Potential Solar Radiation as a Driver for Bark Beetle Infestation on a Landscape Scale

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Abstract: In recent decades, Norway spruce (*Picea abies* L. Karst.) forests of the High Tatra Mountains have suffered unprecedented tree mortality caused by European spruce bark beetle (*Ips typographus* L.). Analysis of the spatiotemporal pattern of bark beetle outbreaks across the landscape in consecutive years can provide new insights into the population dynamics of tree-killing insects. A bark beetle outbreak occurred in the High Tatra Mountains after a storm damaged more than 10,000 ha of forests in 2004. We combined yearly Landsat-derived bark beetle infestation spots from 2006 to 2014 and meteorological data to identify the susceptibility of forest stands to beetle infestation. We found that digital elevation model (DEM)-derived potential radiation loads predicted beetle infestation, especially in the peak phase of beetle epidemic. Moreover, spots attacked at the beginning of our study period had higher values of received solar radiation than spots at the end of the study period, indicating that bark beetles prefer sites with higher insolation during outbreak. We conclude that solar radiation, easily determined from the DEM, better identified beetle infestations than commonly used meteorological variables. We recommend including potential solar radiation in beetle infestation prediction models.

Keywords: *Ips typographus*; national park; *Picea abies*; High Tatra Mountains; solar radiation

1. Introduction

Massive forest mortality events affecting many tree species in the last two decades have prompted concerns that drought, insects, and wildfire may devastate more forests in the coming decades [1]. Mountain spruce forests (*Picea abies* L. Karst.) are shaped by disturbances, ranging in severity from low- to stand-replacing. The main drivers of such disturbances in the Carpathians are wind and bark beetle outbreaks [2,3], the latter usually initiated by extreme weather events [4,5] and affected by forest management [6–8].

In Europe, the European spruce bark beetle (*Ips typographus* L.) is an insect species that often reaches epidemic levels [9,10]. Between outbreaks, beetles persist at small endemic populations in scattered refuges of food. When there is a sudden increase in suitable hosts and favorable weather conditions [11,12], they erupt to outbreak numbers [13–15]. The heat- and drought-induced physiological stress on trees likely triggers the development of forest insects, such as bark beetles [12,16]. The economic consequences of these types of disturbances are of particular importance, especially in Europe, the USA, Canada, and Russia [17].

European spruce bark beetles mostly colonize trees with impaired defenses and their larvae feed on the phloem and cambium cells, thereby increasing the disruption of phloem tissues [18]. *I. typographus* creates infestation spots ranging from several neighboring infested trees to large continuous areas of dead mature trees (Figure 1). The needles of beetle-infested trees fade over time, which allows for the identification of infested trees by optical remote sensing methods [19].
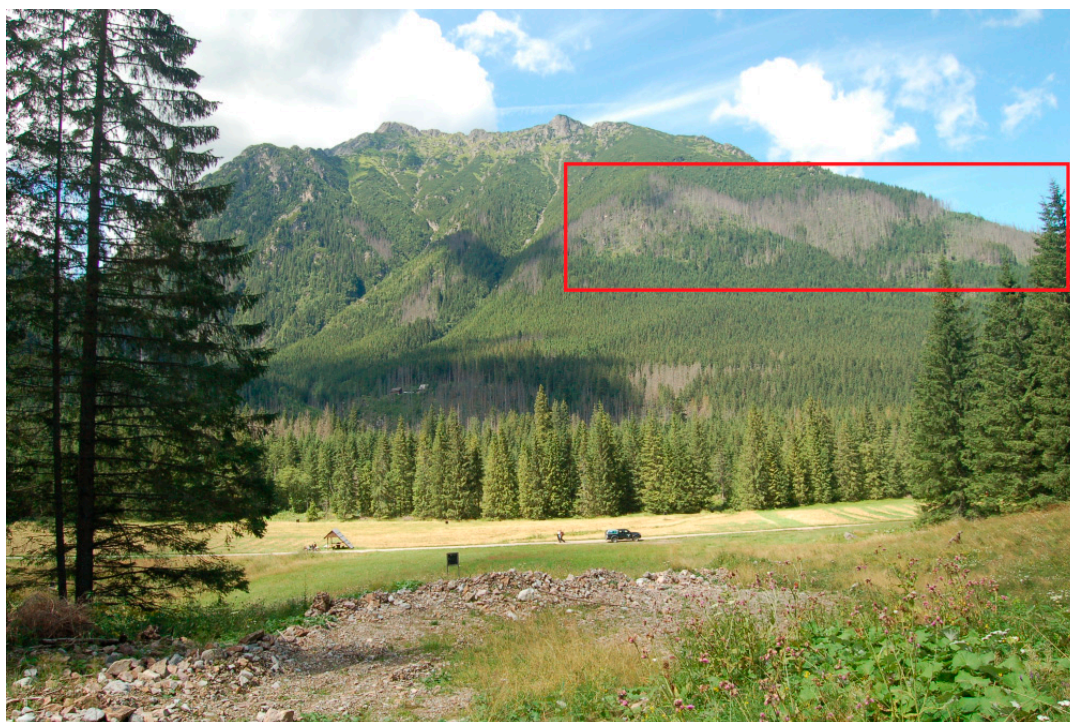

Figure 1. Example of bark beetle–infested trees in the High Tatra Mountains National Park, Slovakia. Bark beetle-infested trees are in the red rectangle (Photo: Pavel Mezei.).

Although *I. typographus* is one of the most studied forest insect pests, its spatiotemporal infestation patterns in mountainous forests are not completely understood due to a variety of biotic and abiotic factors and their interactions. Analysis of the spatiotemporal patterns of bark beetle outbreaks across the landscape in several consecutive years can reveal new insights into the drivers of outbreak development [20,21]. Colonization of new hosts by bark beetles is a key process in the response of insect populations to changing environmental conditions and a key driver of population dynamics. Offspring are forced to emerge and forage for new habitats. The higher the number of simultaneously attacking beetles, the higher the chance of overcoming host tree defense mechanisms. However, experiments studying dispersal across space and time are scarce. Population-level dispersal success is strongly environment-dependent [22–24]. Favorable microclimatic conditions induced by topography, as well as temperature and sunlight, may enhance the probability of local attack [25,26]. Regarding host selection processes in *I. typographus* populations, prior studies listed tree vigor and physiology [15,27,28], forest composition and host characteristics [25,29,30], and the distance from previous infestations [31,32] as the most significant factors influencing the probability that a site will be infested. There is evidence that solar radiation affects infestation patterns of *I. typographus* [26,33,34]. Higher pheromone trap catches at sun-exposed sites [35,36] corresponded to higher infestation occurrences at sun-exposed sites [34,37]. Incoming solar radiation (insolation), received from the sun, is the primary energy source that drives many of the earth's physical and biological processes. Our previous studies, based on forest inventory data, showed the importance of solar radiation [29] and temperature [38] in triggering *I. typographus* induced tree mortality. Here, we examine the environmental conditions of spatially explicit locations of infested trees based on Landsat imagery in a national park zone where no sanitary or salvage logging

has been applied. A better understanding of the drivers of bark beetle spot occurrence is critical to predict outbreak dynamics and future dynamics of subalpine forests. In this work, we use spatially explicit locations of beetle infestations acquired through remote sensing. We used Landsat-derived beetle infestation spots from 2006 to 2014 in the High Tatra Mountains [39] to quantify the contributions of temperature and radiation to spatiotemporal patterns. Further, we tested the effects of these variables according to individual outbreak phases, i.e., incipient, peak, and decline. Specifically, we sought to answer the following three questions: (1) Do bark beetle spots originate at locations with distinct patterns of temperature conditions or potential solar radiation at a landscape level? (2) Which of the tested variables are linked closer to bark beetle spot occurrence? (3) Are temperature or potential solar radiation patterns of landscapes associated with bark beetle population dynamics according to outbreak phases?

2. Methods

2.1. Study Area

The study area is located in the High Tatra Mountains of Central Europe, the highest mountains in the Carpathians, which extend to 2655 m a.s.l. (Figure 2). The High Tatra Mountains are located on the border between Poland on the north and Slovakia on the south. The studied forests are located in two national parks, Tatrzański Park Narodowy (TPN, Poland) and Tatranský národný park (TANAP, Slovakia). Our study area covers 28,532 ha of forests, dominated mainly by Norway spruce (*Picea abies*). The codominant tree species is *Larix decidua* Mill. and admixtures are *Pinus sylvestris* L. and *Abies alba* Mill. The ground vegetation is dominated by *Vaccinium myrtillus* L., *V. vitis-idaea* L., *Calamagrostis villosa*, and *Homogyne alpina* L. Rocky cambisol is the prevailing soil type. Stands are characterized by high altitudinal variability from the lower mountain zone to the timber line, ranging from 700 m to 1700 m above sea level (a.s.l.). The study area is characterized by deep valleys and mountain ridges. Populations of *I. typographus* in the study area are largely univoltine, although favorable weather conditions may allow beetles to complete a sister generation [38,40,41]. The study area was hit by a storm in 2004, after which the bark beetle outbreak began [42].
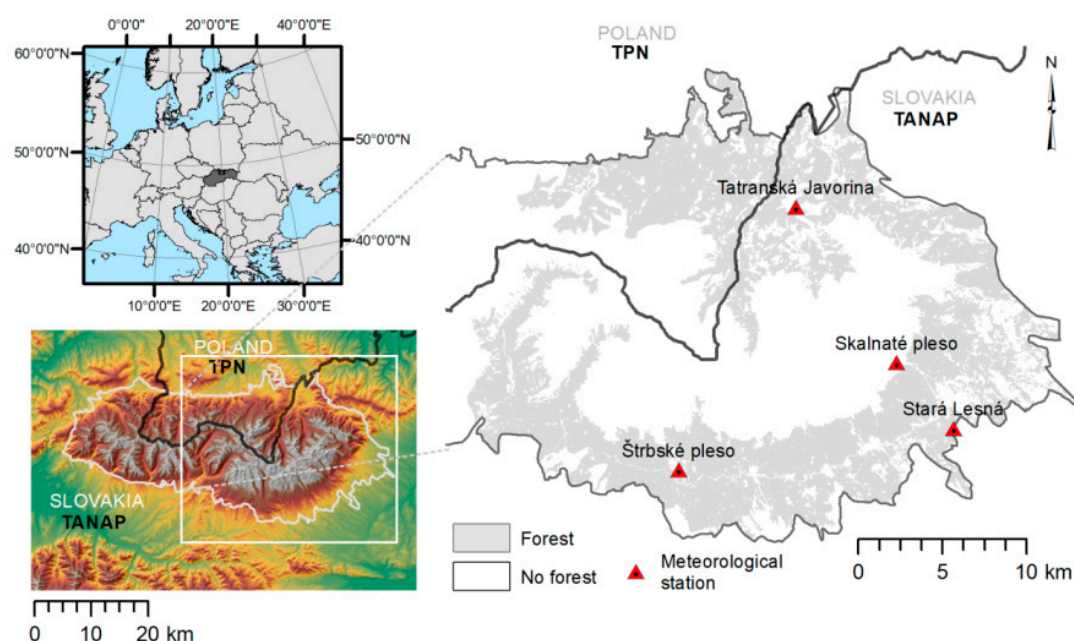

Figure 2. Location of the study area in the High Tatra Mountains. Grey represents the area of forest cover under our investigation; red triangles represent meteorological stations.

2.2. Meteorological and Topographic Data

To understand the potential effects of temperature on bark beetle spot occurrence, we obtained meteorological data comprising two variables previously identified as important for *I. typographus* population dynamics, as follows: (1) Mean air temperature sums (*ATmeanSum*) [43] and (2) maximum daily air temperature sums (*ATmaxSum*) [38,44]. All variables were calculated from the period from 1 April to 31 October [45]. We consider this temporal window as the main season for bark beetles in Central Europe as, outside this period, the temperatures are frequently beyond the developmental threshold of *I. typographus* in the study area. Daily mean and maximum air temperatures were estimated using daily regression analysis, which incorporated elevation and relative solar radiation as predictive variables. For each day, we computed a unique set of regression coefficients based on the aggregated hourly temperature data from 4 stations (Table 1). Estimates of maximum and mean air temperatures were then calculated using appropriate daily regression coefficients, elevation, and estimated solar radiation as input variables [45]. The temperature sums were then calculated by adding all daily temperatures in the period from 1 April to 31 October. Topographic data were derived from the digital elevation model (DEM) with a resolution of 30 m (available from Space Shuttle Radar Topography Mission, http://dwtkns.com/srtm30m). We calculated the potential solar radiation (*PotRad*) (Wh/m^2) using the Area Solar Radiation tool (ArcGIS, Esri, Redlands, CA, USA) using the geographical information system. The Area Solar Radiation tool calculates solar insolation across the entire landscape. It accounts site latitude, elevation, steepness (slope) and compass direction (aspect), daily and seasonal shifts of the sun angle, and effects of shadows cast by surrounding topography [46]. The resulting solar radiation neglects local shading conditions by trees. The calculations were repeated for each day on the input topographic surface, producing yearly insolation maps for the entire study period from 1 April to 31 October.

Table 1. Locations of meteorological stations inside our study area.

Station	Lat.	Long	Elevation
Tatranská_Javorina	20.14361	49.26306	1013
Stará_Lesná	20.28333	49.15	807
Skalnaté_pleso	20.23333	49.18333	1778
Štrbské pleso	20.05	49.117	1322

2.3. Identification of Bark Beetle Infestation

We used freely available Landsat-based land cover classification for the Tatra Mountains from 2005 to 2014 (30 m resolution, see Reference [42] for details and data availability) to create yearly time series of bark beetle infestation patterns. The land cover classification captures the spatial extent of green intact forests and four disturbances types, as follows: Bark beetle-infested trees, fire, clear-cuts, and windthrows occurring in the Tatra Mountains over the study period. From raster data, we extracted bark beetle infestations spots for each year, which represent accurate fine-grain (30 × 30 m) records of the spatiotemporal development of tree mortality due to *I. typographus* outbreak [42]. We further reclassified beetle infestation data into two categories for each year in our 10-year period, as follows: Pixels infested by bark beetles (1) and forest (0). Pixels infested by bark beetles in year, *T*, were removed from the raster layer of the subsequent year, *T+1*.

2.4. Statistical Analysis

A set of a priori models [47] was selected prior to analysis. These models were constructed using climatic variables (*ATmeanSum, ATmaxSum,* and *PotRad*) identified as important for bark beetle population dynamics in order to test which one would best explain the infestation pattern of *I. typographus*. As these three variables highly correlated to each other, we have not used them in multivariate modelling. We divided our analysis into two parts. In the first part, we compared

three models where we extracted cell values from raster images of infestations for each year (0, not infested; 1, infested) and cell values from rasters of temperature and potential solar radiation for each aligning pixel for the same year. We used logistic regression [48] and the *glm* function in R [49] to model the relationship between infestation spots and predictor variables. The information-theory (I-T) approach [50,51] was used to assess three competing models. Apart from selecting the most parsimonious model, I-T model selection also arranges models in order of parsimony. Models were ranked according to the Akaike information criterion (AIC); the most parsimonious model was selected based on the lowest AIC value [47]. We also calculated Akaike weights to arrange candidate models in order of parsimony, where Akaike weight is a number from 0 to 1, providing a measure of the relative likelihood of each model, given the data and candidate model set. For comparison, we included the intercept-only model as a baseline [50]. In the second part of our analysis, we worked with the predictor variable, which was fitted as the most parsimonious according to the above-mentioned criteria. This comprised the analysis of average solar radiation and meteorological values of infested vs. non-infested pixels for each year in the study area. We calculated the average value of the selected meteorological or topographic variables for infested and non-infested pixels for each year and used the Shapiro–Wilks test to test for normality of the data for the whole outbreak period and for particular outbreak phases. We compared the two groups by Analysis of Variance (ANOVA) in case of normality and by the nonparametric Mann–Whitney U test in cases of data deviating from normality. We did this comparison according to outbreak phases and for the whole study period.

3. Results

During the study period (2005–2014), 8945 out of the 28,532 ha of forest was infested by bark beetles (Figure 3a). The first infestations detected by Landsat started in 2006 and the yearly average infested area by bark beetles reached 993 ha. Based on the amount of infested trees, we identified years 2005 and 2006 as the incipient phase (*n* = 2), 2007 to 2010 as the peak phase (*n* = 4), and 2011 to 2014 (*n* = 4) as the decline phase of the epidemics.
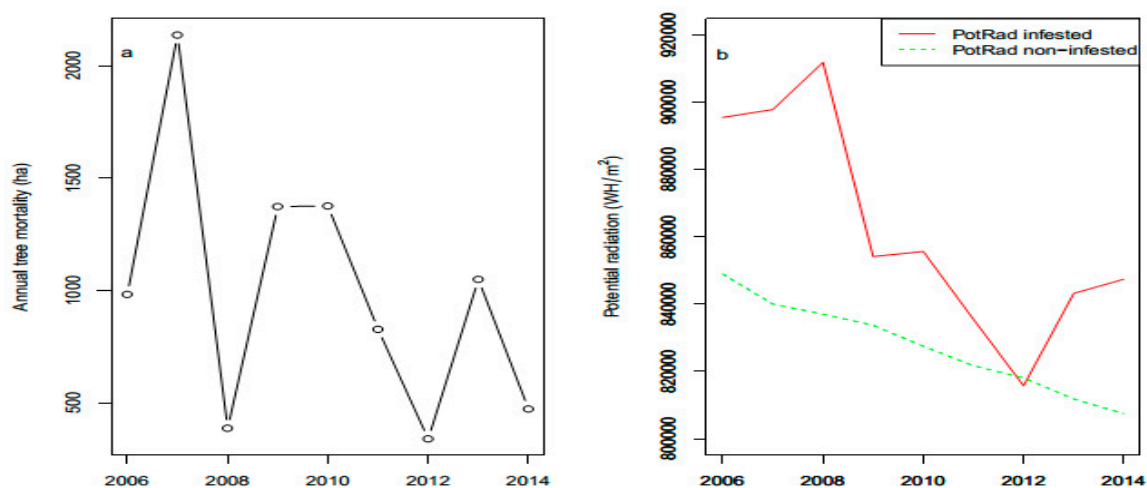

Figure 3. Time series of bark beetle infestations (**a**) and potential radiation of infested and non-infested pixels from 1 April to 31 October in the High Tatra Mountains, 2006–2014 (**b**).

3.1. Environmental Drivers of Insect Infestation

We used logistic regression to model the relationships between the occurrences of bark beetle spots and each of the explanatory variables' maximum temperature sums, mean temperature sums, and potential radiation. We did not create multivariate logistic regression models, since there was a high level of correlation among the three explanatory variables ($r^2 > 0.70$). Instead, we used each variable separately in univariate regression models to analyze their individual relationship with bark

beetle spot occurrences in order to identify the best meteorological predictor. According to the I-T approach, the most parsimonious model was the one with the lowest AIC number and the highest Akaike weight, which was model 3 (Table 2). Potential radiation was the best explanatory variable for *I. typographus* infestations in a mountainous terrain.

Table 2. Model formula and Akaike information criterion (AIC) for the four fitted logistic regression models selected for 2005 to 2014 in the High Tatra Mountains. *I* signifies infestation by bark beetles; * intercept-only model.

Model	Explanatory Variable	AIC	AIC Weight
1	I = meanATsum	711,045.1	0.00
2	I = maxATsum	709,576.3	0.00
3	I = PotRad	709,317.8	1.00
4	I = 1 *	719,125.9	0.00

3.2. Infested vs. Noninfested Spots

We found significant differences between potential radiation of infested vs. noninfested pixels for the whole outbreak period (Figure 4a), as well as for the peak and decline phases (Figure 4b,c). Pixels of infested forests derived from Landsat satellite images received higher loads of solar radiation from 1 April to 31 October than non-infested forests (Figure 3b).
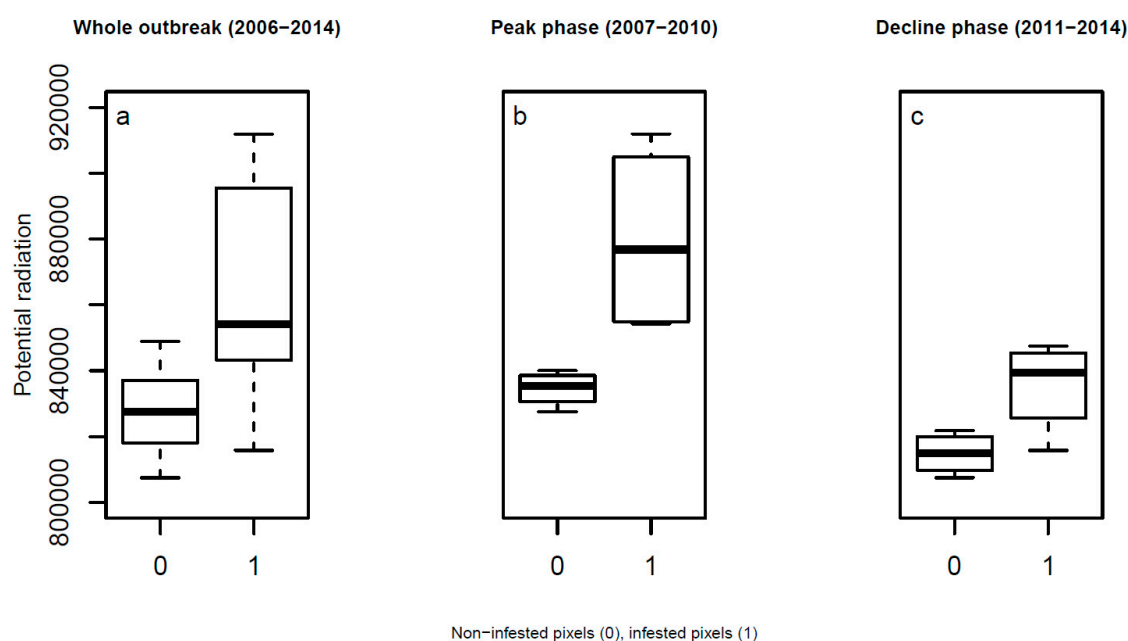

Figure 4. Comparison of potential solar radiation of pixels with noninfested and infested trees during the (**a**) whole bark beetle outbreak (Mann–Whitney U Test: W = 12, $p = 0.01$), (**b**) the peak phase (ANOVA, $F = 9.18$, $p = 0.02$) and (**c**) the decline phase (ANOVA, $F = 7.21$, $p = 0.0363$) in the High Tatra Mountains.

ATmeanSum and *ATmaxSum* showed weaker effects on bark beetle spot occurrence ($p = 0.06$ and 0.07 for the whole period; graphs not shown) than *PotRad*, which is in agreement with the model selection results (Table 2). We did not report the incipient-epidemic phase because it only had two years, which was not sufficient to perform the analysis.

Of all the involved outbreak phases, the peak phase showed the strongest response of bark beetle spots to potential solar radiation (Figure 4b). The post-epidemic phase of an outbreak also showed

differences between infested and noninfested spots of forests (Figure 4c). The time series of potential radiation of bark beetle infestation spots indicates that bark beetles infested the most sun-exposed sites at the beginning of an outbreak (Figure 3b). Infestations started at sun-exposed sites and moved to less sun-exposed areas.

4. Discussion

In recent decades, forests of the High Tatra Mountains have been subjected to large-scale windfall episodes and bark beetle outbreaks. In 2004, a 2.5 million m^3 storm felling occurred and *I. typographus* used the wind-felled trees to build up their population during the first two seasons after the storm [13]. Our study examined bark beetle infestations in a national park zone, where no sanitary or salvage logging was applied, from 2005 to 2014. Newly infested bark beetle spots occurred each year during this period. Previous studies reported higher bark beetle activity with incoming potential solar radiation [26,36]. Our results show that bark beetle spots occurred in sites with higher potential solar radiation loads, especially during peak and decline outbreak phases. Both our analysis approaches (Table 2, Figure 4a–c) show that the occurrence of beetle spots was driven by potential solar radiation.

Bark beetle infestation spots showed a preference for sites with higher potential solar radiation loads (Figure 4a–c). Bark beetle physiology, reproduction, and population dynamics are mainly climate- and temperature-driven [9,41,52]. Other factors, such as natural enemies [35,53] were not considered in this study, mainly due to the lack of data on natural enemies at the landscape scale. In our case, potential solar radiation was shown to be more related to infestation patterns of *I. typographus* than the interpolated meteorological variables' mean or maximum temperature sums. We attribute this finding to the effect of solar radiation on microclimatic conditions, especially bark temperatures, for the beetle development and the attractiveness of trees to bark beetles [34,36,45]. Important to note is the possible inhibitory effect of very high temperatures on bark beetle development. The lower developmental threshold is 8.3 °C, whereas temperatures above 38.9 °C inhibit beetle development [54]. The average temperatures of stems in the study area are reported to be in the range suitable for bark beetle development [55].

It has been assumed that a stressed physiological state of trees leads to outbreaks of phloem-feeding insects, since impaired protein synthesis can lead to increased nitrogen compounds in phloem and the attractiveness of phloem increases. If phloem transport ceases, the plant might die, because carbon cannot be delivered to tissues of infested trees [18,30,56]. Forest decline events are particularly sensitive to temperature [57] and topographic exposure and south- and west-facing trees encounter an enhanced probability of bark beetle damage [58].

Landscape-scale analysis of mountain pine beetle outbreaks showed that bark beetle occurrence is strongly affected by heat [44,59]. Outbreaks of cambium-feeding beetles follow droughts [27] and often become more severe in overmature trees under stress [56]. In the High Tatras, Norway, spruce is a naturally dominant tree species, with examples of old-growth mountain spruce forests in harsh conditions. Our hypothesis offers an explanation for the initiation of beetle infestation spots, which occurred at sites with the highest levels of incoming solar radiation. The association between bark beetle spots and radiation observed here supports the idea that stressed trees may promote the rapid growth of bark beetle populations. Drought is regarded as a main stressor triggering the development of epidemic bark beetle populations [28,60,61]. While we did not directly measure drought indices, we note that higher radiation is usually associated with warmer temperatures, which tend to co-occur with drought.

Topography is a major factor determining the the spatial variability of insolation over the landscape. Variation in elevation, orientation (slope and aspect), and shadows cast by topographic features all affect the amount of insolation received at different locations. This variability also changes with the time of day and the time of year and, in turn, contributes to the variability of the microclimate, including factors such as air and soil temperature regimes, evapotranspiration, snow melt patterns, soil moisture, and light available for photosynthesis. Higher levels of incoming radiation facilitate insect development [54,62].

Using potential solar radiation as one of the factors affecting the occurrence of bark beetle spots offers an alternative to direct measurement of variables on the landscape scale. Forest practitioners and managers are often in situations where they need to decide on future management actions. Although several decision-support systems for bark beetles exist [24,45,63–65], they are often not available in particular countries or require extensive data, programming skills, or software. Calculation of potential solar radiation is widely available in most geographical information systems [66] and can provide a fast method for selecting the most exposed sites for potential future bark beetle infestations on a landscape scale. Solar radiation can easily be integrated with other GIS data and can help model physical and biological processes as they are affected by the sun.

Contrary to the expectation that warmer temperatures would favor bark beetle outbreaks [65], bark beetle spot occurrence was not strongly linked to temperature sums, although we were not able to test the effect of daily temperatures on the emergence (swarming) of beetles. Mean and maximum temperature sums proved to be less connected to bark beetle spots than potential solar radiation. In the analysis of infestation phases and infested vs. noninfested pixels, both meteorological variables reached very small p-values, on the margin of statistical significance ($p < 0.1$). We do not consider these results trivial and we think they should not be dismissed because of their "nonsignificance" [67]. The statistical modeling was based on data on bark beetle infestations from Landsat satellite images, while air temperatures were interpolated for the whole landscape from the available meteorological stations. We think that a p-value slightly above the 0.05 threshold can have biological meaning, which is supported by other studies [68]. An insufficient number of meteorological stations may be one reason for the finding that potential radiation outperformed temperature sums and our previous findings related to the importance of maximum temperature sums [38]. As temperature parameters are biologically viable, they should not be excluded in future research; they just were not among those chosen as the best representatives for describing bark beetle-infested spots in the study area.

Forest naturalness can also play part in the susceptibility of trees to bark beetles [69]. Most of our study area consisted of near-natural forests at higher elevations. Slope class and soil type can be used to assess the susceptibility of trees to bark beetles when meteorological data are not available [70].

5. Conclusions

We found that initiation of beetle infestation spots strongly depends on solar radiation loads, especially during peak and decline phases of beetle outbreak. While previous findings emphasized the importance of climate variables on bark beetle population dynamics, our results highlight the applicability of easily GIS-derived solar radiation maps to predict the incidence of beetle infested trees during the peak and decline phase of *I. typographus* beetle outbreaks. Our simple approach might help forest practitioners identify places with the highest risks of beetle infestations in following years.

Forest managers could use solar radiation information to pro-actively monitor sun-exposed stands or stands adjacent to clear-cuts and edges to improve the efficacy of detection and mitigation to slow down the development of bark beetle outbreaks. A positive response of bark beetle spots to solar radiation at the landscape scale has been clearly demonstrated in this study. The fundamental mechanisms underlying the responses of trees and insects should be fully explored by studying the distribution of radiation in forests and its effect on individual trees by examining the behavioral responses of beetles.

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