radiation can be present during infestations at the individual tree scale (Hroššo et al., 2020), which was not examined here. The common trigger for bark beetle epidemics is wind, which causes an abrupt increase in excess fallen trees suitable for beetle breeding (Okland et al. 2016; Mezei et al., 2017). The major difference between our study area and Europe is the terrain - in central Europe, mountain ranges with deep valleys create different local climates (Mezei et al., 2019; Pirtskhalava-Karpova et al., 2024).

Therefore, stand characteristics, such as the percentage of different conifers on the stand, and their age, should be considered as the main factors for the presence and severity of tree damage. The percentage of Yezo spruce (24.2% influence factor for presence, Fig. 6a, c) in composition and age of Yezo spruce (13.6%), were the main triggers that began the massive outbreak in Phase I. The influence of these factors increased further in Phase II of the outbreak (Fig. 8a, b).

Nevertheless, it is crucial to distinguish outbreaks in Yezo spruce-Sakhalin fir forests from outbreaks in Glehn spruce forests, as these forests exhibit different stand structures and outbreak patterns. Glehn spruce forests predominantly consist of 80% Glehn spruce stands, whereas Yezo spruce-Sakhalin fir forests are more mixed and have a larger proportion of deciduous trees in their composition (FID, 2007). The study results from landscape-level and tree-level analyses, which are based on field data, suggest that Glehn spruce stand may have lower

resistance to the infestation of the spruce bark beetle. This susceptibility may be due to physiological factors or ecological conditions, such as reduced diversity within Glehn spruce stands. The average area of beetle-killed tree spots is twice as extensive in Glehn spruce forests (Glehn spruce - 0.2 ha, Yezo spruce - 0.06 ha). Bark beetle damage affected 16.5 ha of Glehn spruce, which represents 8% of the entire Glehn-dominant forest, and 23.2 ha of Yezo spruce, which comprises 2% of the total Yezo-dominant forest. Field data collected during the 2021 fieldwork revealed a substantial percentage of Glehn spruce stands in the grey stage of attack, while Yezo spruce was in the red stage.

Therefore, the distinct physiological traits of Glehn and Yezo spruce must also be taken into account. Glehn spruce, characterised by its slow growth, long needle life, and lower nutrient demand for growth and development, has low shade tolerance due to the reduced photosynthetic activity of its needles. In contrast, Yezo spruce exhibits a higher photosynthetic capacity and a more rapid growth rate under normal conditions. Consequently, Glehn spruce and Yezo spruce are classified as slow- and fast-growing spruce species, respectively (Lambers et al., 1998; Kayama, 2004; Kayama et al., 2007). In addition, our field observations show that in some places species such as the Glehn spruce are growing in lines that appear to be artificially planted. This may be a result of the activities of Japanese loggers in the last century. Japanese foresters carried out logging in areas of the southern part of the reserve (~60 ha) before the Second World War, as described in the forest inventory data (FID, 2007). However, we don't have any information on reforestation in these areas.

The influence of tree mortality from the Sakhalin fir age variable diminishes throughout the outbreak. The fir age has a 13.3% influence on tree mortality for presence in Phase I. The probability of infestation decreases with increasing age. This contrasts with the Yezo spruce, where the probability of infection increases with age (Fig. 6c, e). The Sakhalin fir age influences tree mortality by 9% in Phase II, but the chart of the probability of infestation is flatter (Fig. 8e).

Tree diameter is highly correlated with the age of the tree (Table S1), which suggests that the dependence of tree mortality on Sakhalin fir age could be a factor in the fir bark beetle's shift to attacking trees with larger diameters throughout the outbreak. Studies conducted on Siberian fir (*Abies sibirica* Ledeb.) and Veitch's fir (*Abies veitchii*) have shown that fir bark beetles attack weakened, small-diameter trees under endemic conditions, and can switch to attacking healthy, large-diameter fir trees under epidemic conditions. The population of fir bark beetles increased, leading to the beetles attacking trees with larger diameters (Takagi et al., 2018; Debkov et al., 2020).

Infestation of Sakhalin fir by European spruce bark beetle (*I. typographus*) was observed during the fieldwork, but it is not a common occurrence. There are two sources that point out that Sakhalin fir could be a host tree for this bark beetle species (Maslov, 2010; CABI, 2022). However, we have not found any studies examining the shift in host tree preference from spruce to fir by the spruce bark beetle during an outbreak. Several hypotheses regarding spruce bark beetle attacks on Sakhalin fir should be considered: (1) The fir bark beetle starts attacking weakened, smaller diameter fir trees. These trees grow under the canopy (Debkov et al., 2020). (2) Fir trees can be infested by the fir bark beetle for 3–4 years before tree death. (3) Sakhalin fir trees were attacked first by the fir bark beetle, and the spruce bark beetle attacked weakened fir trees, resulting in fir death. (4) The death of the top canopy trees increases solar radiation under the canopy and increases water stress for fir trees, thus exposing them to spruce bark beetle infestation.

Nevertheless, further field research is necessary to study the influence of these two bark beetle species on Sakhalin fir mortality. The existing field studies do not provide sufficient data for a comprehensive assessment. The association between the presence of deciduous trees and reduced tree mortality due to bark beetle infestations is particularly intriguing.

4.4. Potential limitations of the study

Sentinel 2 images with a spatial resolution of 10 m were employed for the standing tree mortality identification. This technique becomes more common in analysing bark beetle outbreaks (Abdullah et al., 2018) as it provides higher resolution than the 30 m resolution of the LANDSAT images (Meddens et al., 2013; Senf et al., 2015) and gives us more precise information on tree mortality. Hence, identifying individual dead spruce or fir trees using this spatial resolution is still not possible, as one pixel may encompass 4–5 mature trees. A pixel containing only one dead tree crown will, with a high probability, not be identified as belonging to the standing tree mortality class. However, as time progresses and more trees within the same pixel become infested, it will likely be identified as an infested area.

Forest inventory data were spatially divided by subcompartments as the lowest level forest inventory unit; consequently, our statistical analysis was based on the subcompartment level. It should be noted that the forest inventory data were collected in 2006 and have not been updated; thus, a 15-year difference introduces possible inaccuracies in stand variables, but less so in environmental variables. Mostly, the changes are associated with individual trees grow in height and diameter, which can change the forest's volume and biomass. Changes in canopy cover, altered forest structure, changes in species composition are not reported in the forest inventory data (FID, 2007). Mortality events were already excluded by using Global Forest Change (Hansen et al., 2013) dataset 2007–2015 – small losses, 2015–2021 excluded by classifying Sentinel 2 images of tree cover loss due to bark beetle mortality.

In our study, we posited that a significant bark beetle outbreak following a windfall was the primary cause of conifer tree mortality. This assertion was substantiated by visual inspections of test plots and the observed pattern of dead wood emergence post-windthrow. However, it is important to note that tree mortality was mapped using satellite imagery and we did not directly observed the transition of bark beetle infestation from windthrown trees to standing trees in the field as was done by Hroššo et al. (2020). In addition, it is noteworthy that a larger sample size of study plots would yield more robust data, particularly in evaluating various bark beetle species. We theorise that the presence of any other potential abiotic or biotic stressors might lead to increased bark beetle attacks on trees under outbreak conditions, given that these beetles typically target stressed trees. This limitation is compounded by the remoteness of Kunashir Island and environmental challenges such as dense cloud cover and frequent fog events, so high-resolution annual remote sensing is needed to further investigate the relationship between bark beetles and tree species in this study area. In this context, our study mainly examined the influence of topographic and stand variables on bark beetle damage. However, we did not investigate the effects of climate variables and beetle pressure, mainly due to the limitations of our dataset, which is restricted to two outbreak phases.

4.5. Practical implementations

Our results are important to understand and manage bark beetle outbreaks in mixed stands, particularly concerning invasive species. We identified the primary factors contributing to the initiation of beetle infestations and their subsequent spread (Table 3), including tree age, tree species proportions in forest compartments, and their height. Compared to the more substantial effects of environmental factors (terrain, solar radiation, etc.), these attributes can be modulated by forest management to reduce the risk of bark beetle infestation. It can be especially helpful in identifying vulnerable areas during ongoing bark beetle outbreaks. From a forest management perspective, our research contributed to knowledge about the important invasive species and quarantine pest *P. proximus* in the European Union (EU) (de la Peña et al., 2020). Climatic changes and transportation of unbarked wood,

which refers to logs that have not had their bark removed, along the Trans-Siberian Railway create conditions for the active westward migration of the fir bark beetle. Since the traditional habitat of the fir bark beetle in Russian Far East is climatically similar to that of Western Europe, there are no obstacles to bark beetle reproduction in the conditions of such countries as northern Spain, Ireland, Scotland, northern Italy, northern Türkiye, etc. (EPPO, 2014).

Our study highlights a potential mechanism of fir infestation, initially by the fir bark beetle and subsequently by the spruce bark beetle. Research by other scientists shows the possibility of fir bark beetle attack on spruce (Mandelstam and Popovichev, 2000; Chikhshaeva, 2008). Thus, the invasion of fir bark beetle in Europe may increase the damage from spruce bark beetle outbreaks and endanger the spruce forests of Europe.

The results of this study can be utilised by local biodiversity conservation. One of the primary objectives of Kurilskiy Nature Reserve is to safeguard the habitat of the fish-owl (*Strigiformes: Strigidae: Ketupa blakistoni*). The fish-owl typically inhabits coniferous forests along rivers (Hayashi, 2009). A reduction in the area of coniferous forests, resulting from disturbances, will likely lead to a decline and fragmentation of the fish-owl habitat. Consequently, this may potentially cause a decrease in its population in the future. Spatial gaps created by disturbances are filled by the wide-sweeping growth of dwarf bamboo species (*Sasa* spp.) on the Kuril Islands archipelago (Popov, 1969). Unfortunately, dwarf bamboo thickets impede forest recovery and then can cause a decrease in the forested area on the island (Kornikov et al., 2019). The cover of dwarf bamboo species (*Sasa* spp.) prevents mainly Sakhalin fir regeneration, and to a less extent affects Glehn spruce restoration (Krestov et al., 2003).

The methodology outlined in this study offers a viable tool for analysing extensive areas that are affected by bark beetle outbreaks in Russian Far East. This approach can be effectively employed to map and assess the risk of tree mortality caused by bark beetles across large forest expanses, leveraging time-series of high-resolution remote sensing imagery. The data we have used in this study are from freely available datasets (Sentinel-2, Global Forest Change dataset), and can be processed by commercial (ArcGIS) or open source software (QGIS, 2022). These methods are versatile and can be adapted for a variety of environmental monitoring tasks in the Kurilskiy Nature Reserve, including but not limited to biodiversity conservation.

5. Conclusion

We show that tree mortality by bark beetles in Kunashir Island forests was preceded by wind disturbance. Our study provides, for the first time, evidence of the changing importance of the drivers of tree mortality, during the bark beetle outbreak in Yezo and Glehn spruce forests. The most important factor for wind disturbances on the island was the height of the Yezo spruce, and for the bark beetle outbreak the factors were the percentage and age of Yezo and Glehn spruce. These results can be used to forecast mortality in mixed-species forests. Additional data are needed to retrospectively infer yearly bark beetle population dynamics.

In addition, we found evidence of changing the host tree to Sakhalin fir by a spruce bark beetle (*I. typographus*). We cannot conclude whether this is due to bark beetle epidemics and whether this behaviour occurs at low beetle numbers (endemic beetle population). Additional data are needed for the analyses of infestation of Sakhalin fir by two species of bark beetle (*I. typographus*, *P. proximus*), and a description of the mechanisms of infestation.

Our findings thus highlight a general need for improved assessments of the role of biotic mortality agents in Kunashir Island forests, particularly in mixed-species forests, which allow comparisons between co-occurring tree species during the same disturbance event.

CRedit authorship contribution statement

Aleksandr Karpov: Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Rastislav Jakuš:** Conceptualization, Funding acquisition, Methodology, Project administration, Writing – review & editing. **Maria Potterf:** Writing – review & editing. **Pavel Mezei:** Conceptualization, Formal analysis, Methodology, Visualization, Writing – review & editing. **Aleksei Trubin:** Conceptualization, Formal analysis, Methodology, Visualization, Writing – review & editing. **Nana Pirtskhalava-Karpova:** Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft, 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

Data will be made available on request.

Acknowledgement

This research was founded by:

Grant no. QK1910480, “Development of integrated modern and innovative diagnostic and protection methods of spruce stands with the use of semiochemicals and methods of molecular biology”, financed by the Ministry of Agriculture of the Czech Republic.

Grant no. CZ.02.1.01/0.0/0.0/15_003/0000433, “EXTEMIT-K” financed by the Operational Program Research, Development and Education (OP RDE).

Grant no. 43950/1312/3165 “The study of relationship between spruce stand insolation and bark beetle attack with the use of LIDAR data” financed by Internal Grant Agency FFWS CULS in Prague.

Grant no. 43950/1312/3152 “Prediction of bark beetle outbreak spreading using TANABBO system” financed by Internal Grant Agency FFWS CULS in Prague.

We thank also projects APVV–18–0347 and VEGA1/0606/22 for providing financial support for this work.

We also extend our sincere thanks to the Kurilskiy Nature Reserve for supplying the forest inventory data essential for our analysis.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2024.121774](https://doi.org/10.1016/j.foreco.2024.121774).

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3.4 Spruce bark beetle phenological modelling and drought risk within framework of TANABBO II model

Published as: Pirtskhalava-Karpova, N., Karpov, A., Trubin, A., Koreň, M., Blaženec, M., Holuša, J., & Jakuš, R. (2024). Spruce bark beetle phenological modelling and drought risk within framework of TANABBO II model. In *Ecological Modelling* (Vol. 496, p. 110814). Elsevier BV. <https://doi.org/10.1016/j.ecolmodel.2024.110814>

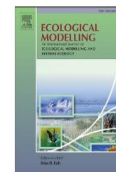
The operational part of TANABBO II produced daily 30 m maps that combined the PHENIPS phenology model with drought metrics to track spruce bark beetle pressure across the Horní Planá study area. Predicted swarming periods coincided closely with peaks in pheromone-trap catches collected in 2014 and 2015, with mismatches of only a few days. The Cumulative Transpiration Deficit Index (CTDI) proved to be the strongest single predictor of beetle activity. GAMs including CTDI explained almost half of the variation in trap numbers in 2014 and about one sixth in 2015.

Pixels where the CTDI threshold was exceeded and the swarming stage was active were classified as high risk in the operational module of TANABBO II. Overall, the study shows that the integration of high-resolution meteorological interpolation with phenological modelling can identify in advance the stands most susceptible to drought-enhanced bark beetle outbreaks and provide managers with actionable maps of outbreak risk during each generational swarming period.



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Ecological Modelling

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Spruce bark beetle phenological modelling and drought risk within framework of TANABBO II model

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ARTICLE INFO

Keywords:

Spruce bark beetle
Phenological modelling
Drought risk assessment
Drought indices
Bark beetle outbreak

ABSTRACT

Global warming plays a major role in the disruption of forest ecosystems by bark beetle outbreaks. Decreasing precipitation and more frequent droughts create the conditions for water stress in trees. The Eurasian spruce bark beetle (*Ips typographus* L.) is more dangerous for Norway spruce (*Picea abies* (L.) Karst.) forests in Central Europe under these conditions, because even healthy trees under water stress have a lower probability of survival during massive spruce bark beetle outbreaks. This critical issue highlights the importance of targeted research and intervention strategies in affected regions; hence, this study has a focus on the Horní Planá region in Central Europe, which is managed by the Military Forests and Farms of the Czech Republic (VLS).

The study presents the results of the drought risk assessment of the operational part of TANABBO II and its validation. TANABBO is a high spatial resolution risk assessment tool for spruce bark beetle infestation in Central European forests, incorporating 30 m spatial resolution and extensive meteorological data, which outperforms existing models in its ability to accurately predict bark beetle activity based on the PHENIPS phenological model. The operational part integrates environmental factors such as global radiation, temperature, precipitation and, in particular, water stress, which is assessed by using a transpiration deficit. The drought risk assessment included the calculation of Drought Indices (DI) and Cumulative Transpiration Deficit Indices (CTDI) on a daily basis, and the estimation of spruce bark beetle swarming time using the PHENIPS model. The risk assessment was validated by comparing it with the number of bark beetles caught in traps and the value of the drought index. Generalised additive models (GAM) were used for validation, with the most effective models incorporating the CTDI. The model with the highest predictive accuracy achieved an adjusted R-squared value of 0.478. The study highlights the critical role of high-resolution environmental data in understanding and managing bark beetle outbreaks, particularly in the context of climate change.

1. Introduction

Climate change is escalating at a more rapid pace than has been suggested in prior predictions. This acceleration is causing an increase in drought, temperature extremes, and wind storm events, with significant impacts on forest ecosystems, insect populations, and tree survival during mass bark beetle outbreaks (Bale et al., 2002). Furthermore, the rise in average temperature is extending the vegetation season and the period of bark beetle development, reducing the mortality of overwintering beetles, and leading to earlier beetle swarming, thereby increasing the bark beetle population and the number of generations

(Safranyik and Linton, 1998; Negron and Popp, 2009; Bentz et al., 2010; Robbins et al., 2021). Knowledge regarding the biology, ecology, and population dynamics of the spruce bark beetle (*Ips typographus* L.) has enabled the formulation of effective forest management strategies to mitigate beetle attacks, particularly in the early stages of an outbreak (Wermelinger, 2004).

In Central Europe, the peak flight activity period of the spruce bark beetle extends from April to September (Baier et al., 2007), with the season divided into spring (May to mid-June) and summer (mid-June to August) periods (Faccoli and Stergulc, 2004). The beetle's flight activity is temperature-dependent, with an optimal range between 16 °C and 31

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<https://doi.org/10.1016/j.ecolmodel.2024.110814>

Received 14 June 2024; Received in revised form 20 July 2024; Accepted 26 July 2024

Available online 6 August 2024

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°C (Lobinger, 1994). The temperature range is also critical for the development of bark beetle eggs into mature beetles under bark and for oviposition rates (Wermelinger et al., 1999). The resilience of the spruce bark beetle population is highly contingent on environmental conditions; increased solar activity and higher temperatures at the landscape and tree level can enhance the likelihood of a spruce bark beetle attack in a given location (Jakuš et al., 2011; Kautz et al., 2013). Spruce bark beetle outbreaks are caused by rising temperatures due to local changes in forest cover and global climate change (Seidl et al., 2017).

The ongoing climatic shift, characterised by increased temperatures and reduced precipitation, is affecting the defences of spruce stands (Netherer et al., 2019). Clearcuts and wind damage create gaps in the forest canopy, reducing collective shade and increasing understory temperatures. Adaptation to the altered conditions in new forest gaps and edges takes a minimum period of two months. In such situations, water stress prompts the emission of biogenic volatile organic compounds, including terpenes, attracting bark beetles (Marešová et al., 2020). It is noteworthy that this undermines the tree's resistance to bark beetle attacks (Jönsson et al., 2007; Strižbrská et al., 2022). Studies by Korošková et al. (2022) and Koontz et al. (2021) have shown that sustained water deficiency significantly undermines spruce resilience against bark beetle invasions, and is closely correlated with increased bark beetle attacks. Hence, areas with higher solar radiation experience more drought stress, weakening spruce trees' defence mechanisms and making them more susceptible to bark beetle attacks.

The occurrence of water stress is significantly influenced by factors such as the amount of precipitation, solar radiation, soil temperatures and properties, and the depth of the soil layer, which affect water capacity and moisture evaporation rates (Jakuš et al., 2017). Norway spruce increases the emission of volatile terpenoids that attract spruce bark beetles and influence their host selection (Schiebe et al., 2012). Moreover, these trees have weaker defences and are prone to infestations. Higher temperatures enhance bark beetle oviposition rate, and accelerate bark beetle development and maturation. To address these climate-driven vulnerabilities and their impacts on forest ecosystems, various modelling tools have been developed. These models aid in predicting and understanding the complex interactions of climate, tree physiology, and bark beetle behaviour.

Central to these developments is the PHENIPS model, which employs daily meteorological data to calculate effective temperature sums for predicting spring swarming, infestation, and the development of new generations under the bark (Baier et al., 2007). PHENIPS has been the foundation for subsequent model developments (Hlásny et al., 2011; Berec et al., 2013; Stadelmann et al., 2013; Temperli et al., 2013; Pasztor et al., 2014; Mezei et al., 2017). Seidl et al. (2007) developed a variation of this model, assessing tree susceptibility to bark beetle attack under water stress conditions. This model incorporates data on forest biomass structure, solar radiation, bark temperature, stand leaf area related to evapotranspiration, and soil moisture content for accurate predictions. The spruce bark beetle prediction model was integrated into the two other models, PICUS and EFISCEN, used for simulating disruptions in Alpine regions (Seidl et al., 2007, 2009).

Recent research has produced various models for predicting bark beetle infestations, each with unique approaches and focuses. Huang et al. (2019) classified these models into three categories: Agent-Based Models (ABMs), Forest Landscape Models (FLMs), and Dynamic Global Vegetation Models (DGVMs). ABMs provide highly accurate simulations of bark beetle and host tree interactions at the tree level, including beetle distribution, tree defence, aggregation, and tree colonisation (Burnell, 1977; Berryman et al., 1989). However, ABMs are limited by their local applicability and exclusion of vegetation, and climate dynamics studies via DGVMs offer different spatial resolutions, from stand to continental levels, and integrate bark beetle phenology and distribution models into vegetation dynamics models. The FATES-IMAP is an example of a DGVM (Fisher et al., 2015). The integration of ecological models with bark beetle disturbance simulations has significantly

improved our understanding of forest dynamics under various environmental stresses. Jönsson et al. (2012) and Temperli et al. (2013) used the LPJ-GUESS and LandClim models, respectively, to study vegetation changes due to bark beetle impacts, focusing on tree growth and forest structural dynamics in response to climate variables such as temperature, precipitation, and solar radiation. Similarly, Netherer et al. (2019) and Matthews et al. (2018) employed the PHENIPS-TDEF model to assess the development of spruce bark beetle broods and the impact of water stress on spruce stands, with the TDEF module evaluating water stress and its dual influence on bark beetle phenology and tree physiology.

Despite significant advances in modelling spruce bark beetle dynamics and forest ecosystem responses to climate change, existing models often lack the integration of high-resolution spatial data and comprehensive environmental factors, especially in the Central European context. The combination of the phenological model and water stress analysis enables the identification of the most vulnerable forest areas at the time of spruce bark beetle swarming. The present research addresses these gaps by incorporating detailed spatial analysis and interpolation of meteorological data across diverse forest landscapes.

TANABBO was developed for the conditions of Central Europe and was tested for the area in the High Tatra mountains (Jakuš et al., 2005) more than 10 years ago, and was then upgraded to the TANABBO II. This system improves spruce forest protection measures, including spatially predicting spruce bark beetle outbreaks for the coming year and assessing drought risk on a daily basis. Thus, the software includes prediction and operational modules (Jakuš et al., 2017). Ďuraciová et al. (2020) provide a comprehensive description of the prediction module for spatial outbreak forecasting. This article focuses on implementing the operational part of TANABBO II to assess the risk of drought-induced spruce stand infestation.

Drought risk assessment in TANABBO II is based on meteorological data, solar radiation, soil moisture content, and spruce bark beetle phenology. The operational module performs spatial analyses of these factors, interpolating data such as average and maximum air temperature, precipitation, and daily sums of solar radiation from weather stations across the study area. Bark temperatures are calculated from meteorological data to model bark beetle phenology and water deficit for drought risk assessment. The PHENIPS model calculates the period for the first and subsequent bark beetle generations, based on the summed effective air and bark temperatures (Baier et al., 2007; Jakuš et al., 2017). Areas that are most susceptible to infestation, are identified through daily modelling of spruce bark beetle phenology and water stress.

The aim of our work has two objectives: (i) to introduce the drought risk assessment algorithm of the operational part of TANABBO II, and (ii) to validate these risk assessment results with field data.

2. Materials and methods

2.1. Study area

The study area (see Fig. 1) is the Horní Planá region (Czech Republic) in Central Europe, which is managed by the state enterprise of Military Forests and Farms of the Czech Republic (VLS). This state enterprise is responsible for managing a total land area of 19,960 ha, of which 16,569 ha are covered by forests, 203 ha are occupied by a water reservoir, and the rest is comprised of grassland that is used for military activities. The topography of the region is characterised by hills with variations in elevation ranging from 100 to 150 m. The majority of the study area is situated between 600 and 800 m above sea level, with the highest point being Lysá Mountain at an elevation of 1228 m above sea level (a.s.l.). Part of the area falls within the Bohemian Forest (the Šumava Mountains), while another part is within the Šumavské podhůří (i.e., Šumavské Piedmont), a huge complex with highland to montane characteristics. The average annual temperature in the region ranges from 5

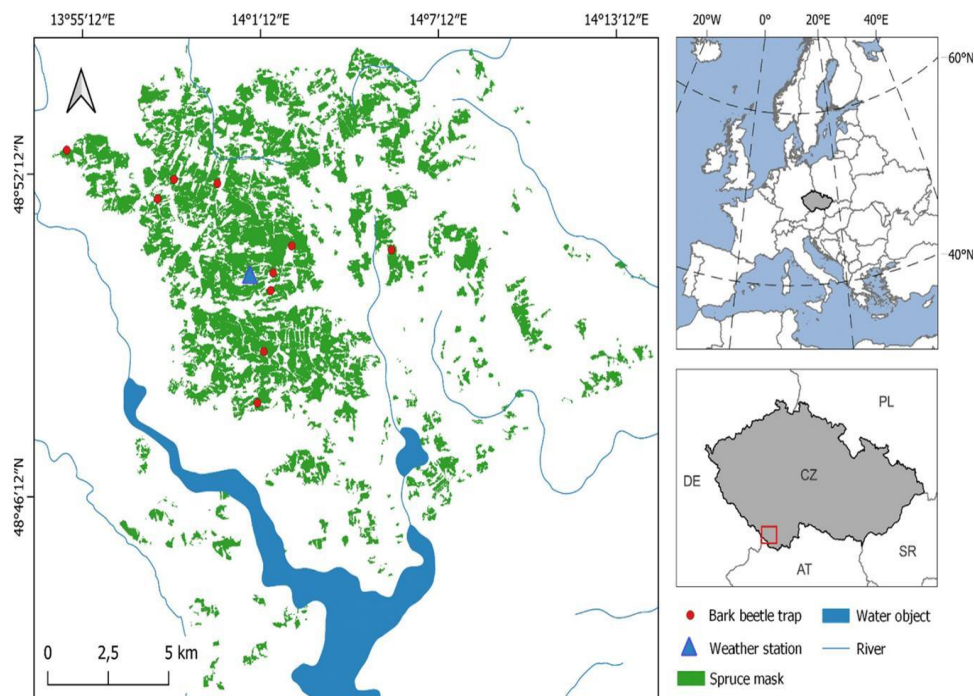


Fig. 1. Study area. Horní Planá region, Czech Republic.

to 7 °C, and the annual precipitation ranges from 700 to 800 mm (Culek et al., 2013).

The dominant tree species in the forests of this region is the Norway spruce (*Picea abies* (L.) Karst), accounting for 69 % of the tree composition. It is frequently found alongside silver fir (*Abies alba* Mill., 6 %) and European beech (*Fagus sylvatica* L., 5 %). Scots pine (*Pinus sylvestris* L., 12 %) is common at lower elevations. Forest stands younger than 40 years of age cover approximately 23.5 % of the area, while stands older than 100 years of age account for 32 %. The natural conditions in the region are represented by altitudinal zones ranging from Querceto-Fagetum to Fageto-Piceetum forests. The forests form extensive complexes in higher altitudes, surrounded by meadows and pasturelands.

Spruce forests in the Horní Planá region are primarily affected by snow, bark beetles, and notably wind disturbances, with windthrows being the most significant in recent years. The occurrence of windfall trees and bark beetle infestations has contributed to approximately 50 % of the total forest damage. Bark beetle outbreaks in the study area align with patterns observed in bark beetle populations across the Czech Republic, with peaks recorded in the mid-1980s and mid-1990s. A prolonged outbreak commenced in 2003, following an intense drought that affected Central Europe as a whole (Rouault et al., 2006). This outbreak was further triggered by Wind Storm Kyrill in 2007 (Fink et al., 2009). Since 2015, a new bark beetle outbreak has emerged, resulting from drought conditions and prolonged warm vegetation seasons.

2.2. TANABBO II

This research employed TANABBO II (see Fig. 2), which is an Open Source Software (OSS) that is seamlessly integrated within the GRASS GIS system (grass.osgeo.org), and which adheres to the European Union Public License (EUPL) agreement (<https://joinup.ec.europa.eu/collection/eupl/eupl-text-eupl-12>). TANABBO II is composed of three primary modules, all accessible through GRASS GIS and developed using Python (TANABBO, 2024). The first module provides support for data input and

editing. The second, a prognostic module, is dedicated to forecasting spruce bark beetle infestations. The third, an operational module, incorporates the PHENIPS model (Baier et al., 2007) for bark beetle phenology. This third module offers insights into the current status of spruce bark beetle populations, including critical phases such as the onset of swarming and infestation stages, along with development patterns. Additionally, TANABBO II includes submodules that calculate various environmental parameters. These include solar radiation, air and bark temperatures, and drought indices, which are essential for a comprehensive ecological analysis.

2.3. Meteorological, forest data and digital elevation model

Data from the forest management plan, as detailed by Duračiová et al. (2020), were integral to the present study. The data encompassed various parameters, including the age structure of the forest, percentage of spruce, stand density, and overall wood volume. A spruce mask was generated with spatial resolution 30 m based on forest inventory spatial layer on order to identify areas that are more vulnerable to infestations. The spatial resolution of the spruce mask is 30 metres, as with the other input data. This mask specifically targeted forest units that are characterised by a minimum of 50 years of age and a significant percentage of spruce, due to their higher susceptibility to infestations. For the PHENIPS model, essential meteorological data inputs included average and maximum temperatures, precipitation levels, and solar radiation. These meteorological variables were calculated on the basis of data received from a weather station installed in the study area at an elevation of approximately 1100 metres above sea level. These variables are crucial for accurately predicting spruce bark beetle infestations. A Digital Elevation Model (DEM) was derived from the ASTER Global Digital Elevation Model with resolution of 30 m, obtained from NASA's Earth Observing System Data and Information System (NASA, 2024).

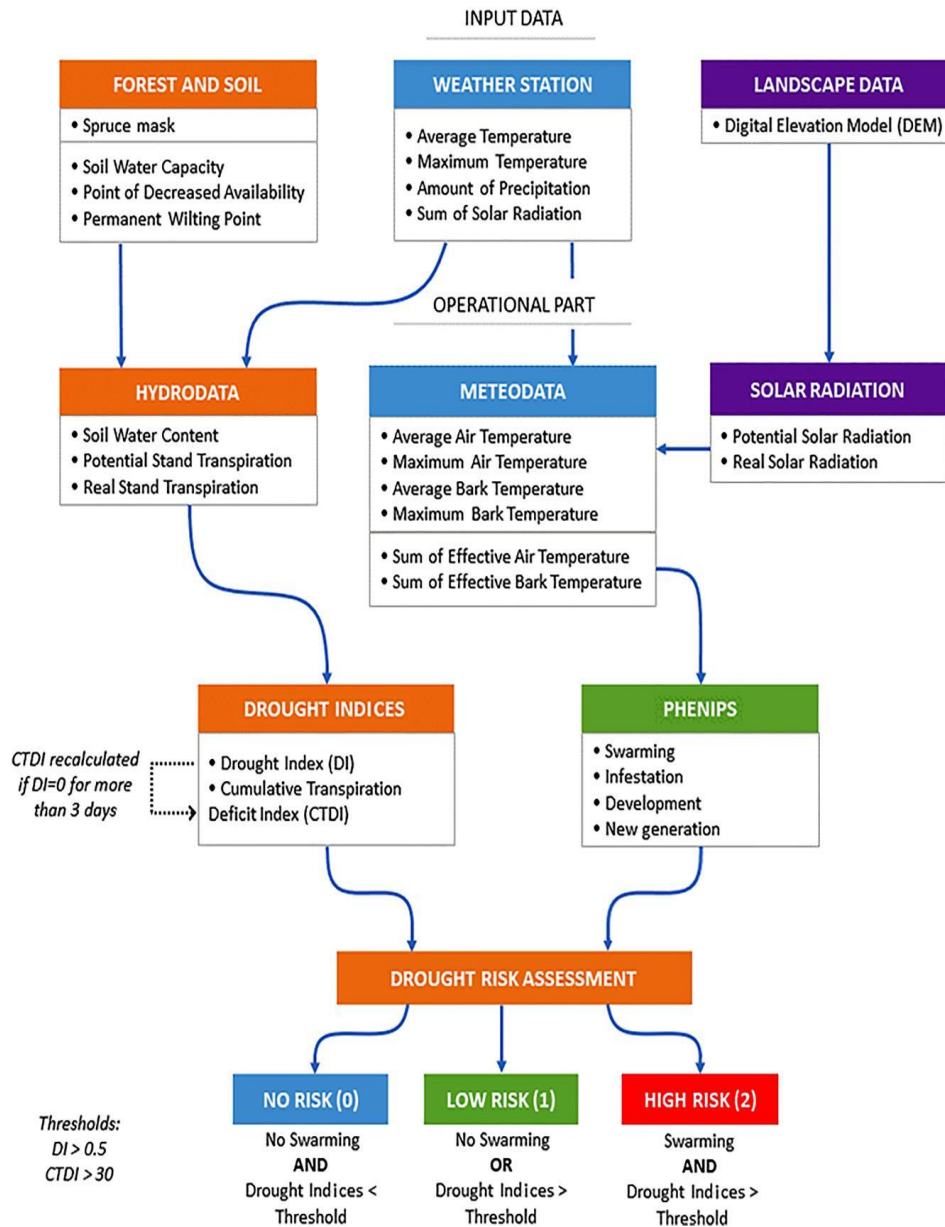


Fig. 2. Drought risk assessment workflow in TANABBO II.

2.4. Phenological modelling

TANABBO II features a specialised module that is designed for the spatial modelling of spruce bark beetle development. This module employs a modified version of the phenological model, PHENIPS, which relies on meteorological data, including average and maximum air temperatures. The PHENIPS model operates within a specific annual timeframe, from 1st April (day 92) to 30th October (day 304). Within this period, the model performs daily calculations to create spatial layers. These layers represent the cumulative effective air and bark temperatures (S4–8), which are key factors in understanding bark beetle development.

The model then generates spatial layers which offer insights into

several critical stages of the bark beetle lifecycle. These stages include the timing of swarming, the onset of spruce infestation, the development of the bark beetle under the bark, and the number of generations produced. According to the PHENIPS model, swarming is initiated when the cumulative effective air temperature surpasses 60 °C, and the maximum temperature exceeds 16.5 °C. Infestation is indicated when the effective air temperature sum goes beyond 140 °C. The development stage is determined by the cumulative effective bark temperatures, with a threshold of 557 °C marking completion.

2.5. Calculation of drought indices and assessment of drought risk

Drought indices play a crucial role in indicating water stress, which is

a key contributor to bark beetle infestation. Our drought risk assessment incorporates both forest inventory and meteorological data (Baláz et al., 2009), while taking into account factors such as soil type and depth, global radiation, air temperature, and precipitation. The model for soil water balance is conceptualised as a reservoir system. In this system, precipitation serves as the water input, while stand transpiration represents water loss. The daily Real Stand Transpiration (RST) is determined by considering the Potential Stand Transpiration (PST; S9; Turk, 1961) and the soil Water Content (WC; S10). If WC falls below the volume required by PST, this is an indication of water stress for the stand.

This research employs two key parameters for assessing the drought risk in tree stands: the Drought Index (DI) and the Cumulative Transpiration Deficit Index (CTDI). DI is calculated as the ratio of RST to PST, indicating the availability of moisture. CTDI, on the other hand, quantifies the absolute water deficit, accounting for the difference between PST and RST. Both DI and CTDI provide insights into the current water availability and the duration of the water deficit. Detailed formulas for DI and CTDI calculations are available in the supplementary materials (S11–12). A DI value exceeding zero suggests a water deficit, while CTDI tracks the accumulated deficit. Specifically for spruce stands, a DI value of zero sustained over three consecutive days resets the CTDI.

The drought risk assessment integrates drought modelling with the spruce bark beetle phenological model. A high risk of infestation in spruce stands is indicated when both the DI and CTDI indices exceed thresholds ($DI > 0.5$, $CTDI > 30$) and the spruce bark beetle is in the swarming stage within that specific pixel. Low risk is when drought indices exceed thresholds or bark beetle swarming stage in a given pixel. Spatial layers for risk assessment are calculated daily, assigning pixel values of 0 - no risk, 1 - low risk, and 2 - high risk of infestation.

2.6. Beetle count and drought indices connectivity

Field data on the number of bark beetles caught in traps were collected during the growing season at ten sites in 2015 and six sites in 2014. Data on the number of bark beetles caught in pheromone traps were included in our datasets. Subsequently, specific characteristics of the forest management unit, such as the percentage of spruce and the age of the forest, were extracted for each trap location based on the forest management plan. Additionally, we incorporated the distance of each trap to the nearest area of significant forest loss in the previous year, defined as a location with two or more pixels of loss. Furthermore, for each observation, we extracted the values of the DI and CTDI indices, corresponding to the specific date and location from the relevant spatial layer. To create the variable 'beetle_lag', we transformed the collection date of beetles from each trap. This was done by subtracting the earliest date in the year when beetles were collected, thereby standardising the data to reflect the time lag in beetle capture.

2.7. Statistical analysis

Before the analysis, data were checked for missing values, outliers, autocorrelation, and collinearity. During data exploration, we plotted the response variable with each covariate to check the relationship between them. Based on the data exploration, the relationship between the number of beetles in traps and the explanatory variables was analysed using Generalised Additive Models (GAMs). A set of a priori models (Dochtermann and Jenkins, 2011; Rosen, 2016) were selected prior to analysis (Table 2), in order to test which model would best explain the number of *I. typographus* in traps. These models were constructed using previously known variables that were identified as important for bark beetle population dynamics, mainly climatic variables, and this is consistent with the previous work of Trubin et al. (2022) and Mezei et al. (2017).

For the GAMs, the Information-Theoretic (I-T) approach was used to assess competing models. The models were ranked according to the

Akaike information criterion (AIC) for a small sample dataset. The delta AIC (ΔAIC) represents the difference in the AIC between a given model and the best-performing model in a set of candidate models; the most parsimonious model was selected based on the lowest ΔAIC value. Models with $\Delta AIC < 2$ can be considered as good as the best, while models in the ΔAIC range of 2–7 are also plausible. We also calculated Akaike weights to arrange candidate models in order of parsimony, where the Akaike weight is a number from 0 to 1, thus providing a measure of the relative likelihood of each model, given the data and the candidate model set. This weight can be considered the probability that a given model is the best-approximating model (Burnham et al., 2011).

As some of the variables were highly correlated, we used the threshold of $r = 0.7$ to select variables. All data manipulations, plotting, calculations, and statistical analysis were performed in VSCode 1.73.1 in Jupiter Notebook using Python programming language (ver. 3.11.1; Rossum and Drake, 2010) with pandas 1.5.0, Matplotlib 3.6.0, statsmodels 0.15.0, pygam 0.5.5, scikit-learn 1.3.0.

3. Results

The TANABBO II phenological model has been important in identifying the significant life cycle stages of the spruce bark beetle in the study area, including swarming, infestation, and development. The daily geospatial layers were generated using the PHENIPS model. Each pixel was assigned a numerical value to represent the progression through the beetle's stages. Drought indices DI and CTDI were calculated daily using the Meteo module to provide further insight during the study period.

3.1. Phenology model

One aspect of this research involved analysing the phenology model PHENIPS, which is integrated into the TANABBO software, using real data on spruce bark beetle activity. The data from traps indicate that spruce bark beetle activity was highest during two periods: from mid-May to mid-June (day of year 142–162) in 2014, and from mid-July to mid-August (day of year 196–230) in 2015. It is noteworthy that our trap data for 2014 are restricted to days 114–224, and for 2015 are restricted to days 121–224. The data from traps in 2014 showed the highest bark beetle activity during the first swarming period, while in 2015, the highest activity was observed during the third swarming period, according to the phenology calculated using the PHENIPS model. However, the catches and densities of bark beetles were relatively low, and this is likely due to the overall low population densities in the area.

The relationship between spruce bark beetle activity during the 2014 and 2015 trapping periods and meteorological data, specifically precipitation and maximum air temperature, is shown in Fig. 3. An increase in the maximum temperature leads to an increase in the number of bark beetles captured, while precipitation decreases the capture rate of bark beetles. The time lag between the bark beetle swarming period (duration of swarming), calculated from the PHENIPS phenological model and the beetle trapping data, is shown in Fig. 4. The time lag is the number of days from or to the nearest bark beetle swarming period, calculated using the phenological model. This metric is crucial, because the greater the distance away from the modelled swarming period, the lower the number of bark beetles caught in traps. These findings highlight the impact of environmental conditions on beetle activity, and demonstrate the effectiveness of the PHENIPS model in predicting these dynamics.

3.2. Drought risk assessment

The core outcomes of the operational component of TANABBO II include daily-calculated drought risk assessment layers that provide information on areas at high risk of spruce bark beetle infestation. A pixel is classified as high risk if the drought index value exceeds the established threshold, and the phenological model indicates that the

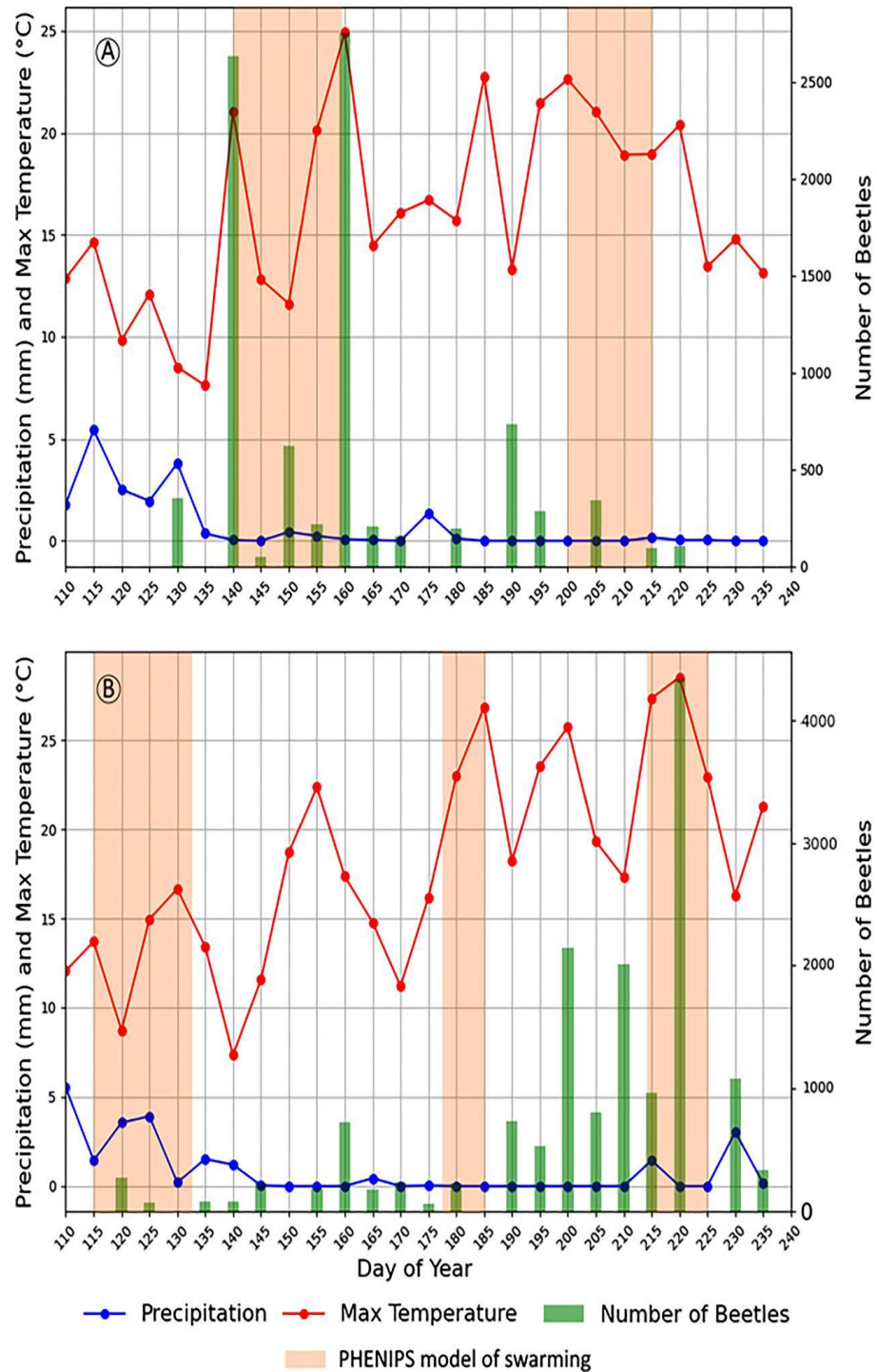


Fig. 3. Spruce bark beetle trapping, maximum air temperature and precipitation with swarming periods predicted by PHENIPS for years A - 2014 and B - 2015.

bark beetle is in the swarming stage on that day. Fig. 5 illustrates the drought risk assessment based on the CTDI drought index on 29th June 2015 (the 180th day of the year), which aligns with the second bark beetle swarming period. Additionally, drought index values and the

corresponding number of captured bark beetles for 2014 and 2015 are detailed in Fig. S1.

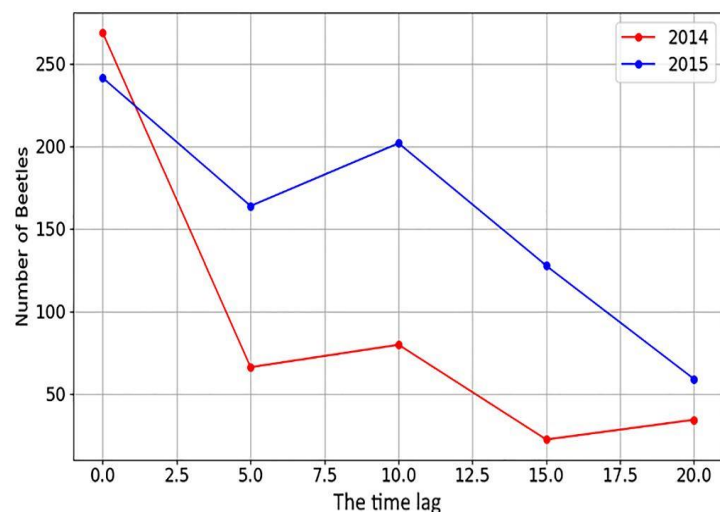


Fig. 4. Time lag of spruce bark beetle activity (average number for five-day lag) compared to PHENIPS model predictions for years 2014 and 2015.

3.3. Validation

We tested the data on bark beetle counts throughout our study period (i.e., for each year, separately) for autocorrelation; the ACF function did not reveal trends between *I. typographus* numbers in traps.

The TANABBO II drought risk assessment is based on drought index values and the occurrence of bark beetle swarming within a pixel. Field data were gathered on the number of bark beetles caught in traps. Minimal Time to Next or Previous Swarming and the drought index values (DI and CTDI) were calculated, to be included in the models. We used GAM regression in order to investigate the relationship between the number of bark beetles and meteorological, stand, and phenological variables (Table 1).

Based on Akaike's information criterion, Model 1 emerged as the most parsimonious model (Table 2). The insights gleaned from our model (Table 3) indicate that the Average daily air temperature on the current day, Average daily precipitation on the current day, and Cumulative Transpiration Deficit Index, have a relationship with the changes in *I. typographus* number in the trap in 2014 (Fig. 6). Higher Average daily air temperature on the current day resulted in more beetles in the trap; nevertheless, higher Average daily precipitation on the current day and Cumulative Transpiration Deficit Index resulted in less beetles in the trap.

In the analysis of *I. typographus* number in the trap in 2014, we identified a total of 7 models that exhibited a ΔAIC of less than 7, indicating a substantial level of support relative to the best model. When assessing the prevalence of variables within these models, Average daily air temperature and CDTI emerged as the most recurrent variables, featuring all 7 models. Minimal Time to Next or Previous Swarming, Average daily precipitation on the current day, Drought Index, daily of solar radiation on the current year, Percentage of spruce in forest management unit, Age of trees in forest management unit, and solar appeared once in the list of best models, except for Model 2. The sorting of these variables, from the most frequently used to the least, provides insights into their relative importance in the models, based on the criterion that we applied.

Based on Akaike's information criterion, Model 1 emerged as the most parsimonious model (Table 4). The insights gleaned from our model (Table 5) indicate that the Cumulative Transpiration Deficit Index, have relationship with the changes in *I. typographus* number in the trap in 2015 (Fig. 7). Higher Average daily air temperature on the current day resulted in more beetles in the trap; nevertheless, higher

Average daily precipitation on the current day and Cumulative Transpiration Deficit Index resulted in less beetles in the trap.

In the analysis of *I. typographus* number in the trap in 2015, we identified a total of 29 models that exhibited a ΔAIC of less than 7, indicating a substantial level of support relative to the best model. When assessing the prevalence of variables within these models, CDTI emerged as the most recurrent, featuring all 29 models. All other variables appeared 7 times in the list of best models, except model 2. The sorting of these variables, from the most to the least frequently used, provides insights into their relative importance in the models, based on the criterion that we applied.

4. Discussion

4.1. Model results and pheromone trap catches

In this study, spruce bark beetle catches in pheromone traps were used to validate the predictive accuracy of the PHENIPS model for the phenological stage of swarming. The close alignment between trap data and model predictions over a period of two years confirms that the PHENIPS model is an accurate tool for predicting spruce bark beetle swarming periods. The study utilised GAM models to examine spatial and temporal variations of bark beetle activity. The results indicated that the CTDI, in addition to average temperature and precipitation, was a significant factor in determining beetle numbers in traps. The different relationship between the number of captured beetles and the CTDI in 2014 and 2015 reflects the climatic variability between two years and differences in the phenology of spruce bark beetle development. These shifts demonstrate the complexity of ecological systems, and highlight the necessity for multi-year datasets to improve our understanding and predict bark beetle swarming activity. The negative relationship in 2014 supports the idea that drought stress increases beetle activity, while the positive relationship in 2015 suggests that other environmental or biological factors also play a role.

This study has a limited temporal scope of trap data and lacks direct water stress measurements at the stand level. These constraints highlight the importance of long-term data and direct measurements of environmental stressors to improve understanding of the relationship between spruce drought stress and beetle activity. Many research studies demonstrate that drought stress affects the defence mechanisms of Norway spruce, making stands more susceptible to beetle attack, and that this stress influences the behaviour of spruce bark beetles. The

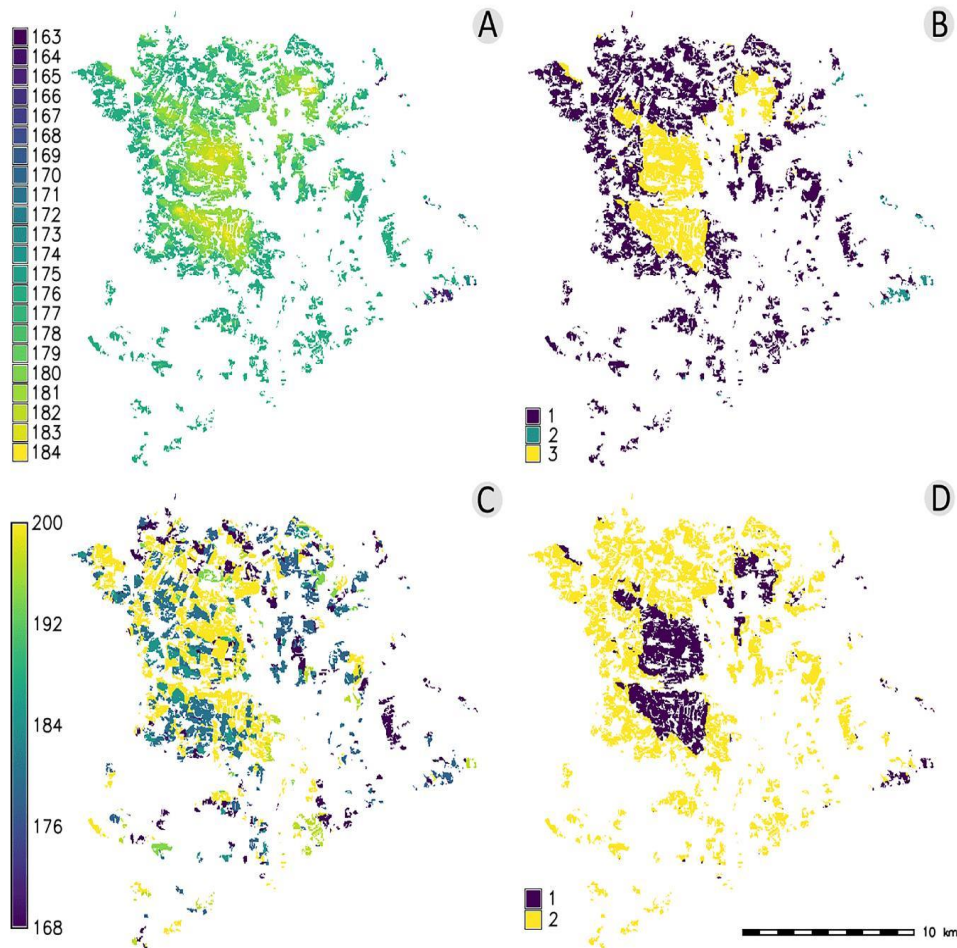


Fig. 5. TANABBO II modelling results: A - swarming second generation; B - spruce bark beetle stages at day 180 (1 - swarming, 2 - infestation, 3 - development); C - calculated CTDI drought index at 180 day of the year; D - drought risk assessment based on CTDI (0 - no risk of infestation, 1- low risk of infestation, 2- high risk of infestation).

Table 1
Variables used in the study area in years 2014 and 2015.

Name in model	Variable	Unit of measure
beetles	Number of bark beetles on particular day in particular trap	
beetles_lag	Minimal time to next or previous swarming	days
temp_avg	Average daily air temperature in the current day	degrees Celsius
precip	Average daily precipitation in the current day	millimetres
ctdi	Cumulative Transpiration Deficit Index	millimetres
di	Drought Index	
solar	Daily solar radiation	Watt.m ² . Hour ⁻¹
percent	Percentage of spruce in forest management unit, where trap installed	percent
age	Age of trees in forest management unit, where trap installed	years

emission of biogenic volatile organic compounds, including terpenes, under water stress attracts the spruce bark beetle. In addition, trees under stress, primarily due to water deficit, exhibit decreased resin flow, which is a crucial defense mechanism against bark beetle colonisation. Our study confirms that water stress significantly increases the

Table 2
Proposed seven best GAM regression models used to study bark beetle number in the trap in 2014.

Model	Combination	AIC	ΔAIC	AIC weight
1	Beetles = s(temp_avg) + s(precip) + s(ctdi) + ε	766.0756	0	0.469951
2	Beetles = s(temp_avg) + s(ctdi) + ε	769.0926	3.017032	0.103971
3	Beetles = s(temp_avg) + s(ctdi) + s(percent) + ε	769.2318	3.156195	0.096983
4	Beetles = s(beetles_lag) + s(temp_avg) + s(ctdi) + ε	769.3606	3.284981	0.090934
5	Beetles = s(temp_avg) + s(ctdi) + s(age) + ε	770.3603	4.28473	0.055161
6	Beetles = s(temp_avg) + s(ctdi) + s(solar) + ε	770.5612	4.485581	0.049891
7	Beetles = s(temp_avg) + s(ctdi) + s(di) + ε	770.6938	4.61819	0.04669

susceptibility of spruce stands to infestation, with drought conditions being the most effective predictor of spruce bark beetle presence as measured by trap captures. Research by [Temperli et al. \(2013\)](#) has

Table 3

GAM model equation estimating the variation in *I. typographus* number in the trap as a function of the Average daily air temperature on the current day, Average daily precipitation on the current day, and Cumulative Transpiration Deficit Index in 2014 within the study area.

Parameter	Estimate	p-value	Model values
Intercept	157.640865	0.010159*	Adjusted R-squared: 0.478
temp_avg	21.314221	0.000002*	
precip	-169.896036	0.031328*	
ctdi	-0.624389	0.000007*	

highlighted that stressed trees, especially those experiencing severe drought stress, produce less defensive resin compared to moderately or non-stressed trees. Resin flow is a critical defense mechanism against the colonisation of trees by bark beetles (Christiansen et al., 1987; Baier et al., 2002). Severe drought stress can result in lower production of

defensive resin in spruce and pine trees, in comparison to moderate or non-stressed trees (Netherer et al., 2015; Korolyova et al., 2022). This is a key consideration, as unstressed trees have greater resources available for resin production. The success of tree survival, therefore, depends not only on the level of water stress, but also on the defensive capacity of the host trees (Nelson et al., 2008).

Another important factor influencing bark beetle outbreaks is the number of generations that can develop annually. A strong negative relationship between voltinism and higher elevation was observed in Switzerland by Jakoby et al. (2019). In this study, an increase in the number of spruce bark beetle generations was modelled across the elevation gradient from 400 to 4000 m a.s.l. with increasing average temperature under climate change conditions for the 21st century. The predicted increase in bark beetle generations is expected to be more pronounced at lower altitudes, while a pre-shift in spring swarming is expected at higher altitudes. The TANABBO model is critical in

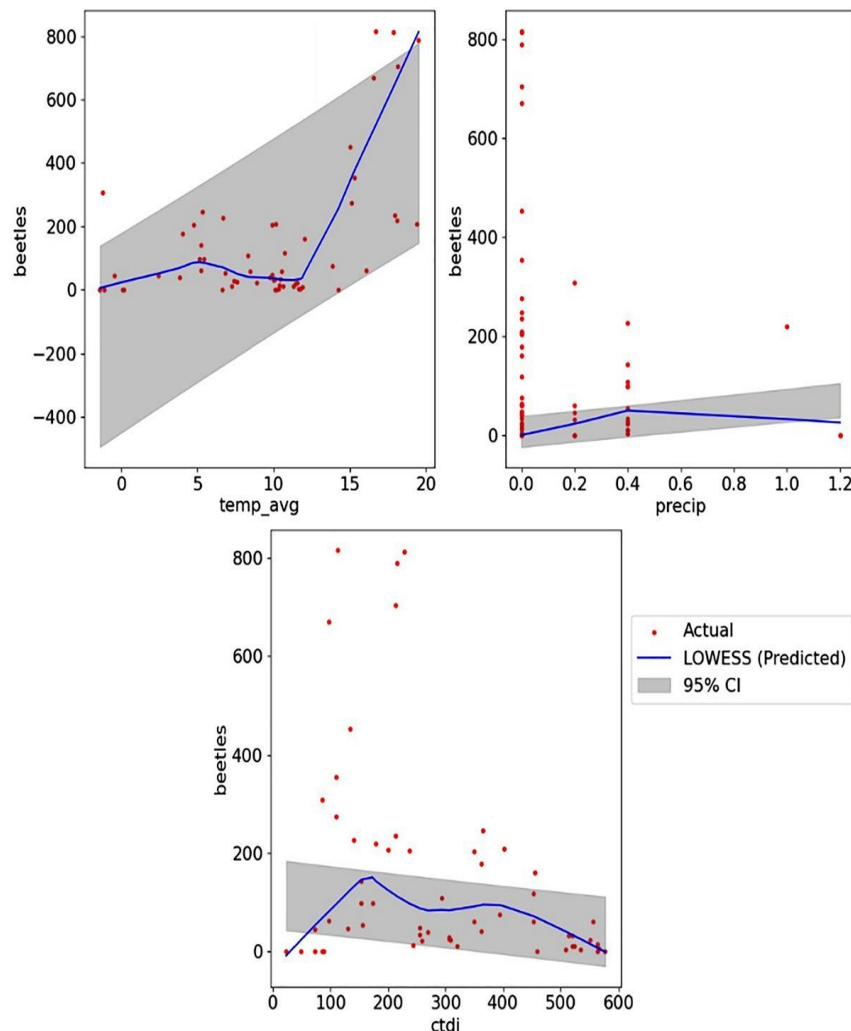


Fig. 6. The result of fitting the most parsimonious model (Table 3) for the relation between the *I. typographus* number in the trap, the Average daily air temperature on the current day, Average daily precipitation on the current day, and Cumulative Transpiration Deficit Index (CTDI) in the study area in 2014. The graphs illustrate the association between each predictor variable and the response variable with Locally Weighted Scatterplot Smoothing (LOWESS, blue line) with 95 % confidence intervals (marked grey) and actual values (red dots).

Table 4

Proposed eight best GAM regression models used to study bark beetle number in the trap in 2015. All plausible models are presented in Supplementary Materials (Table S1).

Model	Combination	AIC	ΔAIC	AIC weight
1	Beetles = $s(ctdi) + \epsilon$	1148.259	0	0.109768
2	Beetles = $s(beetles_lag) + s(ctdi) + \epsilon$	1148.94	0.680586	0.078107
3	Beetles = $s(temp_avg) + s(ctdi) + \epsilon$	1149.84	1.580427	0.049807
4	Beetles = $s(precip) + s(ctdi) + \epsilon$	1149.843	1.584134	0.049715
5	Beetles = $s(ctdi) + s(age) + \epsilon$	1149.966	1.706597	0.046762
6	Beetles = $s(ctdi) + s(solar) + \epsilon$	1149.987	1.727827	0.046268
7	Beetles = $s(ctdi) + s(percent) + \epsilon$	1149.991	1.731792	0.046177
8	Beetles = $s(ctdi) + s(di) + \epsilon$	1150.251	1.992311	0.040537
9	Beetles = $s(beetles_lag) + s(ctdi) + s(age) + \epsilon$	1150.415	2.156251	0.037347
10	Beetles = $s(beetles_lag) + s(temp_avg) + s(ctdi) + \epsilon$	1150.57	2.310574	0.034573

Table 5

GAM model equation estimating the variation in *I. typographus* number in the trap as a function of the Average daily air temperature on the current day, Average daily precipitation on the current day and Cumulative Transpiration Deficit Index in 2015 within the study area.

Parameter	Estimate	p-value	Model values
Intercept	16.911338	0.727392	Adjusted R-squared: 0.16
ctdi	0.614860	0.000107*	

predicting the potential number of spruce bark beetle generations based on meteorological data, allowing us to assess the impact of climate change on bark beetle development at different altitudes. The model can show how changes in precipitation can affect the drought stress of spruce stands and consequently the risk of infestation. Additionally, an extended growing season and increased average temperatures reduce winter mortality of bark beetles. Austarå and Midtgaard (1986), Faccoli (2002), and Lekander (1972) estimated winter mortality rates for mature bark beetles at 40 %, while immature bark beetles can experience mortality rates of up to 100 %. Mezei et al. (2017) found that rising temperatures during the growing season contributed to the expansion of bark beetle populations, and the emergence of new infestations in the High Tatras National Park in Slovakia. Additionally, decreased

precipitation intensifies tree water stress, thereby reducing tree defense mechanisms against bark beetle attacks. Taken together, these findings highlight the important role of climate change, particularly increase in temperature and changes in precipitation patterns, and influence on bark beetle life cycles and spruce forest susceptibility to infestation.

Rising average temperatures and more frequent droughts are having an impact on other conifer species. Howe et al. (2022) investigated the irruptive dynamics of the western balsam bark beetle (*Dryocoetes confusus* Swaine) in subalpine fir (*Abies lasiocarpa* Hook) forests over a twenty-year period. The research of those suggests that the drivers of western balsam bark beetle outbreaks in British Columbia are an extended growing season, warmer temperatures, and increased drought stress (Howe et al., 2022). These findings align with similar studies conducted by Aukema et al. (2008), Hart et al. (2014), Preisler et al. (2012), Seidl et al. (2017), Orgis et al. (2020), Pollard et al. (2020) and Harvey et al. (2021). Moreover, drought stress negatively impacts the tree defences of subalpine fir against the western balsam bark beetle (Bleiker et al., 2005).

4.2. Comparison of phenological and drought simulation models

Two phenology models of *Ips typographus* were developed for Central Europe and Scandinavia (Baier et al., 2007; Jönsson et al., 2007). The phenological model PHENIPS simulated *Ips typographus* brood development and was developed for regions with mountainous conditions. The phenological model of Jönsson et al. (2007) was developed for Scandinavian boreal forest conditions, and it assumed the development of *Ips typographus* according to degree-day requirements calculated from gridded daily temperature data for sun-exposed and shaded conditions of the forest.

The PHENIPS model, central to various research developments, uses daily meteorological data to calculate effective temperatures for predicting bark beetle swarming, infestation and development (Baier et al., 2007). This model formed the basis for subsequent models. For example, Orgis et al. (2019) developed the RITY-2 phenology model based on the PHENIPS model. There are several important differences between the PHENIPS and RITY phenology models. RITY-2 modelling starts on 7th March and ends on 31st October. The start of spring swarming is with a lower threshold of 14.5 °C and a sum of effective temperatures of 53.0 degree-days. The infestation threshold is 155.6 degree-days. Bark beetle brood development is assessed using a non-linear function on the effective thermal sum with a time step of 30 min, a minimum temperature of 8.3 °C, and a maximum temperature of 38.9 °C. This phenological model was developed for the territory of Slovakia.

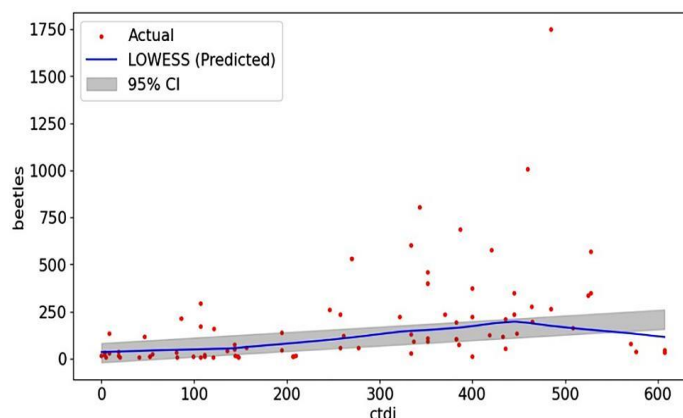


Fig. 7. The result of fitting the most parsimonious model (Table 5) for the relation between the *I. typographus* number in the trap and Cumulative Transpiration Deficit Index in the study area in 2015. The graphs illustrate the association between each predictor variable and the response variable with Locally Weighted Scatterplot Smoothing (LOWESS, blue line) with 95 % confidence intervals (marked grey) and actual values (red dots).

Meteorological data from the Integrated Nowcasting through Comprehensive Analysis (INCA) were incorporated into RITY-2. The model's output layers simulate bark beetles' outbreaks at a spatial resolution of 1 km for generations and assess their potential impact on forests, informing about the deployment of pheromone traps and trap trees.

The second factor in the difference between the models is the use of additional models for drought assessment, stand development, and the influence of additional factors on spruce stands. Netherer et al. (2019) and Matthews et al. (2018) used the PHENIPS-TDEF model for the assessment of brood development of *Ips typographus* and the influence of water stress on the infestation susceptibility of spruce stands. The drought stress of spruce trees is assessed in the module TDEF based on transpiration deficit, which equals the difference between the potential and actual transpiration of tree stands. The TDEF model calculates the transpiration deficit of spruce stands based on weather data according to elevation, slope, and aspect of the forest stand. This calculation starts from the first day of 5 consecutive days when the daily average temperature exceeds 5 °C for a snow-free period. Transpiration deficit has a dual influence on bark beetle phenology and the physiology of trees, and the water balance simulator PHENIPS-TDEF helps in the identification of potential tree drought stress in forest areas co-occurring with beetle flight (Netherer et al., 2019).

Temperli et al. (2013) integrated a bark beetle disturbance model into the forest landscape simulator LandClim, which is a climate-sensitive forest succession and landscape model, that simulates the dynamic of forest landscapes. Forest dynamics are determined by temperature, precipitation, soil types, fire and wind disturbances, and forest management (Schumacher et al., 2004; Schumacher and Bugmann, 2006). The prognosis of bark beetle attacks was based on previous assessments of bark beetle susceptibility (Netherer and Nopp-Mayr, 2005) and the phenology model PHENIPS (Baier et al., 2007). This model was integrated into the LandClim simulator for the prediction of bark beetle disturbance and forest dynamics in conditions of massive bark beetle outbreaks, climate change, and wind disturbance.

Robbins et al. (2021) developed the model of bark beetle phenology, population dynamics, and attack on trees for western pine beetle (*Dendroctonus brevicornis*) distribution on ponderosa pine (*Pinus ponderosa*) in California, USA. The insect mortality and phenology model (IMAP) was calculated on the daily minimum and maximum temperature of the environment and calculated bark temperature, which determines the stage of beetle development under bark (Goodsman et al., 2018). IMAP includes simulation bark behaviour such as beetle oviposition, beetle flight initiation, and beetle population, and takes into account beetle overwinter mortality.

This comprehensive comparison with various phenological models underlines the diverse approaches and methodologies that are employed in understanding and predicting spruce bark beetle dynamics. These models integrate a range of environmental variables, from meteorological data to tree physiology, bark beetle phenology, highlighting the complexity of forest ecosystems and the intricate relationships between climate, tree health, and spruce bark beetle dynamics. The evolution of these models, including advancements in capturing the dual influence of drought stress and the detailed simulation of bark beetle life cycles, reflects a growing understanding of the multifaceted nature of forest management.

4.3. Limitations of data and study design

The TANABBO II model represents a significant advance in phenological modelling of spruce bark beetle dynamics and drought assessment. However, it is important to recognise certain limitations in the data and study design that may influence the interpretation of the results. Firstly, the TANABBO II reliance on data from a single weather station poses a limitation, especially in large areas with varying mountainous conditions. Temperature and solar radiation are adjusted based on the DEM to account for vertical temperature gradients and potential

solar radiation alterations caused by terrain. However, relying on only one meteorological station for precipitation data in large, topographically diverse areas presents a significant challenge. Mountainous regions have highly variable precipitation; hence, relying on a single station may not capture the full range of conditions. In addition, the water loss model focuses exclusively on stand transpiration and does not take into account runoff or infiltration into the groundwater body. This can affect the accuracy of the model of drought risk assessment.

In addition, the model does not distinguish between the forest edge and the forest interior when calculating the potential solar transpiration of stands. This distinction is important because the forest edge has a different solar radiation exposure compared to the forest interior and, therefore, the forest edge has a different potential stand transpiration. These limitations highlight the need for further research to improve the accuracy and applicability of the model. Future developments could include the integration of more detailed spatial data, the inclusion of microclimatic variations in different forest sections, log-transforming a dataset (ensuring handling of non-positive values appropriately before transformation) and the improvement of the computational methodology to allow for more complex environmental simulations.

4.4. Practical implementation

The practical application of the TANABBO II model is significant for forest management and spruce bark beetle control strategies, such as the installation of pheromone traps, trapping devices, and defining high-risk infestation areas. This model promptly assesses the current risk of infestation during the growing season, providing information on spruce bark beetle swarming and the onset of tree infestation in spring and summer periods. This methodology is intended for utilisation by forest owners, forest managers, state forest administrations, forest research institutes, and universities to develop early protective measures against massive spruce bark beetle outbreaks. The utilisation of TANABBO II contributes to cost reduction in protection measures, by efficiently deploying traps and trapping devices in the most susceptible areas of infestation.

5. Conclusion

The TANABBO II model represents a significant advance in the field of spruce bark beetle management, particularly in the context of one-year bark beetle outbreak forecasting. The operational part of TANABBO II introduced drought indices for risk assessment of infested spruce stands during the vegetation period and spruce bark beetle swarming phases. Assessment of water stress in spruce stands is a critical element in predicting bark beetle outbreaks. These forecasts enable the evaluation of various weather scenarios to determine the potential development of spruce bark beetle outbreaks. The results of this research highlight the importance of drought indices, as demonstrated in our study, in predicting the number of bark beetles captured in traps at different locations within the study area, thereby validating our forecasting approach. Future research should focus on refining these models, exploring their applicability in different ecological contexts, and integrating them into broader forest management frameworks.

CRedit authorship contribution statement

Nana Pirtskhalava-Karpova: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Aleksandr Karpov:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Data curation. **Aleksei Trubin:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Milan Koren:** Writing – review & editing, Writing – original draft, Software, Methodology, Data curation. **Miroslav Blaženec:** Writing – review & editing, Writing – original draft, Software, Methodology, Data curation.

Jaroslav Holuša: Writing – review & editing, Writing – original draft, Software, Methodology, Data curation. **Rastislav Jakuš:** Writing – review & editing, Writing – original draft, Supervision, Software, Project administration, Methodology, Data curation, Conceptualization.

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

Data will be made available on request.

Acknowledgement

This research was funded by: Development of integrated modern and innovative diagnostic and protection methods of spruce stands with the use of semiochemicals and methods of molecular biology. NAZV – Ministry of Agriculture – Czech Republic QK1910480. Grant no. CZ.02.1.01/0.0/0.0/15.003/0000433, “EXTEMIT-K” financed by the Operational Program Research, Development and Education (OP RDE). Grant no. 43950/1312/3165 “The study of relationship between spruce stand insolation and bark beetle attack with the use of LIDAR data” financed by Internal Grant Agency FFWS CULS in Prague. Grant no. 43950/1312/3152 “Prediction of bark beetle outbreak spreading using TANABBO system” financed by Internal Grant Agency FFWS CULS in Prague. Project VEGA (2/0155/22) Norway spruce (*Picea abies*) resistance to bark beetle attack in condition of changing climate.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2024.110814](https://doi.org/10.1016/j.ecolmodel.2024.110814).

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4. Discussion

Spruce-dominated forests across Europe are increasingly exposed to disturbances driven by prolonged drought, extreme heat, and mass outbreaks of spruce bark beetle. These combined factors reinforce each other and accelerate the decline of spruce forests (Seidl et al., 2016). This dissertation presents four studies that demonstrate the use of multiscale remote sensing approaches to analyse this disturbance at stand and landscape levels. These approaches integrate satellite imagery, airborne thermography, hyperspectral imagery, LiDAR data, solar radiation simulation, drought modelling, and ground-based sap flow measurements. These integrated methods provide an understanding of tree responses at different scales, from individual crowns to entire landscapes. Consequently, these studies emphasise the importance of forest management and proactive mitigation strategies based on regular monitoring using remote sensing technology.

4.1 Solar radiation and canopy temperature under normal and stressed conditions

Articles 1 and 2 were designed to analyse the influence of solar radiation on canopy temperature in relation to tree water stress, which may affect the predisposition to spruce bark beetle infestation. The first study focuses on the relationship between solar radiation and crown temperature in conjunction with spruce tree parameters, crown openness to forest gaps, and area of the nearest forest gaps. The second study analyses relationships among crown temperature, spectral indices, solar radiation and sap flow between the forest edge and roof groups, which represent thermal and drought stress conditions for mature spruce trees, and the control group without additional stress. Additionally, this analysis includes information on both attacked and non-attacked spruce stands affected by spruce bark beetles. The identification of attacked spruce trees occurred during a field survey conducted one month after the hyperspectral and thermal airborne remote sensing survey.

Article 2 found that crown temperature is not a definitive predictor of water stress according to statistical tests between spruce trees under drought stress conditions and a control group. The spectral vegetation index is more sensitive to water stress in spruce trees in this study. In addition, this spectral index differs significantly between attacked and non-attacked spruce trees in the group under drought stress. Although crown temperature does not differ statistically between these groups, attacked spruces exhibit higher temperatures than non-attacked spruce crowns.

The results of this study do not show thermography data as a key factor in detecting water stress in spruce stands, but other studies have found thermography to be important in detecting bark beetle and disease infestations in spruce stands and other tree species. Zakrzewska and Kopeć (2022) found that spruce stands under water stress and bark beetle attack exhibited higher canopy temperatures compared to healthy stands. Smigaj et al. (2019) found a correlation between canopy temperature depression and disease levels in Scots pine (*Pinus sylvestris*), which has needle blight caused by the fungus *Dothistroma septosporum*. Smigaj et al. (2023) reviewed several studies that investigated the thermal response of different tree species under drought stress conditions. These studies used satellite, airborne, and UAV-mounted sensors and revealed significant differences in the tree canopy under stressed and unstressed conditions. Although the results of Dunn's post hoc test indicate that there is no significant difference in crown temperatures between drought-stressed and non-stressed spruce stands in this study (Article 2), the results of sap flow modelling suggest that this factor is important. According to Singh et al. (2025), sap flow is an important indicator of drought conditions. Crown temperature is consistently included in parsimonious models alongside trunk diameter, canopy density index, potential solar radiation and soil water potential. This highlights the importance of crown temperature in predicting sap flow, and the linear relationship between this predictor and the prediction variable reflects a strong association.

Article 1 was designed to investigate the factors influencing canopy temperature and to compare canopy temperature with simulated solar radiation. This study demonstrates the effect of tree height, crown area, crown density, the area of the nearest forest gaps and crown openness to the south on spruce crown temperature. A similar analysis was applied to determine the relationship between these factors and simulated solar radiation, based on the voxel approach and LiDAR point cloud. However, the relationship between simulated solar radiation and canopy temperature was found to be non-linear and unable to fully explain temperature variations. The canopy temperature of a standalone spruce tree decreases with increasing height. In contrast, the same trees in forest interiors show positive temperature gradients, as the lower canopy is shaded by the upper layers (Webster et al., 2018). Foliage fully exposed to the sun in the upper canopy usually has a higher temperature because it receives more solar radiation. These leaves have a higher transpirational cooling rate under higher solar radiation, which decreases the canopy temperature under non-water-stressed

conditions (Reinert et al., 2012). The complexity of modelling solar radiation is illustrated by this example, which shows how canopy temperature and simulated solar radiation can vary.

4.2 Solar radiation as a driver of bark beetle outbreaks

This dissertation investigates the mortality of spruce trees during bark beetle outbreaks. Tree mortality was detected by satellite-based analysis with the objective of assessing the influence of stand characteristics and landscape factors on infestation, according to the phases of the bark beetle outbreak. Article 3 is closely related to these objectives, using satellite-derived data to map and classify spruce mortality specifically by outbreak phases. This research adopted the methodologies used by Mezei et al. (2014a, b). The interpretation of the results of Article 3 highlights that stand characteristics, particularly the composition and age structure of conifer species, are more important determinants of infestation severity than solar radiation. It should be noted that the reference study and this study were carried out in different geographical regions with different climates. Although solar radiation, slope and altitude were significant predictors of infestation in previous studies, their roles vary due to the topographical and climatic conditions of this study region, which are characterised by low altitude, high precipitation and a marine climate.

The influence of meteorological factors is also covered in Article 4 of this thesis. An important aspect of this research is the simulation of bark beetle swarming times based on daily temperature sums, which identifies periods of highest infestation risk and correlates closely with pheromone trap data in this study. Solar radiation is a direct and indirect driver of outbreaks. Spruce stands in landscapes with higher levels of solar radiation can have higher bark surface temperatures, thereby accelerating the development of beetle broods under the bark. High radiation levels can also increase drought stress in spruce stands, thus impairing their ability to produce defensive resin (Netherer et al., 2015). Drought stress promotes the infestation of spruce stands. The combination of meteorological parameters, such as daily air temperature and precipitation, and modelled bark temperatures, at a spatial resolution of 30 metres, enables swarming time and areas at risk of infestation to be detected more accurately. This information can be used to identify the time and location of new hotspots in more vulnerable spruce forest areas (Duračiová et al., 2020).

4.3 Limitations of the research

A critical technological concern relates to the use of thermography in forest environments due to technical and atmospheric limitations of the sensor. Research shows that thermal sensors mounted on UAVs can be sensitive to temperature changes due to sensor heating during the survey, which can affect the thermal image values. Atmospheric conditions such as humidity, wind, and cloudy weather pose a challenge to obtaining accurate surface temperatures (Smigaj et al., 2023). These factors highlight the limitations of using thermal infrared data to monitor forest health. The results presented in Article 1 using the DigiTHERM thermal sensor show a potential overestimation of the thermal values measured at a distance of more than 25 metres from the centre of the image.

The availability of remote sensing and ground sensor data imposes limitations in characterising the physiological response of spruce trees under thermal and drought stress in Article 2. These gaps limit the ability to capture seasonal changes during the vegetation period and to provide time-series data analyses. These limitations relate to the lack of sap flow sensor data in 2022, and to only a single hyperspectral and thermographic survey of the ŠLP area in August 2023. In addition to these limitations, there is a lack of comprehensive ground-based observations of the health of the trees, such as the percentage of foliage discolouration and crown defoliation in Articles 1 and 2. However, LiDAR-derived canopy metrics can approximate this gap to some extent (Solberg et al. 2009); more detailed ground-truth data would strengthen the interpretation of physiological stress responses in Norway spruce.

Free satellite imagery is available at a spatial resolution of 10 m through Sentinel-2. Although Sentinel-2 offers higher resolution than the Landsat constellation, a single 10-metre pixel can still encompass several mature trees, making it difficult to identify individual crown mortality (Article 3). However, recent studies demonstrate adequate accuracy for detecting bark beetle infestation based on these satellite images (Abdullah et al. 2018). Higher-resolution satellite images could provide a more detailed map of spruce infestation and mortality. Also, frequent high cloudiness in coastal areas such as Kunashir Island makes it difficult to select suitable images for forest monitoring.

Finally, the TANABBO II model in Article 4 is limited by its dependence on a single weather station. Although temperature and solar radiation inputs are adjusted for topography, precipitation data in mountainous regions have complex patterns that cannot be fully captured

by measurements from that single location (Bertoncini and Pomeroy, 2025). This limits the model's ability to provide highly localised drought assessments. As a result, the accuracy of phenological projections of spruce bark beetle swarming periods may be reduced (Baier et al., 2007).

4.4 Future studies

Despite significant advances in the monitoring of bark beetle outbreaks, current methods still have limitations in terms of robustness and transferability. Kautz et al. (2024) point out that previous studies have produced inconclusive results regarding the optimal spectral range or indices for infestation detection, as specific approaches often provide reliable results only within limited geographical or temporal contexts. Therefore, future studies should explore the integration and fusion of different remote sensing data. These may include thermal, infrared, radar and LiDAR data. In parallel, there is a need to improve the quality and consistency of ground-truth datasets. This combined approach could support the development of more universally applicable and robust detection systems.

The quality of ground-truth data can be significantly improved by using dual- or multi-wavelength terrestrial laser scanning (TLS), which is able to measure forest structural characteristics in detail and capture spectral signatures via intensity data (Junttila et al., 2019). These sensors provide the opportunity to measure biochemical properties of foliage such as chlorophyll and water content with high accuracy (Zhu et al., 2015, 2017) which can be used to detect *Ips typographus* infestations even at an early stage (Junttila et al., 2019). The resulting high-density point clouds of spectral and structural data can serve as robust ground-truth datasets, significantly improving the accuracy of models calibrated using remote sensing data from satellite platforms. This integration enables accurate mapping of water-stressed or infested trees over large spatial areas and provides essential training and validation datasets required for robust modelling and the accurate detection of infestations.

Future research should prioritise data fusion methods that exploit the combined strengths of different remote sensing data. Ortiz et al. (2013) demonstrated the effectiveness of integrating RapidEye satellite imagery with TerraSAR-X radar data in assessing the health of spruce forests affected by bark beetle infestation. Complementary to optical approaches, Synthetic Aperture Radar (SAR) coherence time series have proven effective in detecting forest harvesting associated with bark beetle damage, as shown by Washaya and Hlásny (2024). The integration of airborne laser scanning (ALS) metrics with satellite optical data has

also significantly improved the accuracy of forest monitoring, with notable improvements in biomass estimation, species classification accuracy and monitoring of urban forest variables (Borghi et al., 2025). Future forest monitoring practices will significantly benefit from recently launched hyperspectral satellite missions such as Environmental Mapping and Analysis Program (EnMAP), Copernicus Hyperspectral Imaging Mission for the Environment (CHIME) (Nieke et al., 2023; Buschkamp et al., 2023). In addition, the Italian Space Agency's compact hyperspectral payload PLATiNO-4, as part of a larger constellation, aims to provide performance comparable to larger satellites, thereby improving forest monitoring with high-resolution hyperspectral data adaptable to different environmental applications (Ansalone et al., 2024). Emerging smaller platforms, such as the UAE's Sharjah-Sat-2 (carrying the Hyperscape100 camera), will further contribute to global forest health monitoring capabilities (Faroukh et al., 2024; Sulaiman et al., 2024).

Understanding the interactions between thermal, drought stress and the response of Norway spruce, particularly at early stages of infestation, could further improve the early detection of stressed trees and bark beetle infestations in Norway spruce stands. Future studies focusing on the thermal responses of spruce in relation to forest edges and varying canopy densities, combined with accurate solar radiation simulations (e.g. voxel-based modelling approaches), will improve the assessment of spruce stand conditions. High-resolution solar radiation models that take microclimatic variability into account, particularly in mountainous regions and areas with diverse forest structures, can significantly improve projections relating to the timing of bark beetle swarms, the severity of infestations and the number of bark beetle generations.

5. Conclusion

This study used ground sensor and airborne remote sensing data to investigate the physiological and thermal responses of Norway spruce at the crown level. Changes in crown temperature, spectral indices and sap flow were identified and used to detect water stress and potential susceptibility to bark beetle attack. Another part of the research evaluated the influence of stand characteristics, topographic conditions and climate on bark beetle outbreaks at a landscape level. The study shows how water deficit indices and simulated swarming periods of bark beetles can be used to identify areas that are more susceptible to bark beetle infestations.

Integration of ground sensor data and airborne remote sensing. Higher solar radiation and canopy temperatures at forest edges indicated thermal stress. The increased bark temperatures near the edges may prevent infestation of spruce stands by *Ips typographus* by exceeding the upper thermal tolerance of the species. Conversely, severe drought reduced sap flow, indicating the vulnerability of Norway spruce to water stress. Spruce stands under drought showed distinct spectral signals and an increased risk of bark beetle infestation. Mature stands showed measurable responses to thermal and drought stress, reflected in lower sap flow rates and higher canopy temperatures, but spectral indices showed promise in detecting water stress and early signs of forest decline.

Crown temperature and simulated solar radiation. Crown characteristics, canopy density, and forest gaps affected local microclimates. Tree height and southern canopy openings substantially influenced crown temperature. The non-linear relationship between solar radiation and crown temperature underscores complex interactions among stand structure, solar input, and transpiration.

Climate data, drought indices and swarming time. Drought indices were found to be reliable predictors of bark beetle activity levels, based on the results of bark beetle catches in pheromone traps. Water deficit indices could also be used to quantify the susceptibility of spruce to attack. Forecasts of spruce bark beetle phenology and incorporation of drought indices can provide valuable information on potential infestation areas and timing of bark beetle swarming.

Influence of stand and landscape factors. Stand height and spruce age are found to be important factors in bark beetle outbreaks. Wind damage served as a trigger for outbreak development and species composition influenced the overall susceptibility of the forest.

Highlighting the different drivers of outbreaks under different environmental conditions, solar radiation was less influential in hilly areas and marine climates than in mountainous areas of central Europe.

These results indicate that combining physiological monitoring with stand and landscape level assessments can improve the detection of stressed spruce and clarify how different factors such as solar radiation, drought and spruce tree characteristics affect spruce stand infestation and bark beetle outbreaks.

5.1 Practical implementation

The use of thermography to measure canopy temperatures and sensors in the infrared spectrum to assess spectral properties of Norway spruce holds promise for early detection of water stress and potential identification of bark beetle infestation. Thermography can serve as an additional tool for detecting water stress in spruce stands, but its effectiveness depends on a clear understanding of the thermal response of spruce under different landscape conditions, stand characteristics, crown openness near forest gaps, and overall canopy density. Potential solar radiation calculated from high-resolution LiDAR point clouds can assist in the identification of these conditions, providing a meaningful comparison with thermographic survey data and improving the detection of water-stressed trees. This method enhances the discrimination of stressed trees. Remote sensing tools enable rapid assessment of tree health over large areas, thus facilitating early detection of infestation and supporting sustainable forest management.

In addition, this study provides practical insights into the generation of thermal image mosaics. As shown in Article 1, which used the DigiTHERM thermal sensor, pixel values in thermal images are influenced by their distance from the centre of the image. Specifically, distances greater than 25 m have a significant effect on temperature values. This threshold can be used as a useful parameter to minimise bias and improve the accuracy of thermal mosaics.

The integration of meteorological data, such as daily temperature and precipitation, enhances the ability to identify areas susceptible to bark beetle infestation. For example, the TANABBO II operational model calculates drought indices and spruce bark beetle phenology on a daily basis and at a spatial level. The combination of simulated beetle swarming time periods and drought indices can indicate areas of spruce stands at high risk of infestation and

the time of potential infestation. This data can be used to support decision making for the protection of spruce forests and the optimal installation of pheromone traps.

Comparative studies of spruce bark beetle outbreaks in different geographical and climatic regions, such as Kunashir Island with a maritime climate and mountainous regions in Slovakia with a continental climate, reveal different factors influencing outbreak development. This comparative data are crucial for formulating adaptive strategies to protect spruce forests and mitigate future outbreaks. In addition, monitoring on Kunashir Island indicates significant potential ecological and biodiversity impacts from bark beetle disturbance.

6. Reference

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7. Supplementary material

Supplementary files are available in the electronic version of this PhD thesis. These files contain additional tables, formulas and figures associated with the published articles. The following sections provide an overview of the supplementary content for each paper.

7.1 Article I (chapter 3.1)

Table S1 - Correlation of variables.

Figure S1 - Function of the influence of each predictor on average temperature crown BRT modelling, including solar radiation as a variable.

Figure S2 - Scatter plots, distribution, correlation, and regression between variables using Robust Linear Model.

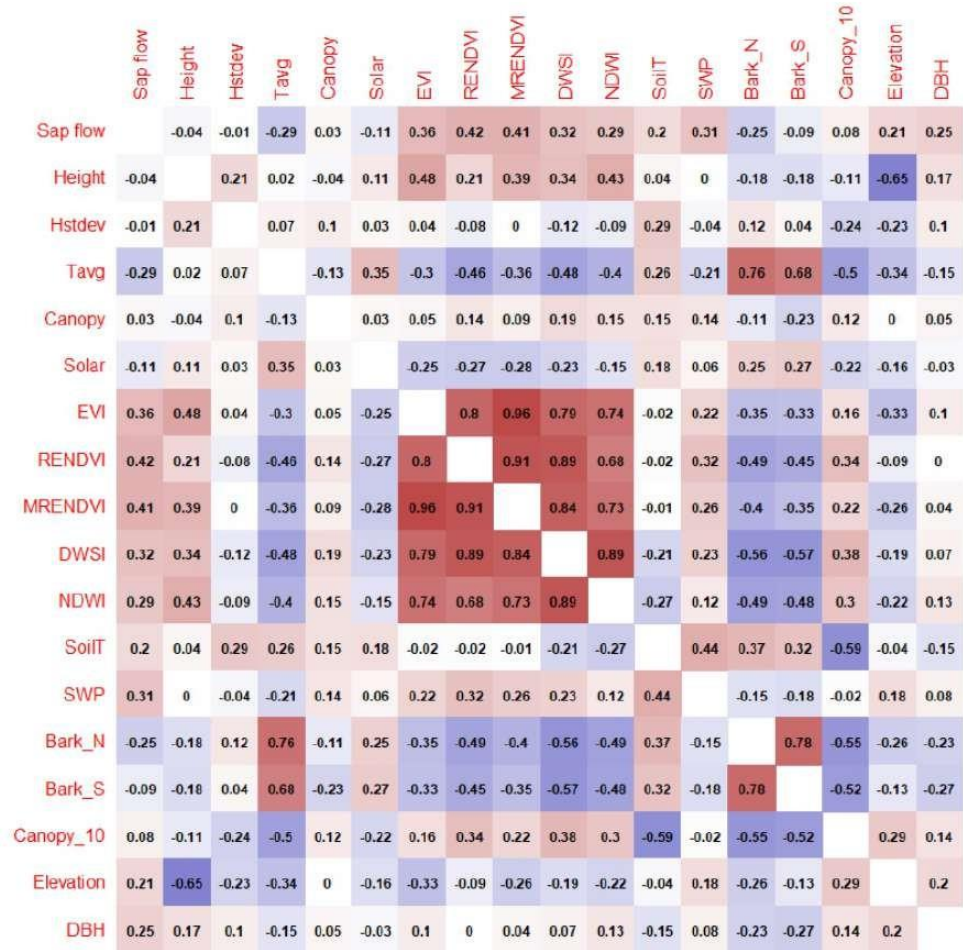
Figure S3 - Box plots of spruce crown and variables across groups defined by surrounding gap area and canopy openness conditions. FI - gaps area $< 2 \text{ m}^2$, openness from south side $< 5\%$, SFE - gaps_area $> 10 \text{ m}^2$, openness from south side $> 10\%$, NSFE – gaps area $> 10 \text{ m}^2$, south openness $< 10\%$, openness from non-south sides > 10 .

The Supplementary Material for this article can be accessed online at:

<https://ars.els-cdn.com/content/image/1-s2.0-S0378112725000659-mmc1.docx>

784 **Supplementary Materials**

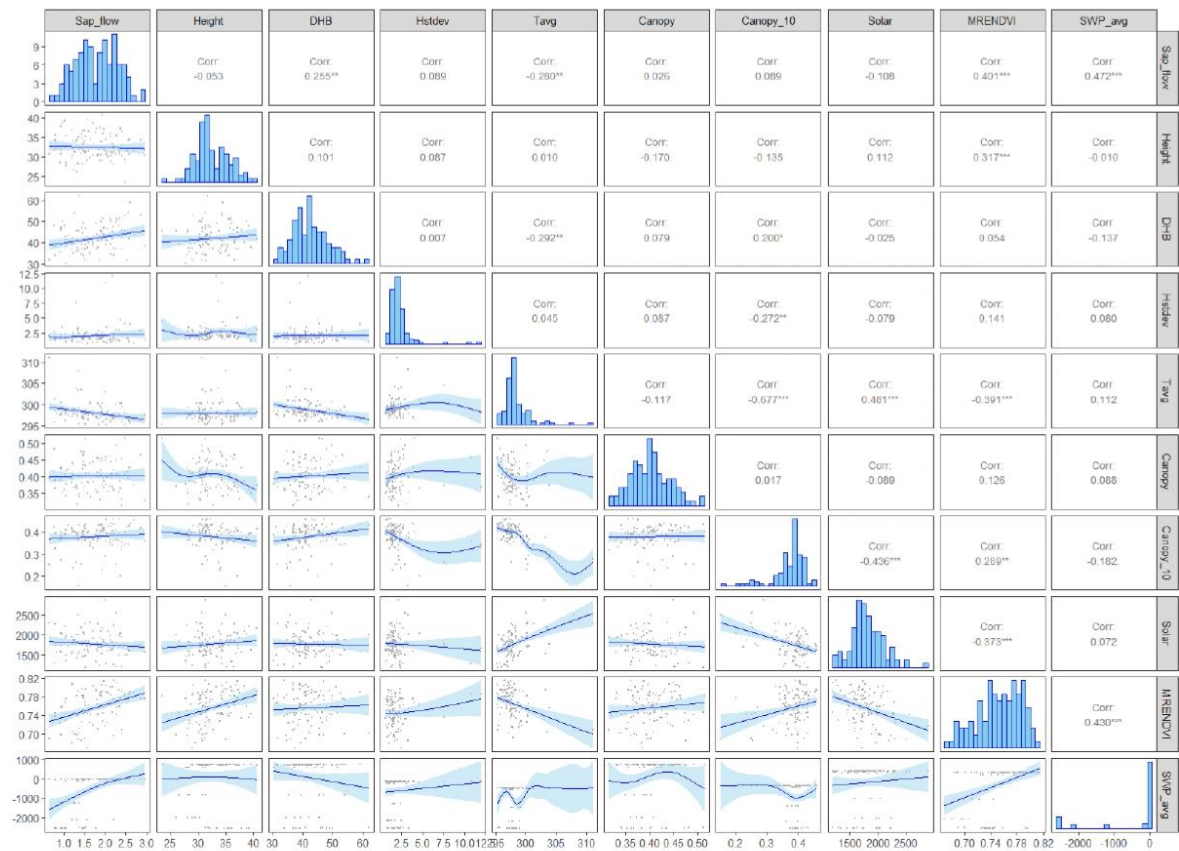
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787 **Fig. S1.** Correlation matrix of variables in the dataset.

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790 **Fig S2.** Scatter plots, distribution, correlation, and regression between variables using GAM. The square root transformation was used to normalize the
 791 distribution of the Sap flow variable.

792 **Table S1**
793 Formulas of spectral indexes

N	Index abbreviation	Index	Formula	Source
1	EVI	Enhanced Vegetation Index	$2.5 * \frac{(NIR - R)}{(NIR + 6 * R - 7.5 * B + 1)}$	Huete et al., 2002
2	RENDVI	Red Edge Normalized Difference Vegetation Index	$RENDVI = \frac{\rho_{750} - \rho_{705}}{\rho_{750} + \rho_{705}}$	Gitelson and Merzlyak, 1994; Sims and Gamon, 2002
3	MRENDVI	Modified Red Edge Normalized Difference Vegetation Index	$MRENDVI = \frac{\rho_{750} - \rho_{705}}{\rho_{750} + \rho_{705} - 2 * \rho_{445}}$	Datt, 1999; Sims and Gamon, 2002
4	DWSI	Disease-Water Stress Index	$DWSI = \frac{\rho_{802} - \rho_{547}}{\rho_{1657} + \rho_{682}}$	Galvao et al., 2005
5	NDWI	Normalized Difference Water Index	$NDWI = \frac{(\rho_{857} - \rho_{1241})}{(\rho_{857} + \rho_{1241})}$	Gao, 1995; Jackson et al., 2004

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796 **Table S2**
797 ANOVA and Kruskal Wallis test results for groups Edge, Roof, Control.

Parameter	ANOVA			Kruskal Wallis		
	F-statistic	p-value	Significant	H-Statistic	p-value	Significant
Sap_flow	22.54955	0.000013	Yes	14.48181	0.000003	Yes
Height	1.536296	0.463871	No	0.407291	0.666508	No
Hstdev	0.59184	0.743847	No	1.828062	0.165851	No
DBH	3.023819	0.220489	No	2.510144	0.086169	No
Tavg	40.34203	0.000000	Yes	44.05976	0.000000	Yes
Elev*	0.01207	0.988004	No	0.000386	0.984334	No
Canopy	4.585972	0.100965	No	0.84799	0.431214	No
Canopy_10	46.45807	0.000000	Yes	102.5872	0.000000	Yes
Solar	1.136284	0.566577	No	2.420253	0.093891	No
EVI	32.37587	0.000000	Yes	20.77298	0.000000	Yes
RENDVI	48.48916	0.000000	Yes	41.00898	0.000000	Yes
MRENDVI	39.50046	0.000000	Yes	33.37278	0.000000	Yes
DWSI	50.125	0.000000	Yes	23.87592	0.000000	Yes
NDWI	31.66755	0.000000	Yes	13.9044	0.000004	Yes
Soil	40.31603	1.76E-09	Yes	71.20406	9.62E-16	Yes
SWP	23.10093	9.63E-06	Yes	129.9463	1.56E-20	Yes
Bark_N	21.58502	2.06E-05	Yes	5.197386	0.007694	Yes
Bark_S	27.27459	1.2E-06	Yes	15.26243	2.82E-06	Yes

798 * Without Roof group

799 **Table S3**
800 Post-Hoc test (Turkey test) based on Dunn's test results

Parameter	Comparison	P (Unadjusted)	P (Bonferroni Adjusted)	Significance
Sap_flow	Edge - Control	0.0721	0.2162	No
Sap_flow	Edge - Roof	0.0021	0.0063	Yes

Sap_flow	Control - Roof	0.0000	0.0000	Yes
Tavg	Edge - Control	<0.0001	<0.0001	Yes
Tavg	Edge - Roof	0.0010	0.0031	Yes
Tavg	Control - Roof	0.0052	0.0155	Yes
Canopy_10	Edge - Control	<0.0001	<0.0001	Yes
Canopy_10	Edge - Roof	<0.0001	<0.0001	Yes
Canopy_10	Control - Roof	0.1560	0.4679	No
EVI	Edge - Control	<0.0001	<0.0001	Yes
EVI	Edge - Roof	0.1421	0.4263	No
EVI	Control - Roof	<0.0001	<0.0001	Yes
RENDVI	Edge - Control	<0.0001	<0.0001	Yes
RENDVI	Edge - Roof	0.1621	0.4863	No
RENDVI	Control - Roof	<0.0001	<0.0001	Yes
MRENDVI	Edge - Control	<0.0001	<0.0001	Yes
MRENDVI	Edge - Roof	0.0621	0.1864	No
MRENDVI	Control - Roof	<0.0001	<0.0001	Yes
DWSI	Edge - Control	<0.0001	<0.0001	Yes
DWSI	Edge - Roof	0.1881	0.5644	No
DWSI	Control - Roof	<0.0001	<0.0001	Yes
NDWI	Edge - Control	<0.0001	<0.0001	Yes
NDWI	Edge - Roof	0.0425	0.1275	No
NDWI	Control - Roof	0.0006	0.0019	Yes
Soil	Edge - Control	0.0000	<0.0001	Yes
Soil	Edge - Roof	<0.0001	<0.0001	Yes
Soil	Control - Roof	0.0004	0.0011	Yes
SWP	Edge - Control	0.1473	0.4420	No
SWP	Edge - Roof	0.0003	0.0008	Yes
SWP	Control - Roof	<0.0001	<0.0001	Yes
Bark_N	Edge - Control	0.000002	0.000006	Yes

805 **Table S5.**
806 Best GAM models used to study relationship between sap flow and stand tree characteristics, landscape factors, spectral index, crown temperature.

Combination	Adjusted R-squared	Deviance explained	p-value	F-value	edf	RMSE	AIC	ΔAIC	AIC weight
DBH + Tavg + Canopy + SWP_avg	0.483408 01859536 1	0.53162 827802 1869	0.0014, 5e-04, 0.0401, 0	8.5867, 12.9337, 2.9276, 14.0453	1.4726 , 1, 2.2232 , 5.1985	0.355785 50907672	106.2881 39771387	0	0.6879293352402 1
Height + DBH + Tavg + SWP_avg	0.454629 19251405 1	0.49558 751966 5891	0.0528, 3e-04, 0.0013, 0	3.844, 14.1406, 10.985, 13.3098	1, 1, 1, 4.9608	0.369220 52330280 7	110.3531 32195807	4.064992424 42003	0.0901243073412 487
DBH + Canopy + Solar + SWP_avg	0.454788 91039879 6	0.50507 778213 5527	0, 0.0294, 0.0278, 0	21.0766, 3.1962, 3.4574, 13.9512	1, 2.2088 , 1.5443 , 5.0241	0.365730 68272904 5	111.9535 5804485	5.665418273 46288	0.0404868401005 349
DBH + Tavg + SWP_avg	0.436925 45010654	0.47274 870446 98	7e-04, 0.0012, 0	12.3381, 11.1598, 12.864	1, 1, 4.7438	0.377486 78229428	112.6574 3491312	6.369295141 73343	0.0284753428994 849
DBH + Tavg + MRENDVI + SWP_avg	0.442389 83930291 3	0.48509 417593 3217	0.0011, 0.0081, 0.2021, 0	11.2248, 7.1343, 1.571, 11.9336	1, 1.1272 , 3.1571 , 2.8337	0.373041 22062628 2	112.8705 75961448	6.582436190 06134	0.0255968174966 617

DBH + Tavg + Solar + SWP_avg	0.443728 90478721 8	0.48864 291028 7934	5e-04, 0.0075, 0.4353, 0	12.9243, 7.4602, 0.7506, 12.9728	1, 1, 1.7586 , 4.8	0.371753 49692582 8	113.0117 86699216	6.723646927 82932	0.0238518708912 88
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808 **Table S6.**

809 Best LR models used to study the relationship between sap flow and stand tree characteristics, landscape factors, spectral index, crown temperature.

Combination	Adjusted R-squared	R2	p-value	RMSE	AIC	delta_AIC	AIC_weight
DBH + Tavg + SWP_avg	0.374177298 03574	0.3918892 6129888	0, 0.0026, 0.0013, 0	0.4054004792 86813	120.4365554 86209	0	0.2107709722 97499
DBH + Tavg + Canopy + SWP_avg	0.373683851 250996	0.3973184 22901902	0, 0.0022, 0.001, 0.34, 0	0.4035867312 47323	121.4769785 59064	1.04042307285 449	0.1252811696 12281
Height + DBH + Tavg + SWP_avg	0.373317531 970215	0.3969659 26990207	0, 0.3563, 0.002, 0.0014, 0	0.4037047387 34731	121.5395423 37883	1.10298685167 331	0.1214228010 79136
DBH + Tavg + MRENDVI + SWP_avg	0.372686598 614238	0.3963588 02440116	0, 0.0025, 0.0141, 0.3869, 0	0.4039079091 76896	121.6472139 44198	1.21065845798 847	0.1150587509 36409
DBH + Tavg + Canopy_10 + SWP_avg	0.371837104 347815	0.3955413 64561105	0, 0.0027, 0.0033, 0.4343, 0	0.4041812983 39532	121.7920130 14628	1.35545752841 821	0.1070229545 97525
DBH + Hstdev + Tavg + SWP_avg	0.371308244 118914	0.3950324 61321974	0, 0.0028, 0.4683, 0.0012, 0	0.4043514058 41388	121.8820600 98056	1.44550461184 691	0.1023112664 82611
DBH + Tavg + Solar + SWP_avg	0.368226053 967814	0.3920665 80233179	0, 0.0027, 0.0063, 0.8634, 0	0.4053413696 4001	122.4053508 19878	1.96879533366 879	0.0787575729 697462
Height + DBH + MRENDVI + SWP_avg	0.359071528 984608	0.3832575 09022925	0, 0.05, 2e-04, 0.005, 0	0.4082675444 36967	123.9446754 16067	3.50811992985 724	0.0364781021 582913
DBH + MRENDVI + SWP_avg	0.340805207 387052	0.3594616 63781758	0, 3e-04, 0.0241, 0	0.4160691207 61361	125.9954164 60574	5.55886097436 463	0.0130833655 42828

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DBH + Solar + MRENDVI + SWP_avg	0.338434083 012481	0.3633988 34596916	0, 3e-04, 0.4289, 0.0955, 0	0.4147884322 08088	127.3356943 06093	6.89913881988 377	0.0066939403 6931554
DBH + Canopy + MRENDVI + SWP_avg	0.338314599 343026	0.3632838 59745176	0, 2e-04, 0.4357, 0.021, 0	0.4148258874 375	127.3550175 48014	6.91846206180 459	0.0066295774 8032664

811 **Table S7.**

812 Best GAM models used to study the relationship between crown temperature and stand tree characteristics, landscape factors, spectral index, sap flow.

Combination	Adjusted R-squared	Deviance explained	p-value	F-value	edf	RMSE	AIC	ΔAIC	AIC weight
Sap_flow + Canopy + Canopy_10 + Solar	0.6498114 63	0.697135 963	0.0117, 0.011, 0, 0.0207	6.6117, 6.7364, 9.7089, 2.4974	1, 1, 7.0635, 5.2614	1.2728931 46	387.93910 76	0	0.344250376
Canopy + Canopy_10 + Solar + MRENDVI	0.6472779 45	0.701061 94	0.0223, 0, 0.0156, 0.2269	5.4055, 9.0124, 2.4987, 1.8559	1, 7.2294, 6.4102, 1.5235	1.2646160 82	390.21964 55	2.280537928	0.11006821
DBH + Canopy + Canopy_10 + Solar	0.6410719 06	0.689434 966	0.0572, 0.0213, 0, 0.0172	3.7099, 5.4852, 8.9091, 2.7787	1, 1, 7.2453, 5.0375	1.2889746 42	390.54163 77	2.602530041	0.093700564
Height + Canopy + Canopy_10 + Solar	0.6469551 95	0.701796 148	0.2931, 0.0088, 0, 0.0068	1.2375, 7.1767, 10.1254, 3.0703	1.5955, 1, 7.3259, 6.5443	1.2630621 44	390.56166 55	2.622557879	0.092766937
Hstdev + Canopy + Canopy_10 + Solar	0.6433249 53	0.694789 957	0.1463, 0.0142, 0, 0.018	2.1465, 6.2548, 10.2756, 2.5372	1, 1, 7.4121, 5.8827	1.2778135 95	390.70474 59	2.765638313	0.086362199
Canopy + Canopy_10 + Solar	0.6412515 81	0.691245 467	0.0129, 0, 0.0092	6.4287, 10.0874, 2.7032	1, 7.387, 6.3848	1.2852119 81	390.89406 72	2.954959609	0.078562102
DBH + Canopy_10 + Solar + MRENDVI	0.6341023 65	0.685057 298	0.0298, 0, 0.035, 0.1289	4.874, 7.614, 2.4358, 2.4599	1, 7.0378, 5.1642, 1.5596	1.2980274 27	392.99697 28	5.057865168	0.027451935
Canopy + Canopy_10 + Solar + SWP_avg	0.6367490 28	0.690730 519	0.0133, 0, 0.0102, 0.8896	6.383, 9.7621, 2.9273, 0.0194	1, 7.3476, 6.4047, 1	1.2862832 88	393.03341 87	5.094311123	0.026956209
Canopy_10 + Solar + MRENDVI	0.6305678 01	0.684000 282	0, 0.0135, 0.1327	8.5046, 2.5562, 2.1197	7.1206, 6.4621, 1.7485	1.3002038 34	394.49477 18	6.55566416	0.012981654

DBH + Hstdev + Canopy_10 + Solar	0.6273888 8	0.677632 877	0.0412, 0.1668, 0, 0.026	4.2874, 1.9423, 8.5424, 2.5754	1, 1, 7.2362, 5.0572	1.3132380 76	394.55368 24	6.614574775	0.012604852
DBH + Canopy_10 + Solar	0.6244892 72	0.672128 368	0.0321, 0, 0.0115	4.7349, 8.3903, 2.9846	1, 7.2092, 5.2385	1.3244025 74	394.67393 94	6.734831755	0.011869278

813

814 **Table S8.**

815 Best LR models used to study the relationship between crown temperature and stand tree characteristics, landscape factors, spectral index, sap flow.

Combination	Adjusted R-squared	R2	p-value	RMSE	AIC	delta_AIC	AIC_weight
Sap_flow + DBH + Canopy_10 + Solar	0.535988182 09781	0.5534980 62018648	0, 0.0261, 0.0531, 0, 0.0031	1.5455382888 5811	408.8225090 39167	0	0.1384961467 97177
DBH + Canopy_10 + Solar + MRENDVI	0.535788407 787796	0.5533058 26361842	0, 0.0106, 0, 0.0133, 0.0267	1.5458709588 5429	408.8685665 9658	0.04605755741 30644	0.1353431933 53948
Sap_flow + Canopy_10 + MRENDVI + SWP_avg	0.530337839 857168	0.5480609 40239916	0, 0.0051, 0, 0.0046, 0.0128	1.5549199418 3301	410.1175949 35971	1.29508589680 347	0.0724791950 520933
Sap_flow + Height + Canopy_10 + Solar	0.529670000 029626	0.5474183 01915301	0, 0.0043, 0.1239, 0, 0.0044	1.5560250644 7491	410.2696363 60575	1.44712732140 823	0.0671735012 803794
Sap_flow + Canopy_10 + Solar	0.523243980 265828	0.5367370 75163965	0, 0.0055, 0, 0.0059	1.5742795970 0903	410.7655686 53496	1.94305961432 883	0.0524212842 649332
Sap_flow + Canopy_10 + Solar + SWP_avg	0.527189317 800112	0.5450312 30335957	0, 0.0021, 0, 0.0067, 0.1757	1.5601231736 3009	410.8325080 84125	2.00999904495 751	0.0506957956 844498
Sap_flow + Canopy_10 + Solar + MRENDVI	0.526514816 793685	0.5443821 82197697	0, 0.0334, 0, 0.0204, 0.1937	1.5612355952 1797	410.9850430 84115	2.16253404494 785	0.0469731180 551586
Sap_flow + Canopy + Canopy_10 + Solar	0.526278849 160021	0.5441551 1900304	0, 0.0055, 0.2005, 0, 0.0083	1.5616245780 1416	411.0383546 72977	2.21584563380 992	0.0457375529 197401
Sap_flow + Hstdev + Canopy_10 + Solar	0.525637695 036958	0.5435381 59375186	0, 0.0078, 0.2205, 0, 0.0148	1.5626810048 6295	411.1830750 58522	2.36056601935 434	0.0425448789 725249

DBH + Canopy_10 + Solar	0.517517241 704427	0.5311724 14109018	0, 0.0109, 0, 0.0016	1.5837064059 4458	412.0431823 619	3.22067332273 286	0.0276743458 902929
DBH + Hstdev + Canopy_10 + Solar	0.520426743 873503	0.5385238 47878277	0, 0.0146, 0.2053, 0, 0.0051	1.5712407208 2117	412.3520792 20387	3.52957018122 015	0.0237138060 827692
DBH + Canopy + Canopy_10 + Solar	0.518353409 138086	0.5365287 52189479	0, 0.0142, 0.2802, 0, 0.0023	1.5746335231 8077	412.8136742 68469	3.99116522930 143	0.0188263952 843648
Height + DBH + Canopy_10 + Solar	0.518273939 393498	0.5364522 81303177	0, 0.2836, 0.0167, 0, 0.0014	1.5747634219 1252	412.8313273 80537	4.00881834137 004	0.0186609542 627851
Sap_flow + DBH + Canopy_10 + MRENDVI	0.517369548 368301	0.5355820 18241195	0, 0.1395, 0.0637, 0, 0.0293	1.5762409567 6134	413.0320205 20134	4.20951148096 697	0.0168792788 111624
DBH + Canopy_10 + MRENDVI	0.511661369 467752	0.5254822 74105458	0, 0.0198, 0, 0.0031	1.5932881083 1002	413.3340190 40488	4.51151000132 063	0.0145136197 783133
DBH + Canopy_10 + MRENDVI + SWP_avg	0.515560802 559111	0.5338415 26990843	0, 0.0302, 0, 0.0013, 0.1792	1.5791918201 2893	413.4322730 30266	4.60976399109 87	0.0138178399 700455
DBH + Hstdev + Canopy_10 + MRENDVI	0.514909029 704213	0.5332143 49338016	0, 0.0247, 0.1966, 0, 0.0097	1.5802537990 0915	413.5761359 20356	4.75362688118 85	0.0128588085 103263
Canopy_10 + Solar + MRENDVI	0.509729694 171352	0.5236052 68864615	0, 0, 0.025, 0.0278	1.5964362083 5164	413.7564339 95994	4.93392495682 627	0.0117503147 312324
DBH + Canopy_10 + Solar + SWP_avg	0.513554460 33179	0.5319108 95790968	0, 0.0104, 0, 0.0017, 0.6891	1.5824586134 4781	413.8745066 25483	5.05199758631 528	0.0110766989 820618
Canopy_10 + Solar + MRENDVI + SWP_avg	0.512438464 647929	0.5308370 13151781	0, 0, 0.0443, 0.0119, 0.2127	1.5842727993 193	414.1197031 82038	5.29719414287 104	0.0097986579 5416003
DBH + Canopy + Canopy_10 + MRENDVI	0.511750465 350951	0.5301749 76092424	0, 0.0247, 0.3152, 0, 0.0049	1.5853901909 164	414.2705847 18922	5.44807567975 442	0.0090866351 0694612
Hstdev + Canopy_10 + Solar + MRENDVI	0.510490957 849081	0.5289629 97175531	0, 0.284, 0, 0.0422, 0.0488	1.5874337409 7923	414.5462506 76633	5.72374163746 611	0.0079166780 9624986
Canopy + Canopy_10 + Solar + MRENDVI	0.510321728 971457	0.5288001 54293289	0, 0.2914, 0, 0.0293, 0.0374	1.5877081142 729	414.5832354 08446	5.76072636927 87	0.0077716253 0635415

Sap_flow + Hstdev + Canopy_10 + MRENDVI	0.510169074 254863	0.5286532 60132039	0, 0.0439, 0.1642, 0, 0.1016	1.5879555749 6293	414.6165869 17266	5.79407787809 839	0.0076431021 7973168
Sap_flow + Canopy_10 + MRENDVI	0.505587363 769896	0.5195801 74229239	0, 0.0414, 0, 0.0495	1.6031662269 7621	414.6566871 61034	5.83417812186 724	0.0074913831 248717
Sap_flow + DBH + Hstdev + Canopy_10	0.508698842 983882	0.5272385 09286377	0, 0.0201, 0.1232, 0.0864, 0	1.5903369197 9888	414.9372672 14058	6.11475817489 048	0.0065108070 3362708
Sap_flow + Canopy + Canopy_10 + MRENDVI	0.508392324 946369	0.5269435 5796726	0, 0.037, 0.2105, 0, 0.0729	1.5908329403 5258	415.0040026 62977	6.18149362380 927	0.0062971408 205678
Height + DBH + Canopy_10 + MRENDVI	0.507202757 998115	0.5257988 80337809	0, 0.7946, 0.0197, 0, 0.0048	1.5927564852 6507	415.2626030 07639	6.44009396847 196	0.0055333616 2728126
Sap_flow + Hstdev + Canopy_10 + SWP_avg	0.506560117 775293	0.5251804 90689433	0, 0.0021, 0.0822, 0, 0.1641	1.5937946768 4999	415.4020471 87715	6.57953814854 727	0.0051607061 9697423
Sap_flow + Hstdev + Canopy_10	0.501942793 550738	0.5160387 52223831	0, 0.0058, 0.0781, 0	1.6090642596 0846	415.4425463 37068	6.62003729790 121	0.0050572550 4729028
Height + Canopy_10 + Solar + MRENDVI	0.506219860 592233	0.5248530 73400073	0, 0.6059, 0, 0.0222, 0.0726	1.5943440919 3736	415.4758048 4909	6.65329580992 267	0.0049738520 4529228
Sap_flow + Hstdev + Canopy + Canopy_10	0.505802821 236046	0.5244517 71378082	0, 0.0057, 0.1014, 0.1822, 0	1.5950172294 8159	415.5661373 15112	6.74362827594 462	0.0047541996 5969461
Sap_flow + Height + Canopy + Canopy_10	0.505531053 226126	0.5241902 58764763	0, 0.0025, 0.1051, 0.0817, 0	1.5954557336 8532	415.6249623 86676	6.80245334750 89	0.0046164030 004893
Sap_flow + Canopy + Canopy_10 + SWP_avg	0.504870094 146075	0.5235542 41536789	0, 9e-04, 0.1021, 0, 0.1145	1.5965217043 565	415.7678943 06805	6.94538526763 779	0.0042980003 1049682
Sap_flow + Height + Hstdev + Canopy_10	0.504692900 979925	0.5233837 34905211	0, 0.0047, 0.2128, 0.0909, 0	1.5968073540 6879	415.8061797 68449	6.98367072928 153	0.0042165073 3506373

7.3 Article III (chapter 3.3)

Figure S1 - The area of wind damage and the classification of tree mortality caused by bark beetle damage are divided into Phase I and Phase II in the study area. A - Wind damage area and high resolution Google Earth image. B - Classification of tree mortality by Phase I with Sentinel 2 image (top) and high resolution Google image (bottom).

Table S1 - Correlation of variable

Table S2 - Field data of conifer trees by stage in two fields

Table S3 - Error matrix and accuracy statistics of forest classification.

Table S4 - Error matrix and accuracy statistics of the bark beetle damage classification for Phase I 2017-2019.

Table S5 - Error matrix and accuracy statistics of the bark beetle damage classification for Phase II 2020-2021.

The Supplementary Material for this article can be found online at:

<https://ars.els-cdn.com/content/image/1-s2.0-S0378112724000860-mmcl.docx>

7.4 Article IV (chapter 3.4)

Table S1 - All plausible GAM regression models used to study bark beetle number in the trap in 2015.

Figure S1 - Traps data and drought indices in 2015.

Figure S2 - Traps data and drought indices in 2014.

Formulas:

S1 - Correction coefficient for solar radiation:

S2 - Average air temperature

S3 - Maximal air temperature

S4 - Sum of effective air temperatures, degree-day

S5 - Average bark temperature

S6 - Maximum bark temperature

S7 - Effective bark temperature

S8 - Sum of effective bark temperature, degree-day

S9 - Potential Stand Transpiration

S10 - Water Content in soil

S11 - Drought Index

S12 - Cumulative Transpiration Deficit Index

The Supplementary Material for this article can be found online at:

<https://ars.els-cdn.com/content/image/1-s2.0-S0304380024002023-mmcl.docx>