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Author(s): Hroššo, Branislav; Mezei, Pavel; Potterf, Mária; Majdák, Andrei; Blaženec, Miroslav; Korolyova N; Jakuš, Rastislav

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Article

Drivers of Spruce Bark Beetle (*Ips typographus*) Infestations on Downed Trees after Severe Windthrow

Branislav Hroško^{1,2}, Pavel Mezei^{1,3,*}, Mária Potterf^{4,5} , Andrej Majdák¹,
Miroslav Blaženec¹ , Nataliya Korolyova⁶  and Rastislav Jakuš^{1,6}

¹ Institute of Forest Ecology, Slovak Academy of Sciences, Štúrova 2, 960 53 Zvolen, Slovakia; branoh@centrum.sk (B.H.); majdak@ife.sk (A.M.); blazenec@ife.sk (M.B.); rasti.jakus@gmail.com (R.J.)

² Faculty of Ecology and Environmental Sciences, Technical University in Zvolen, T.G.Masaryka 24, 960 53 Zvolen, Slovakia

³ Faculty of Forestry, Technical University in Zvolen, T.G.Masaryka 24, 960 53 Zvolen, Slovakia

⁴ Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FI-40014 Jyväskylä, Finland; mpotterf@jyu.fi

⁵ School of Resource Wisdom, University of Jyväskylä, P.O. Box 35, FI-40014 Jyväskylä, Finland

⁶ Faculty of Forestry and Wood Sciences, Czech University of Life Sciences in Prague, Kamycká 129, Suchbátka, 16500 Prague, Czech Republic; korolyova@fld.czu.cz

* Correspondence: mezei@ife.sk

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Abstract: Research Highlights: Bark beetles are important agents of disturbance regimes in temperate forests, and specifically in a connected wind-bark beetle disturbance system. Large-scale windthrows trigger population growth of the European spruce bark beetle (*Ips typographus* L.) from endemic to epidemic levels, thereby allowing the killing of Norway spruce trees over several consecutive years. Background and Objectives: There is a lack of evidence to differentiate how outbreaks are promoted by the effects of environmental variables versus beetle preferences of trees from endemic to outbreak. However, little is known about how individual downed-tree characteristics and local conditions such as tree orientation and solar radiation affect beetle colonization of downed trees. Materials and Methods: To answer this question, we investigated the infestation rates and determined tree death categories (uprooted, broken, and stump) in wind-damaged areas in Western Tatra Mts. in Carpathians (Slovakia) from 2014–2016, following a windthrow in May 2014. In total, we investigated 225 trees over eight transects. For every tree, we measured its morphological (tree height, crown characteristics), environmental (solar radiation, terrain conditions, trunk zenith), temporal (time since wind damage), and beetle infestation (presence, location of attack, bark desiccation) parameters. We applied Generalized Additive Mixed Models (GAMM) to unravel the main drivers of *I. typographus* infestations. Results: Over the first year, beetles preferred to attack broken trees and sun-exposed trunk sides over uprooted trees; the infestation on shaded sides started in the second year along with the infestation of uprooted trees with lower desiccation rates. We found that time since wind damage, stem length, and incident solar radiation increased the probability of beetle infestation, although both solar radiation and trunk zenith exhibited nonlinear variability. Our novel variable trunk zenith appeared to be an important predictor of bark beetle infestation probability. We conclude that trunk zenith as a simple measure defining the position of downed trees over the terrain can anticipate beetle infestation. Conclusions: Our findings contribute to understanding of the bark beetle's preferences to colonize windthrown trees in the initial years after the primary wind damage. Further, our findings can help to identify trees that are most susceptible to beetle infestation and to prioritize management actions to control beetle population while maintaining biodiversity.

Keywords: *Picea abies*; *Ips typographus*; disturbance; wind; epidemics; GAMM; bark beetle

1. Introduction

Forests worldwide are shaped by natural disturbances [1,2]. Eruptive insect species are considered as one of the main disturbance agents causing changes in ecosystems and affecting people's livelihoods, the economy, and hydrology [3–6]. In Europe, one of the main tree species affected by large-scale insect outbreaks is the Norway spruce (*Picea abies*, [L.] Karst) [7], whose natural habitat belt spans Scandinavian and Eastern European lowlands, montane areas in Central Europe, and large parts of the Carpathian Mts. [8]. Spruce forests in the latter are shaped by infrequent disturbances ranging from low severity events to stand replacing ones, with wind and bark beetle outbreaks being the key drivers [9,10]. Wind disturbances in the Carpathian spruce forests act as resource pulses [11] recorded at the frequency of at least 14 events in the last 200 years [9,10]. Windthrow, a primary disturbance, often leads to bark beetle epidemic population levels. The transition period between a windfall and subsequent outbreak may take from one to three years [12] and can be regarded as a “wind-bark beetle disturbance regime” [13,14]. Although such disturbances are considered calamities in managed forests, the newly formed dead wood enhances biodiversity [15]. In a natural forest, spruce seedling recruitment largely occurs under favorable conditions provided by decaying logs, despite logs only covering a small amount of forest floor [16–18].

The mechanism for how bark beetle populations tend to transition from endemic to outbreak conditions is lacking. Under endemic population levels, bark beetles attack weakened or downed trees and feed on their phloem [3,19]. The latest results show that uprooted trees can maintain constitutive defense for up to seven months after uprooting [20]. Hence, *Ips typographus* (L.) can develop on 17-month old uprooted trees without significant effects on their body mass or fecundity [21]. In mountain conditions, *I. typographus* can attack uprooted trees as long as 3 years after disturbance [22]. The spatial configuration of downed trees can play a substantial role in the transition of a beetle population from endemic to epidemic levels [13,23]. However, a naturally disturbed forest comprises various kinds of downed trees, e.g., uprooted trees and post-breakage stumps retaining root connection to the soil, or broken trees lying on the ground. These groups of trees differ in their desiccation rate, defense capacity, and attractiveness to beetles, i.e., trees connected by roots desiccate slower and therefore serve longer as breeding material compared to broken trees without root connections [22,24].

During the transition from endemic to outbreak beetle population levels, warmer breeding substrate can promote faster life cycles because temperature triggers bark beetle development [25]. Modeling approaches based on temperature conditions [26–29] and solar radiation [26,30,31] are widely used to predict *I. typographus* colonization behavior and population dynamics. In an open stand structure, the radiation is higher and affects the local microclimate. Solar radiation loads tend to be higher in forests affected by windstorms [32] and in open-canopy stands [33,34] than in intact close-canopy forests, modifying microclimatic conditions towards beetle-favorable ones.

Bark beetle outbreaks in the High Tatra Mountains were thoroughly investigated over the past few decades [13,30,35–37]. Most of these works focused on uncovering the trends and driving forces of beetle population at epidemic levels. Yet, we have a limited understanding of how endemic beetle populations initiate wind-blown tree infestation after large-scale windthrow, and what are the tree and environmental factors predicting tree colonization. Previous studies indicate that in small-scale, scattered windthrows, beetles first attack sun-exposed trunks rather than shaded ones [22,24]. However, the large-scale windthrows mainly affect environmental conditions and open the canopy, and therefore can modify the importance of bark beetle infestation drivers.

Our study aims to evaluate bark beetle colonization of individual wind-disturbed downed trees on a large-scale windthrown area over three years (2014–2016) following the wind damage in May 2014. We specifically aimed to (1) evaluate the effects of different tree morphology on colonization by *I. typographus*, (2) assess the effects of environmental, tree, and local microclimatic variables on tree infestations by bark beetles, and (3) assess the suitability of wind-blown trees in time since wind-damage for tree infestation by *I. typographus*.

2. Materials and Methods

2.1. Study Area

The study area is located at Suchá dolina Nature Reserves, in the Western Tatra Mountains in the Tatra National Park, Slovakia. The privately owned Nature Reserve extends over 1585 ha area and is managed according to a strict non-intervention strategy. Our study transects span Suchá dolina valley governed by the village Liptovský Trnovec community forests (Figure 1). The topography is alpine with rocky terrain intermitted by valleys, with elevation ranging from 970 to 1400 m a.s.l. The climate is continental with four distinct seasons and cold winters. Summers in this region are relatively cold and cloudy with the warmest month of July, and the average temperature does not exceed 16 °C. An average temperature below 0 °C is observed during 120–180 days·year⁻¹. Precipitation ranges from 1000 to 1400 mm·year⁻¹. Wind directions are strongly modified by topography. The north-south flow prevails throughout the year, changing only in speed and intensity. The altitudinal gradient accompanied by pronounced changes in climatic conditions through a wide range of topographical patterns results in distinctive vegetation belts. Norway spruce (*Picea abies*) monodominant forest provides a natural habitat for other forest species represented by European beech (*Fagus sylvatica* L.), mountain maple (*Acer pseudoplatanus* L.), fir (*Abies alba* Mill.), and pine (*Pinus sylvestris* L.) [38]. In May 2014, windstorm “Žofia” affected 107 ha of forests and initiated a six-year-long bark beetle outbreak that reached a decline phase by the year 2020.

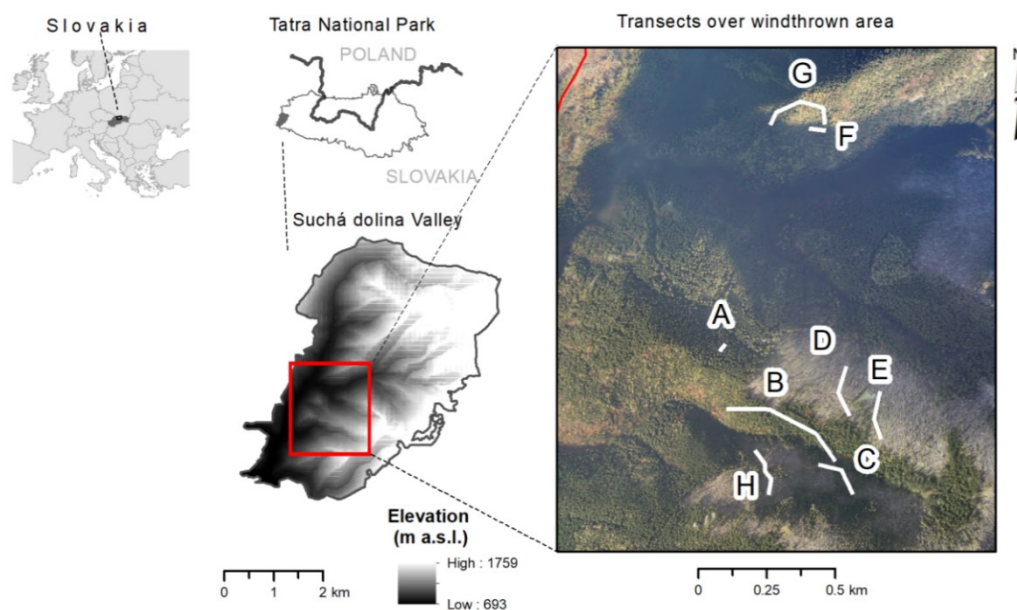


Figure 1. Location of the study area in the Suchá dolina Valley, in the Tatra National Park (Slovakia) located on the Slovak-Polish border and location of A to H transects over windthrown areas.

2.2. Data Collection

We established eight transects in areas affected by windthrow to contain different wind-blown tree damage categories (see below or Figure 2) and different environmental conditions, i.e., open windthrown areas, partially open areas on the edge of large-scale wind-blown trees, and areas under forest canopies. Their length ranged from 23 to 447 m with average length of 198 m. In 2014–2016, we inspected transects during field surveys several times over the study period. Tree systematization and analyses were implemented for three groups of trees affected by windstorm: (a) uprooted trees; (b) broken trees; and (c) stumps (Figure 2a–c). Uprooted trees retained root connection to the soil while broken trees were root-deprived stems lying on the ground. Rooted stem bases lacked trunk and belong into the category of standing stumps.



Figure 2. Examples of windthrown trees in the study site: (a) uprooted tree, (b) broken tree, (c) stump.

Transect locations span the whole range of topographical gradient of the large wind- and beetle-disturbed area. We marked transects by alphabetical letters from A to H. In total, we inspected 225 trees at altitudes ranging from 970 to 1400 m. For every tree, we measured (1) indicators of beetle attack and (2) morphological tree and site characteristics. Indicators of beetle attack recorded presence or absence of *I. typographus* bark beetle attack (IT), location of the attack on the trunk (Position) additional attacking bark beetle species (Species), and year of infestation (Year_of_Attack) (Table 1).

Table 1. Parameters related to bark beetle infestations assessed at each individual tree in our study set-up.

Parameter	Description	Units
IT	Presence/absence of <i>I. typographus</i> attack	Presence/absence
Position	Attack location on trunk: on sun exposed; ground facing side; or dried bark (not suitable for beetle infestation)	IT_sunny, IT_shaded, desiccated
Species	Bark beetle species other than <i>I. typographus</i>	Species name
Year_of_attack	Year of attack	2014, 2015, 2016

Morphological tree parameters included tree height, crown length, DBH, and degree of root connection. Environmental site characteristics measure tree location, altitude, slope and aspect, trunk zenith, canopy openness, and incident solar radiation at the trunk and above-canopy levels (Table 2). To record environmental variables, we measured the position of the trees within the transects A-H using GNSS receiver Trimble Juno SB. Slopes were measured using altimeter SUUNTO PM-5/1520 (Suunto, Finland). Tree and terrain aspects were determined using a compass. We measured solar radiation by hemispherical photogrammetry using a digital image analyzer WinSCANOPY (Regent Instruments Inc., Canada). We constructed hemispherical images for each tree based on the damage type, while images were taken at the base of a tree. We used WinSCANOPY Pro software for image processing and quantification of solar radiation that estimated values of direct, diffuse, and total solar radiation within and above the stand. Solar radiation measurements represent incipient cumulative solar radiation from 1 July to 30 September in $\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$. Environmental and morphological variables of downed trees are listed in Table 2.

Table 2. Environmental and morphological parameters of downed trees ($n = 225$).

Acronym	Description	Units	Type	Min	Max	Mean
Altitude	Tree altitude	[m]	Site	971	1400	1201
Aspect_terrain	Terrain aspect	[°]	Site	5	360	280
Slope_terrain	Terrain slope	[%]	Site	0	55	28
Openess	Canopy openness	[-]	Site	6	95	46
R_O_total	Total solar radiation above canopy	[mol.m ⁻² day ⁻¹]	Site	12	59	44
R_U_total	Total solar radiation under canopy	[mol.m ⁻² day ⁻¹]	Site	2	53	27
Aspct_trunk	Trunk zenith	[°]	Tree	0	350	151
Connection_roots	Degree of root-soil connectivity	[%]	Tree	0	100	40
Crown_length	Tree crown length	[m]	Tree	0	22	7
Crown_Percentage	Crown ratio as a percentage of tree length	[%]	Tree	0	100	30
DBH	Diameter at breast height	[cm]	Tree	13	66	38
Tree_length	Length of tree	[m]	Tree	1	32	16
Slope_trunk	Slope of tree	[°]	Tree	-40	90	17
Zenith_Trunk	Zenith angle of tree	[°]	Tree	0	130	73

We introduced a new variable—trunk zenith—to characterize the degree of tree uprooting as its deviation angle from the vertical position and in its relation to slope exposition, ranging from 0 to 180 degrees. Here, 0 represents standing vertical undamaged tree, 90 a laying tree position parallel to slope contour line, and 180 represents a mathematical scenario opposing the vertical tree, not occurring in real landscapes (Figure 3).

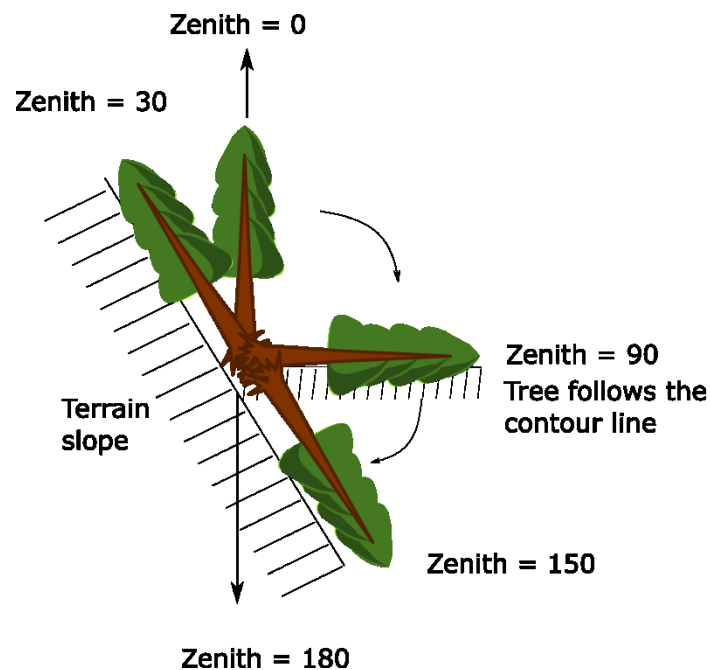


Figure 3. Trunk zenith of a tree lying on a contour line. Trunk zenith angle of a tree lying upward the terrain slope ranges from 0 to 89 degrees. If a tree is located on the contour line, its zenith angle is 90 degrees. Zenith angle of a tree lying downhill ranges from 91 to 180 degrees.

2.3. Statistical Analyses

We inspected all variables for missing values, outliers, and collinearity. To reduce collinearity, all predictor variables were assessed by correlograms. We removed the variables which correlation

coefficients exceeded the threshold of $r > 0.7$ [39]. Infested and non-infested trees were grouped by tree damage category and by year and compared using ANOVA. A post-hoc (Tukey's) test was applied to compare mean values of predictor variables according to the status of the tree (infested vs. non-infested).

We used Generalized Additive Mixed Models, GAMM [40], to determine the effect of downed tree characteristics on bark beetle attack probability. GAMMs can account for expected nonlinear relationships between the response and explanatory variables, as well as for the violations of the independence of measurements taken repeatedly over time and space. GAMMs employ nonlinear smooth function to all, or, as in our example, to some predictor variables. GAMMs allow for the inclusion of random effects that can correct for the lack of independence among individuals. In this instance, we included individual trees as a random effect. The nonlinearity in GAMM was measured by using the Effective Degree of Freedom. Nonlinear effects of the predictor variables on *I. typographus*-caused tree mortality are represented by their effective degrees of freedom, or edfs. Larger values of edf correspond to a higher nonlinearity degree of the modeled effects. Effects were estimated using smoothed functions that show relationships between individual covariates and the response variable while controlling for all other covariates [41,42]. We evaluated predictors of infestations for all downed trees, and individually for the uprooted trees, broken trees, and stumps, as we expected that predictors would be damage-dependent. Count data were fitted using binomial distribution.

All analyses were conducted in R software [43]. Mixed effects were modeled using the 'mgcv' package [40].

3. Results

3.1. Infestation Dynamics by Damage Type

In total, we examined 225 trees in eight transects in three categories: uprooted (156; 69.3%), broken trees (34; 15.1%), and stumps (35; 15.5%) (one broken stem could not be reached in the subsequent visit, therefore the number of stumps and broken trees listed differed by 1 in the subsequent count). Table 2 summarizes all recorded characteristics. We found that the proportion of *I. typographus* infested trees increased over three consecutive years. Upon a three-year monitoring period, 124 uprooted trees (80%) were found to be infested by *I. typographus*, whereas only 16 broken trees (47%) and 8 stumps (24%) were attacked by beetles (Figure 4).

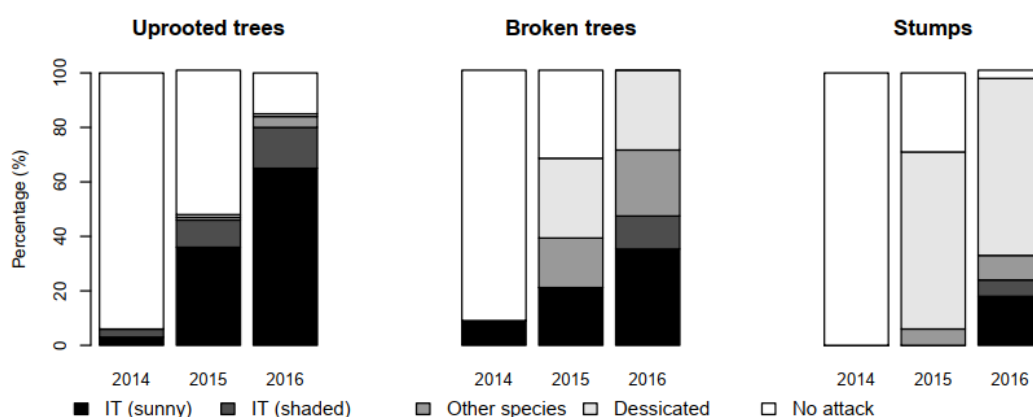


Figure 4. Proportion of downed trees by beetle infestation type and bark desiccation state in the Suchá dolina valley in 2014–2016. “IT (sunny)” stands for *I. typographus* infestations at the sun-exposed sides of a stem. “IT (shaded)” relates to the tree being attacked by beetles at predominantly shaded sides. “Other species” refers to insect infestations by species other than *I. typographus*, which were not analyzed in this study. “Desiccated” refers to a desiccated windthrown tree that has dried up and is not suitable for bark beetle feeding.

In the first post-disturbance year, only a small portion of uprooted trees was attacked (9 trees, 6% of total) (Figure 4, Uprooted trees). Most *I. typographus* attacks took place in the second year (62 infestations) and in the third year (62 infested trees). By the end of the study period, in 2016, most of uprooted trees (101, 65%) were infested on the sun-exposed trunk side, which is considered to be classical bark beetle attack, while less trees (23, 15%) were attacked from the shaded, ground-facing side. Broken trees were less susceptible to *I. typographus* infestations, mainly due to higher desiccation rates (29% of trees vs. 1% of uprooted trees) and larger numbers of successful attacks by other wood-boring insects (24% vs. 4% of uprooted trees). Among the three categories, stumps were the least infested by *I. typographus*.

Deprived of root connections to the soil, broken trees desiccated more frequently than the uprooted individuals, becoming unsuitable food substrate for bark beetles one year after the windthrow, in 2015 (Figure 4). Thus, the share of *I. typographus*-attacked trees appeared to be lower than that of the uprooted ones. However, we observed attacks on the desiccated broken trees by other bark beetle species of the *Curculionidae* (*Col.*) family, such as *Hylastes* sp., *Polygraphus poligraphus* (L.), and *Pityogenes chalcographus* (L.). Species other than *I. typographus* attacked 23% of the sampled wind-blown trees.

Uprooted trees were gradually attacked over the whole study period, mostly on sun-exposed stem sides. 15% of sampled trees were attacked on shaded side, 23% were attacked by species other than *I. typographus*, stumps were only attacked by *I. typographus* in the third year, and only 18% were attacked by *I. typographus*. The infested uprooted trees received two times higher solar radiation compared to non-infested uprooted trees in 2014 (Figure 5c).

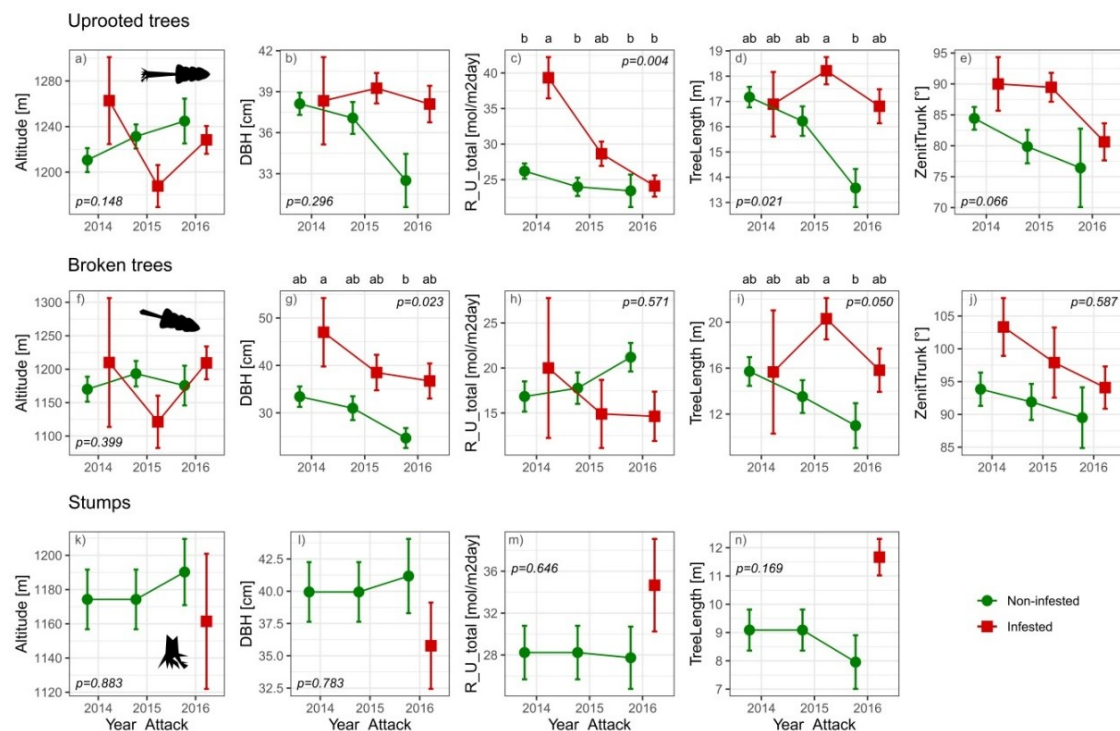


Figure 5. Distribution of wind-broken trees (a–e), uprooted trees (f–j), and stump parameters (k–n) by infestation evidence in 2014–2016. *Altitude* shows elevation of tree position above the sea level; *ZenitTrunk* stands for tree zenith angle calculated as a function of slope and stem orientation; *DBH* means the tree diameter measured at breast height; *R_U_total* denotes total solar radiation under canopy; *TreeLength* stands for the length of a lying tree. ANOVA output for differences between tree parameters followed by group separation (different lower-case letters) according to the Tukey test ($\alpha = 0.05$) is given above for statistically significant differences.

3.2. Environmental and Morphological Parameters of Downed Trees

Only variables which can be assessed for each category of trees and variables, which remained after inspecting for collinearity were used as predictors. These variables were Altitude, DBH, R_U_total, Tree_length, and Zenit_trunk, their maximum, minimum, and mean values can be read out from Table 2.

Mean values of infested and non-infested uprooted trees according to predictor variables and years were analyzed by ANOVA and are shown in Figure 5a–n. Predictors R_U_total (Figure 5c) and TreeLength (Figure 5d) were statistically significant (Tukey post-hoc test) and increasing radiation and tree length increased the infestation probability.

In general, the altitude, DBH, tree length, and trunk zenith had the similar patterns in tree infestation for uprooted and broken trees. Trees at higher elevations, with larger diameter and higher amount of incipient solar radiation were infested in the first summer following the windthrow of May 2014 (Figure 5c). Over time, the diameter size of infested trees clearly decreased for broken trees (Figure 5g) and only decreased slightly for uprooted trees. Yet, the diameter of non-infested trees decreased over whole study period (2014–2016) for both uprooted and broken trees. Wind-broken tree parameter distributions showed that larger diameter trees (DBH, Figure 5g,i) were more susceptible to bark beetle infestations. Accordingly, taller trees were favored over shorter trees, with the highest difference in the second year following the windthrow.

Most sun-exposed downed trees were infested in the first year; yet importance of solar radiation decreased with time over the first year for the broken trees and over two years for the uprooted trees. Contrary to for the uprooted trees, solar radiation did not show a significant effect on bark beetle infestation of stumps. Most of the broken infested trees grew down the slope (trunk zenith > 90) whereas the uprooted trees were oriented uphill, with dominant infestation of trees following the contour lines (Figure 5).

Tree stumps were infested only in the third year (Figure 5, lower row). None of the predictor variables had any effect on beetle infestations of tree stumps, although longer stumps (length: 12 m) were infested by *I. typographus* more often than shorter ones (9 m).

3.3. Morphological and Environmental Effects on Beetle Infestation

After inspecting for collinearity of predictor variables, 8 variables remained and were included in the GAMM model. To estimate the effect of each morphological and environmental variable on probability of bark beetle infestation into the GAMM model, we included predictor variables Crown Length, Year of attack, Crown Percentage, DBH, Connection_roots, Tree length, R_U_total, and Zenith trunk. We found that the most important variables that had positive effects on the number of infested downed trees were the Year of attack, Tree length, Total under-canopy solar radiation, and Trunk zenith (Table 3). Crown Length, Crown Percentage, Connectionroots, and DBH were not found to be significant as predictors of beetle infestations.

R_U_total and Zenith trunk had nonlinear effects. The smooth functions in Figure 6 show the relationship between individual covariates and the response variable, i.e., bark beetle infestations, controlling for all other covariates. Nonlinearity of the predictor variables on tree mortality caused by the spruce bark beetle are listed according to their effective degree of freedom (edf; the higher the edf is, the higher the nonlinearity, see Table 3). Total amounts of received daily solar radiation that exceeded 22 mol/m²day increased the number of infested trees (Figure 6a). Trunk zenith lower than cca 100° was associated with rapid increase in the numbers of attacked spruces, while the trunk zenith that exceeded this threshold level showed a negative relationship with the number of colonized trees (Figure 6b).

Statistically significant variables were identified as Year of attack, Tree length, R_U_total, and Zenith trunk. The Year of attack and Tree length had positive effects on bark beetle attack, i.e., the increasing time, since the tree was wind-blown or broken and increasing tree length increased the probability of the attack.

Table 3. Statistics for Generalized Additive Mixed Model that estimated morphological and environmental effects on tree infestation by bark beetles in 2014–2016. Adjusted $R^2 = 0.554$.

Parameter	Estimate	Std. Error	t-Value	p-Value
Crown length	−0.061523	0.100652	−0.611	0.5412
Year_of_attack	2.354738	0.150526	15.643	<0.01 *
Crown_Percentage	0.002991	0.015845	0.189	0.8503
DBH	0.023468	0.015943	1.472	0.1414
Connection_roots	0.013493	0.009059	1.489	0.1367
Tree_length	0.178461	0.060368	2.956	0.0032 *
Approximate significance of smooth terms (nonlinear variables)				
Parameter	edf	F	p-value	
R_U_total	2.720	5.914	<0.01 *	
Zenith_Trunk	2.436	10.498	<0.01 *	

* indicates statistically significant difference at $\alpha < 0.05$.

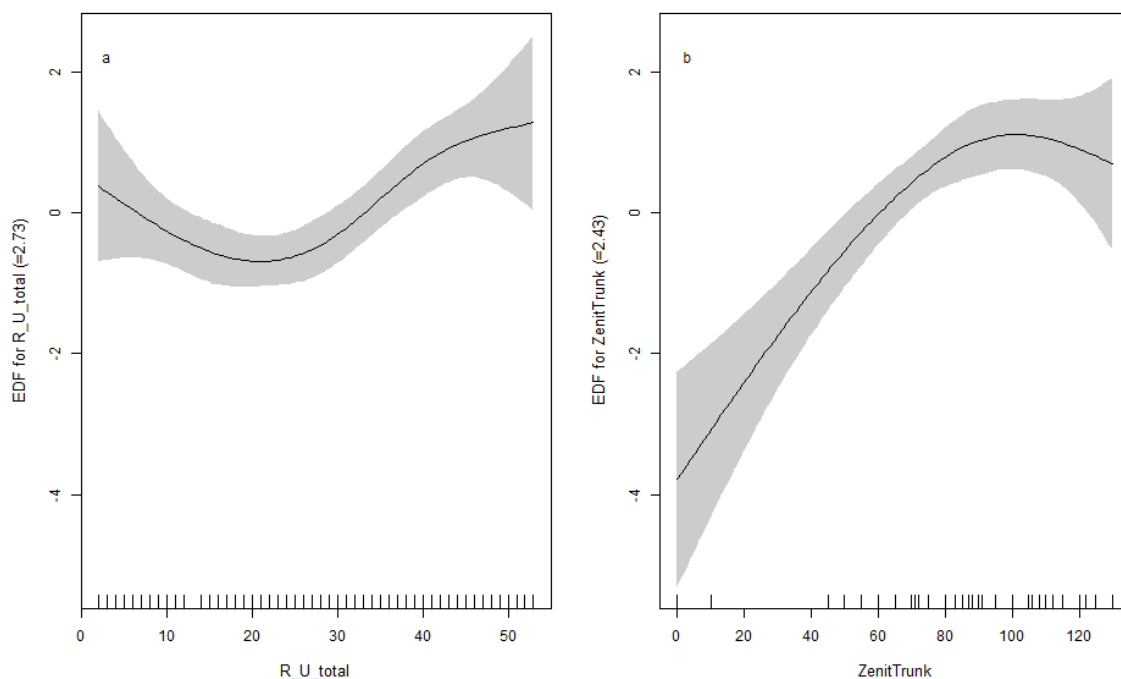


Figure 6. Estimated smooth functions generated for the *I. typographus* infestation of trees GAMM, showing the effect of (a) solar radiation and (b) trunk zenith (only nonlinear variables shown, see Table 3 for the full details of the model). Rug marks along the x-axes illustrate the distribution of solar radiation and trunk zenith values. Shaded areas represent 95% confidence intervals.

4. Discussion

4.1. General *I. typographus* Infestation Patterns

Our results show that 72.9% (164 trees) of all the 225 sampled downed Norway spruce trees were infested by *I. typographus* within three years after the wind disturbance. This corresponds to findings from nearby located Ticha dolina valley, where the wind-blown trees became unavailable as beetle feeding substrate in the second summer after the windthrow [44]. Yet, we found a large difference between the desiccation and infestation rates between uprooted and broken trees: uprooted trees desiccated more slowly compared to broken trees and stumps; up to 70% of uprooted trees were still available as breeding substrate in the second year after the wind damage (Figure 4). We hypothesize that this difference mainly originated because uprooted trees' roots connection was (at least partially)

unaffected and 3 trees retained green needles into the third year after they were wind-blown. Not every broken tree was desiccated in the first year of the study, when they had shaded site exposition or were shaded by surrounding standing trees, they retained their attractiveness for *I. typographus* in the following years.

Our transects were located on sun-exposed slopes with differentiated damage type (uprooted, broken) while trees from Vakula and Zubrik [44] were located prevalingly on the bottom of the shaded valley and without information about the damage type. Therefore, the probability of infestation of downed trees and its availability as a breeding substrate to trigger bark beetle outbreak largely depends on the sun-exposition of downed trees and on the damage type. The importance of the sun-exposition for bark beetle attacks was previously documented for infestation of standing trees located on a freshly open stand edge [37,45,46].

Over the study period, the beetle changed its preferences for the type of tree damage and morphological tree parameters. In the first year, beetles prioritized wind-broken potential hosts over uprooted trees (Figure 4). This is likely because of the presence of the connected root system, allowing trees to partially maintain vital functions and defenses for up to three years after the wind-blown [20,22], and to maintain slower phloem desiccation rates compared to wind broken trees. In the first season, sun-exposed side of the trunks were infested two times more often in broken trees than in uprooted trees; the sun-exposed trunk side became a dominant breeding location for uprooted trees over two vegetation seasons following the windthrow (Figure 4). Infestation of the ground-facing trunk side occurred in the one quarter of infestations in uprooted trees and started in the second summer. This suggests an important switch of locations of *I. typographus* breeding resources depending on solar exposition. We suggest several testable explanations and their effects on beetle population growth: (1) ground-facing shaded bark condition postpones the availability of the high nutritional resources for beetle breeding due to the slower desiccation rate, which supports beetle population growth by exposing new resources sites; or (2) the shaded trunk side provides suboptimal decaying breeding resources that are used only later in the gradation, when the more suitable breeding substrate is exploited. Although initial boring attempts on the ground-facing side of a downed tree stem are uncommon for *I. typographus* colonization behavior on mountainous conditions [22,24], this pattern was reported in spruce stands growing at low elevations outside of their natural habitat [47]. This suggests the role of trunk side sun-exposition in affecting availability of food resources i.e., due to higher temperatures.

We found that 23% of trees were attacked by different species than *I. typographus*. The most important one is attacks by *P. poligraphus*. This bark beetle tended to attack substrate, which is not suitable for *I. typographus* and only 18% of stumps were infested by *I. typographus*.

4.2. Drivers of *I. typographus* Infestation Patterns

Factors influencing infestation of the Norway spruce trees by bark beetles are often studied [48–50] but we lack complete understanding of the changing importance of individual triggers in transiting from the primary disturbance source, usually windthrow [51,52] or drought [53] to the self-driven epidemics, causing landscape level tree mortality [13]. This transition is likely driven both by environmental and tree characteristics; yet the importance of individual factors varies based on local conditions. At the beginning of an epidemic, there is not a sufficient number of beetles to colonize every wind-damaged or drought-stressed tree. Bark beetles utilize the most suitable trees for breeding first. White [54,55] hypothesizes that raising temperatures enhance phloem nutritional values and therefore beetle outbreaks represent a symptom of degrading forests health, not the main cause of tree mortality.

In our case, the main factors influencing the dynamics of *I. typographus* colonization activity on downed trees were tree length, ground level solar radiation, and trunk zenith. Tree length is generally related to tree dimensions and strongly correlates with the diameter at breast height. We found that *I. typographus* preferentially attacked larger trees and infested tree diameter lowers over the following years (Figure 5), which aligns with previous works [22,24]. Interestingly, the same pattern of infestation

of larger trees was reported from infesting standing trees at the beginning of epidemic state [14,56]. Preference for the larger trees correspond to pattern in standing trees infestations where the largest trees are attacked first, thereby increasing the beetle population size.

The nonlinear solar radiation effect on infestation (Figure 6a) can elucidate on a more complex interaction between solar radiation, temperature, tree stems, and beetle infestations. Jurc et al. [57], Akkuzu et al. [58], and Mezei et al. [59] gained higher trap catches on eastern or southern aspects of the slopes, indicating bark beetle preferences for sun-exposed host trees. South- and west-facing slopes have been reported to be more susceptible to *I. typographus* [24].

Our findings oppose the suggested linear effects of solar radiation found in previous studies [22,24]. We suppose that this effect could be partially explained by higher computational performance of statistical methods to account for the existence of the nonlinear relationship between predictors and response variables due to current high-performance computer systems, which was very challenging to develop in the late 1990s.

Our novel variable trunk zenith was found to be an important predictor of beetle attack, especially for uprooted trees (Figures 5 and 6, Table 2). The trunk zenith estimates the angle of a damaged tree relative to the slope (Figure 2), and as such represents the degree of the downed tree-soil root connection. As an example of its usefulness, wind broken trees with no connection to the soil can be shown to have been attacked first (Figure 4). For uprooted trees, the probability of beetle infestation increases over a gradient from very good connection (uprooted trees with a top up to steep slope) to almost no connection (uprooted trees with a top down to steep slope, as seen in Figure 6).

4.3. Management Implications

To minimize the risk of the bark beetle outbreak in commercial forests, at least 80% of individual beetles must be killed or 80% of wind felled trees must be removed [60]. Our results show the importance of considering the type of wind damage (uprooted vs. broken), as the degree of the root connection dictates how long a tree will be available as a suitable breeding substrate. Broken trees become an available breeding resource without any defenses in the first summer after a windthrow, whereas uprooted trees can provide breeding resources for a longer time period (up to 17 months) [20]. We found that stumps played only a minor role in triggering bark beetle outbreak.

5. Conclusions

We found that the *I. typographus* infestations on wind damaged trees after a major windthrow were related mainly to the tree dimensions and received solar radiation. Beetles preferred to colonize larger, sun-exposed, and broken trees over smaller, shaded, and uprooted ones. Our novel variable ‘trunk zenith’, representing the degree of tree uprooting and its connection to the root system, predicts the probability of tree infestation of uprooted trees. Both received solar radiation and trunk zenith exhibited nonlinear variability but in general we concluded that higher radiation, trunk zenith, and larger tree dimensions were the main factors related to an increased probability of beetle infestations. The tree stumps played a negligible role as breeding resources for beetle population growth. Our findings might help to plan salvage logging operations in commercial forests to control development of beetle populations.

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