ORIGINAL PAPER



Patterns, drivers and detectability of infestation symptoms following attacks by the European spruce bark beetle

Markus Kautz¹ · Felix J. Peter¹ · Laura Harms^{1,2} · Stephan Kammen¹ · Horst Delb¹

Received: 14 September 2021 / Revised: 22 February 2022 / Accepted: 25 February 2022 / Published online: 15 April 2022 © The Author(s) 2022

Abstract

Recent outbreaks of the European spruce bark beetle (Ips typographus) in Norway spruce (Picea abies) forests in Central Europe highlight the importance of timely detection and sanitation of infested trees for pest management efficacy. This study provides novel quantitative evidence on the manifestation of infestation symptoms and their visual detectability, to guide accelerated, optimized terrestrial bark beetle monitoring, as well as establishing benchmarks for potential alternative (e.g. sensor-based) monitoring approaches. We employed bi-weekly, individual tree-level assessments on 85 hectares of sprucedominated unmanaged forest over a 2-year period in south-western Germany (detecting a total of 1,176 infested trees). By applying decision tree-type models, we quantified the predictive power of observed symptoms and their correlation with environmental factors and time. Terrestrial detection accuracy and timeliness were high, suggestive of being sufficient to suppress I. typographus outbreak propagation by subsequent sanitation felling. Among the six studied symptoms, boring dust occurred most frequently (in 82% of correctly detected infestations) and is most suitable for timely detection. Total symptom abundance was best explained by two site parameters (slope, Standardized Precipitation-Evapotranspiration-Index) and I. typographus population density, while it was widely independent of tree parameters and time. Though individual symptoms varied over time and among trees, patterns were clearly identified. For instance, infestations in spring were most critical to be timely detected, while increasing crown discoloration and defoliation facilitated detection in late summer and autumn. Findings further imply that hibernation trees would optimally be detected already in late summer with sanitation felling applied before November.

Keywords *Ips typographus* · Terrestrial monitoring · Precise pest management · Detection rate · Time delay · Hibernation trees

Key messages

• We present novel quantitative evidence on the manifestation of infestation symptoms

Communicated by Andrea Battisti.

Markus Kautz markus.kautz@forst.bwl.de

- ¹ Department of Forest Health Protection, Forest Research Institute Baden-Württemberg, Wonnhaldestr. 4, 79100 Freiburg, Germany
- ² Present Address: Department of Forest Nature Conservation, Forest Research Institute Baden-Württemberg, Wonnhaldestr. 4, 79100 Freiburg, Germany

- Overall accuracy and timeliness of terrestrial symptom detection was high
- Boring dust was the most reliable infestation symptom, frequently observed in July and August
- Symptom abundance was mainly explained by site parameters and population density
- Intensive terrestrial infestation monitoring was revealed crucial for timely management

Introduction

Recent outbreaks of the European spruce bark beetle (*Ips typographus*) led to unprecedented amounts of Norway spruce (*Picea abies*) mortality in forests across Central Europe. Within only three years (2018–2020) almost half a billion cubic metres of infested wood and several million

hectares of damaged forest provoked drastic economic and ecological consequences and fostered a rethinking of bark beetle monitoring and management (Hlásny et al. 2021). Enhanced outbreak intensities and frequencies are expected in future decades due to climate change (Seidl et al. 2017) and limited capacities for timely forest management demands further optimization strategies as well as novel techniques for effective pest management (Bentz et al. 2019; Hlásny et al. 2019).

Early-warning systems based on frequent satellite or aerial data (Senf et al. 2017; Zhan et al. 2020), eventually integrated in high resolution risk models (Hais et al. 2016; Duriačová et al. 2020), are promising tools. However, they are not yet sufficiently robust to be applicable. Major drawbacks include insufficient detection accuracy, difficulties regarding the differentiation between I. typographus infestation and other causes of tree mortality, e.g. immediate drought damage, and the temporal delay with which infestations can be reliably detected by remote-sensing products (Hall et al. 2016; Senf et al. 2017). This delay is assumed to vary by weeks to months, depending on *I. typographus* attack density, month of attack, tree physiology, and environmental factors (Kautz 2014). Alternative monitoring approaches may complement terrestrial surveys at a local scale, including sniffer dogs (Johansson et al. 2019) and UAV-based detection systems (Klouček et al. 2019), but they lack operationability at larger scales.

Hence, a frequently and carefully applied terrestrial tree monitoring regime remains indispensable for timely sanitation of trees infested by *I. typographus*. Following the "search and remove" principles as traditionally practiced across Europe (Gmelin 1787), susceptible spruce stands are surveyed frequently and symptoms of infestation are assessed visually. Early symptoms comprise the presence of entrance holes, resin flow from entrance holes and boring dust that occur when the beetles attack the tree, penetrate the bark, and excavate mating chambers and breeding galleries. Another early symptom is the loss of bark scales $(typically < 0.01m^2)$ due to woodpeckers searching for larvae and pupae under the bark to predate on. Gradual needle discoloration and loss of green or discolored needles as well as more extensive bark loss (patches $> 0.01 \text{ m}^2$) are considered late symptoms indicating an advanced stage of infestation with I. typographus emergence likely having initiated already. Such late symptoms are visible only weeks or months after initial attacks by *I. typographus*: the crown starts degrading when the tree's nutrient supply is disrupted by extended larval galleries, partly associated with fungi, that subsequently diminishes these tree's water supply. In addition, large bark patches may fall down due to woodpeckers and beetle maturation feeding (Fig. 1).

The period between successful attack by the parent generation and emergence of the filial generation ranges between ~ 6-12 weeks, primarily depending on temperature (Wermelinger and Seifert 1998). Climate change-induced increases in temperature will result in generally faster *I. typographus* development (Jacoby et al. 2019), and consequentially shorter periods available for timely detection of infested trees and sanitation. To ensure efficacy of management, all measures including detection, sanitation felling and removal of the stem from the forest or alternative brood-depleting measures should be timely employed (Fettig and Hilszczański

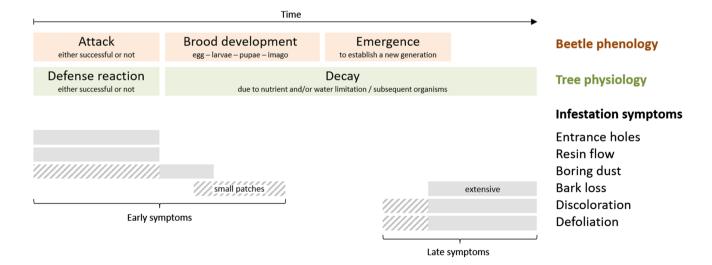


Fig. 1 Conceptual scheme demonstrating the temporal development of *I. typographus* infestation symptoms and its relationship to beetle phenology and tree physiology. Solid grey bars represent typical presence of symptoms; hatched bars represent initial/sparse presence of symptoms. Note that attacks may start at different times and locations

on a tree. Furthermore, symptom presence and progression may vary depending on attack density, tree resistance and temperature. Sanitation is only effective when applied before the emergence of filial beetles 2015), i.e. before the brood starts emerging in order to establish the next beetle generation. Otherwise interventions will prove to be ineffective and a waste of resources.

The management strategy of terrestrial monitoring, sanitation felling, timely removal or brood-depleting of infested trees is considered the backbone of *I. typographus* control measures, mainly preventing subsequent infestations (Stadelmann et al. 2013; Hlásny et al. 2021). However, monitoring is time-consuming and during mass outbreaks management is typically too ineffective to completely stop infestation progress (Stadelmann et al. 2013; Leverkus et al. 2021). The delayed visual signs of infestation within the tree, in combination with insufficient monitoring, sanitation felling and transport capacities often lead to delays exceeding *I. typographus* development period. Moreover, simulation studies have demonstrated that high (> 80%) sanitation rates are required to suppress *I. typographus* outbreak propagation (Fahse and Heurich 2011; Dobor et al. 2020).

Systematic assessments of *I. typographus* infestation symptoms and their development over time are rather scarce. Decision-making in bark beetle management is thus often experience-based due to the absence of empirical evidence. For instance, empirical knowledge is lacking about detection rates, i.e. the portion of infested trees that has been detected (and sanitized) in time. Detection rates are assumed to be highly variable (Hlásny et al. 2019), likely dependent on *I*. typographus population stage, monitoring intensity and quality, as well as on the time of year. Nevertheless, such rates are critical not only for evaluating monitoring and management efficacy, but also to reliably assess the risk of subsequent I. typographus infestation. Ultimately, a better understanding on the spatio-temporal development of infestation symptoms may facilitate the optimization of terrestrial infestation monitoring (i.e. reducing costs while increasing detection efficiency) as well as the development of alternative monitoring approaches. By investigating infestation symptoms comprehensively at the individual tree level in a nature protection area the presented study aims to provide quantitative evidence in order to guide forest practice towards more efficient I. typographus monitoring and management. Specifically, we explored the accuracy and timeliness of terrestrial detection of trees infested by I. typographus, the relevance of single symptoms for a timely detection, the effect of environmental parameters and time of year on its occurrence, as well as the development of symptoms at hibernation trees during autumn and winter.

Material and methods

Study site and data sampling

Field data were collected over two consecutive years in the Black Forest National Park (BFNP; 48.56°N, 8.32°E), a 100 km²-wide protected area in a spruce-dominated mountainous landscape in south-western Germany (Online Resource S1). Due to its protection status since 2014, frequent forest management interventions such as those associated with bark beetle sanitation are prohibited within the core and developing zones. Hence, BFNP facilitates, in contrast to the vast majority of managed European forests, investigation of *I. typographus* dynamics in a large area void of management interventions.

Circular sample plots with a radius of 100 m (= 3.14 ha plot area) were selected and established before swarming onset (April of each study year) according to the following criteria: (a) location within an unmanaged stand primarily consisting of Norway spruce (~80% share) with a mean diameter at breast height > 30 cm, (b) presence of a local beetle source, i.e. a small spot of \leq 20 individual trees currently infested by *I. typographus* (hibernation trees from previous year and/or recently windfelled trees) and (c) absence of large current disturbances (> 20 trees) in a 100 m-buffer outside the plot. In 2018, 15 plots were investigated, and 12 plots in 2019 (from which seven were newly established and five continued from 2018). All plots were 680–870 m a.s.l. (Online Resource S1).

At each plot, every spruce tree was inspected bi-weekly from May to October in 2018 and April-October in 2019. From the practitioner's perspective, our control effort corresponds to a rather intensive monitoring regime, i.e. requiring approximately 20-30 min/ha (except for data recording). Newly infested trees that were detected during these surveys were recorded as 'infested' and infestation symptoms were assessed in detail, such as entrance holes, boring dust, resin flow, bark loss, defoliation or discoloration (Fig. 2; for details see also Online Resource S2). Since infested trees could not be sanitized due to the protective status of BFNP, a verification of brood status within the tree at the time of detection was rendered impossible. Trees classified 'infested' were not inspected continuously during following surveys. Hence, symptom records provide the information on terrestrially visible symptoms at the first instance of detection. To ensure a tree was correctly classified as being successfully 'infested' (i.e. the tree is dying) final assessments were employed at the end of the season in October, as well as in April of the following year (2019, 2020) before emergence of hibernating beetles. The post-season assessment in spring also ensured the detection of trees becoming infested very late in the season and thus not yet showing visual symptoms of infestation in October. Trees classified 'infested' during the bi-weekly surveys, but surviving the attack (i.e. not dying by the subsequent April), were not counted as infested and removed from further analyses of infestation symptoms. Such falsely recorded infestations were considered as a 'false positive' in the accuracy analysis described in Sect. 2.2. Conversely, infested trees that were

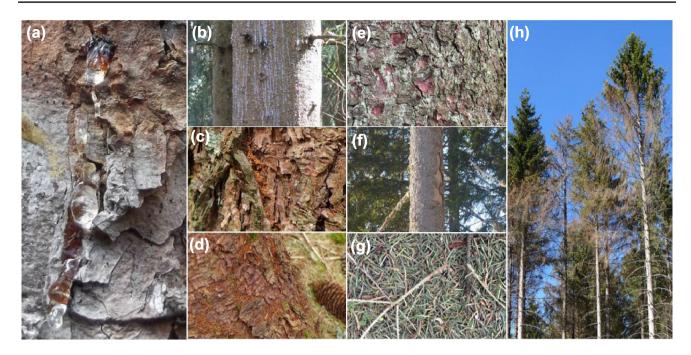


Fig.2 Examples of infestation symptoms: resin flow (a, b), boring dust behind bark sheds (c) or accumulating on the lower bole of the tree (d), and small-scale bark loss (e) indicate an early infestation stage, while extensive bark loss (f), defoliation with green needles

only detected in April of the following year (but not in the year of attack), were considered a 'false negative'.

While the above approach provided information on symptom occurrence at the time of infestation detection, a second analysis addressed the development of hibernation tree symptoms over time. For this reason, a subset of 83 randomly selected trees infested late in the season in 2019 were monitored repeatedly during late autumn and winter 2019/2020. To ensure that brood hibernation within the tree was likely, only trees recorded as newly infested after 15 August 2019 were considered. For hibernation trees, only late symptoms, i.e. bark loss, defoliation and discoloration, were assessed in 20% classes.

Fine-scaled data on plot characteristics were assessed from different sources, such as a digital elevation model, LiDAR-based tree map and climate data (Online Resource S3). Furthermore, *I. typographus* swarming activity around each plot was estimated based on catches recorded weekly in a pair of Theysohn traps baited with Pheroprax® (BASF), which is among the most effective commercially available lures for monitoring *I. typographus* (Šramel et al. 2021). Traps were placed on opposite sides of the plot at a distance of ~ 100 m from the margin of the plot. Due to logistical reasons, traps were installed only by end of April 2018 thereby possibly missing swarming onset that year. In 2019 traps were installed in mid-April (before swarming

found at the bottom (g) and gradual crown discoloration (h) typically occurred delayed at a late infestation stage with beetle emergence likely having initiated already

onset) and collections were terminated by mid-October in both years (after the end of swarming period). Study seasons 2018 and 2019 were characterized by enhanced temperatures, as well as reduced water availability compared to the long-term average (Online Resource S4a, b). This strongly influenced *I. typographus* population density, with local populations exhibiting two-three generations per year (mass outbreak conditions; Online Resource S4c).

Moreover, two reference data sets consisting of timely infestation data from managed forests were gathered to estimate the temporal delay of infestation detection. The first data set covers the buffer zone of BFNP (5,700 ha) in 2018 and 2019, and thus represents a very intense management scenario with weekly to bi-weekly monitoring. In contrast, a second data set comprising 7,000 ha of state forests (available for 2019 only) represents a business-asusual scenario with approximately bi-weekly to monthly monitoring. Both areas are well comparable to the study site as they are located within a relatively short distance (max. 20 km) at 500–1,000 m a.s.l. (Online Resource S1), and exhibit similar stand and site characteristics. For both reference data sets, infested spruce trees were identified during terrestrial monitoring surveys, and the date, location and number of infested trees were recorded on a handheld GPS-based platform.

Data analyses

Detection accuracy

Accuracy performance is displayed by an error (or confusion) matrix representing actual vs. predicted detections of infested trees (e.g. Fawcett 2006). Herein the following instances can be distinguished: True positives are trees that were correctly detected during bi-weekly monitoring surveys, i.e. confirmed dying by final assessments in October or April. False positives are trees that were classified as infested during our surveys, but did not die by the following spring (April). True negatives are trees correctly classified as not infested, i.e. confirmed still healthy in the following spring. False negatives are trees identified infested (dying) only in the following spring but not during bi-weekly surveys in the season of infestation occurrence. Ultimately, we calculated rates referring to these instances, i.e. true positive rate (TPR, = sensitivity), false discovery rate (FDR), true negative rate (TNR, = specificity), and false omission rate (FOR), as well as common total accuracy metrics (ACC, F₁-score; see Online Resource S5 for details).

Modelling

We aimed to answer the following two research questions: (RQ1) Which symptoms are most suitable to detect infested standing trees? and (RQ2) Do symptoms correlate with environmental parameters and/or time of year? For this purpose, we applied two different machine learning algorithms, i.e. boosted regression trees (BRT; Elith et al. 2008) and random forest (RF; Zhou and Qui 2018). Both decision tree-type algorithms are frequently applied in ecology including bark beetle research (Liu et al. 2018; Stereńczak et al. 2020), and we used them here complimentarily as they each hold its

specific advantages and limitations. That is, for instance, a better performance of BRT with unbalanced data (unequal instances for different classes), while RF tends to avoid overfitting. The BRT and RF algorithms were pruned by adjusting the number of nodes of the decision trees (BRT: 3-5, RF: 2-5), for RF the number of decision trees (1,000), and for BRT learning rate (0.01, *n*.trees = 10) and bag fraction (0.5).

Regarding RQ1 we categorized the six infestation symptoms each into three manifestation levels, i.e. absent, sparsely evident and clearly evident (defined in Online Resource S2), to increase model expressive power. Due to the absence of false-positively detected trees in 2018, analysis comprised only 2019 data. To answer RQ2, the initial set of numerous potential predictors (Online Resource S3) was reduced in order to avoid undesired predictor redundancy (Elith et al. 2008). For this purpose, six predictor classes were defined, in which the best performing predictors for each symptom (eight in total) were chosen for the final model by applying backward selection (Tab. 1). This analysis was employed for both study years. Analyses were conducted within the R-Studio environment (RStudio Team 2020), using the packages 'gbm' (Greenwell et al. 2020) and 'randomForest' (Liaw and Wiener 2002).

Results

Infestation occurrence and detection accuracy

A total of 1,265 trees were infested over the 2-year period within our plots (Tab. 2). This translates to an infestation rate of approximately 15% when all spruce trees that could potentially be infested are taken into consideration (≥ 20 cm diameter at breast height). The number of infested trees were four times higher in 2019 compared to 2018. Out of the

 Table 1
 Predictor set used for analyses of infestation occurrence; references refer to infestation predictors only, as references for symptom predictors are lacking. See Online Resource S3 for data sources

Class	Predictor	Description	References
Tree	dbh	Tree diameter at breast height [cm]	Lausch et al. (2011), Blomquist et al. (2018)
	h	Tree height [m], proxy of tree age	Blomquist et al. (2018), Stereńczak et al. (2020)
Stand	h20	Proportion of trees with height ≥ 20 m and < 30 m [%]	Blomquist et al. (2018), Stereńczak et al. (2020)
Site	slope	Slope [°]	Lausch et al. (2011), Sproull et al. (2016)
	SPEI	Standardized Precipitation-Evapotranspiration-Index (Vicente-Serrano et al. 2010) of the month prior to infestation, proxy of tree drought stress	Hart et al. (2017), Senf and Seidl (2018)
Population	рор	Number of currently infested trees within 50 m-distance (weight lin- early decreasing with distance), proxy of actual population density	Lausch et al. (2011), Kärvemo et al. (2014)
Source	dist	Number of previously infested source trees within 50 m-distance (weight exponentially decreasing with distance), proxy of initial population density	Kautz et al. (2011), Økland et al. (2016)
Time	month	Month of infestation detection	Kautz (2014)

Year	Infested standing	Detection accuracy				
	trees	True positive (TPR)	False positive (FDR)	True negative (TNR)	False negative (FOR)	
2018	247	173 (70.0%)	0 (0%)	4,072 * (100%)	74 (1.8%)	
2019	1,018	1,003 (98.5%)	115 (10.3%)	3,393 * (96.7%)	15 (0.4%)	
Total	1,265	1,176 (93.0%)	115 (8.9%)	7,465 * (98.5%)	89 (1.2%)	

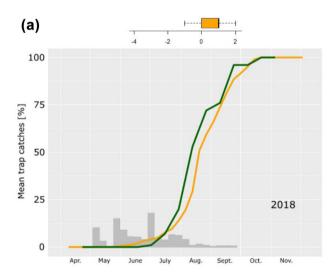
 Table 2
 Error matrix displaying detection accuracy of infested trees; TPR=true positive rate, FDR=false discovery rate, TNR=true negative rate, FOR=false omission rate

*Figure based on LiDAR data, see 'Material and methods'

1,265 infested trees, 93.0% (= TPR) were detected correctly within the same season of infestation occurrence (true positive). The remaining could only be detected in the following spring (false negative, FOR = 1.2%). 115 trees were falsely classified as infested (false positive, FDR = 8.9%), but survived until the following spring. Most false positive trees (93%) were characterized by reduced evidence of symptoms, i.e. showing either none or only a single clearly evident symptom (Online Resource S6a). Total detection accuracy was very high (ACC = 0.98, F₁-score = 0.92), irrespective of the varying infestation levels between study years (ACC $_{2018} = 0.98$, F₁-score $_{2018} = 0.82$; ACC $_{2019} = 0.97$, F₁-score $_{2019}$ = 0.94). Detection rate corresponds to the TPR (93.0%; Tab. 2), when assuming that all correctly detected trees have been detected in time, i.e. before beetle emergence. This rate would slightly reduce to 88.1% when considering any early symptoms only (entrance holes, boring dust, resin flow and/ or sparse, small-scaled bark loss) and would reduce to 75.7% when considering boring dust only. Frequency of infestation detection peaked in late summer in 2018 and 2019, resulting in a typical sigmoidal-shaped curve of cumulative infestation (green line in Fig. 3).

Time-delay of infestation detection

Pheromone-baited trap catches used as a proxy of bark beetle swarming activity totalled 216,243 *I. typographus* in 2018 (i.e. 468 individuals per trap and week) and 436,601 *I. typographus* in 2019 (863 individuals per trap and week). In 2018, 70% of trap catches occurred by early July, but only 1% of infested trees were recorded by early July (green line in Fig. 3a). Nearly all swarming occurred before the mid of August (96% of yearly trap catches). In contrast, almost half of the infested trees were detected after mid-August. In



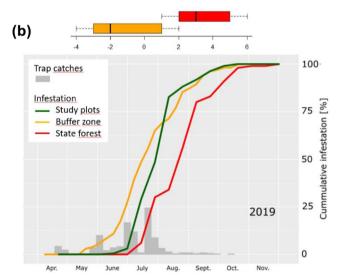


Fig. 3 Cumulative proportion of infested trees (right-handed y-axis) detected in the study (green, $n_{2018}=173$, $n_{2019}=1,003$; bi-weekly recorded), compared to an intensive monitoring regime employed in the buffer zone of BFNP (yellow: $n_{2018}=3,820$, $n_{2019}=4,684$; daily recorded) and to a business-as-usual monitoring regime employed in surrounding state forests (red: n=1,294, only available for 2019; daily recorded) for the years 2018 (**a**) and 2019 (**b**). Horizontal box-

plots show temporal shift in weeks compared to study data (colors according to the line plot; box and whisker based on values at each 10% step of cumulative infestation). As reference, weekly recorded trap catches from our study (mean of 22 traps in 2018 and 2019) are displayed as grey bars (left-handed y-axis; for April 2018 no data available)

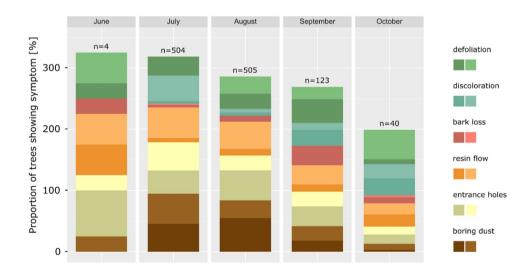
2019, similar patterns were observed: 46% of trap catches occurred by early July while only 5% of infested trees were detected by early July (green line in Fig. 3b). From early August onwards, very few beetles were caught in the traps (8%), but 49% of infested trees were detected after early August. We also observed a delay between intensive and business-as-usual monitoring: while cumulative infestation curves show little difference ($\sim 1-2$ weeks, except for May–June 2019) between both intensive monitoring scenarios (study, BFNP buffer zone), business-as-usual monitoring (state forest) was delayed 2–5 weeks (median=3 weeks) compared to the study (boxplot in Fig. 3b).

Symptom patterns and modelling

The occurrence of different infestation symptoms varied throughout the season (Fig. 4), as well as among individual trees (Online Resource S6). While from June to August early symptoms such as resin flow, entrance holes and boring dust dominated, they were of minor importance later in the season when attack frequency had been reduced and late symptoms became visible (September–October). An individual tree typically showed two or more symptoms, independent of time of season (Fig. 4; Online Resource S6b). Hence, infested trees had a low probability of displaying only one symptom (10.4%, see Online Resource S7). The majority, i.e. 75.4%, of infested trees were recognized by at least one clearly evident symptom. In July, trees showed the highest number of different infestation symptoms (3.4 symptoms in average), and in August the highest number of clearly evident symptoms was recorded (1.6, Fig. 4). The association of symptoms was mainly determined by its categorization into early and late symptoms. For instance, boring dust was typically associated with entrance holes (in 83.1% of its occurrence, and in 67.6% of all infested trees) and bark loss was most often associated with defoliation (in 88.8% of its occurrence; Online Resource S7).

Among all symptoms boring dust contributed most to reducing model error for BRT as well as RF (*RQ1*; Tab. 3). This early-stage symptom is also most frequently occurring (in 81.5% of all correctly detected infestations; Online Resource S7), and thus it can be considered the most reliable symptom characterizing *I. typographus* infested trees. In contrast, bark loss (in BRT) and discoloration (in RF) contributed least to reducing the model error. Overall, ranking of both models agree well, except for the two least-ranked symptoms.

Site parameters (slope, SPEI) and *I. typographus* population density (pop) were best predictors in explaining overall symptom abundance, while individual tree parameters (dbh,



different infestation symptoms in correctly detected infested trees over time in 2018 and 2019 (n = 1,176). Symptoms are differentiated into sparse and clear evidence (light and dark shading, respectively). Values > 100% indicate simultaneously occurring symptoms per average infested tree

Fig. 4 Relative occurrence of

Table 3 Ranking of infestation symptoms regarding model contribution (BRT = boosted regression trees; RF = random forest), suitability for management and visual detectability (+ positive, ○ neutral, – negative). Overall ranking concludes all particular ratings

Symptom	BRT (relative influence)	RF (mean decrease accuracy)	Suitability	Visual detect- ability	Overall ranking
Boring dust	1 (43.4%)	1 (166.0)	++	+	1
Defoliation	2 (26.9%)	2 (80.8)	0	+	2
Entrance holes	3 (16.3%)	3 (68.7)	0	-	3
Resin flow	4 (9.6%)	4 (31.0)	++	-	3
Bark loss	6 (1.4%)	5 (29.0)		++	5
Discoloration	5 (2.5%)	6 (5.3)	0	_	5

h) as well as time (month) were least influential predictors (*RQ2*; Fig. 5). Boring dust mainly occurred in July–August (Fig. 4), under high *I. typographus* population density and at drought-stressed areas with SPEI values below -1 (Online Resource S8). Resin flow correlated with flat terrain. Bark loss and needle discoloration were most abundant in late season (Fig. 4), both associated with low SPEI values and high *I. typographus* population density. In contrast, the amount of defoliation was mainly independent of tree parameters and time.

Development of symptoms in hibernation trees

Hibernation trees experienced a substantial and mostly continuous increase in discoloration, defoliation and bark loss during subsequent autumn and winter months. For example, the percentage of hibernation trees with > 20% discoloration increased from 42% in October to 75% in March (Fig. 6a), while over the same period trees with > 20% defoliation increased from 51 to 84% (Fig. 6b), and trees with > 20% bark loss from 11 to 34% (Fig. 6c).

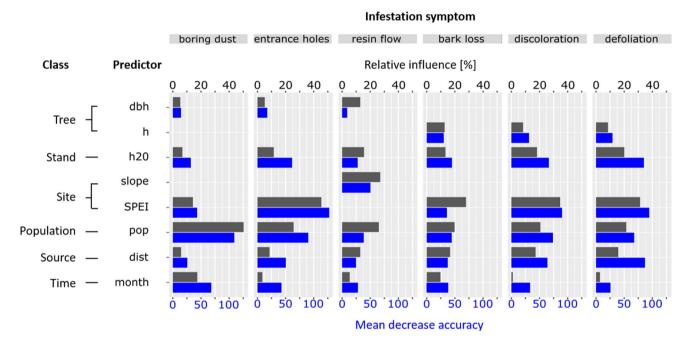


Fig. 5 Predictor importance for symptom occurrence applying boosted regression trees (grey, upper scale; expressed by relative influence) and random forest (blue, lower scale; expressed by mean decrease accuracy)

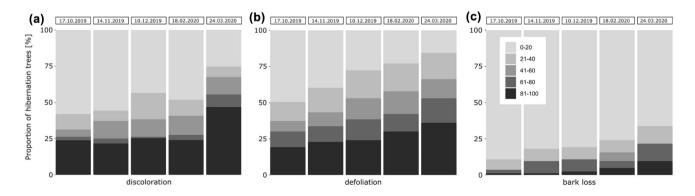


Fig. 6 Development of discoloration (a), defoliation (b) and bark loss (c) in hibernation trees (n=83) from October 2019 to March 2020. Legend indicates the degree (%) of symptom manifestation. Discon-

Discussion

Boring dust was clearly the most reliable symptom for a correct detection of infested standing spruce trees. This symptom was ranked first by both modelling approaches, is highly suitable as early-stage symptom, a specific indicator for recent successful attacks and relatively easily perceptible during terrestrial monitoring (Tab. 3). Three out of four infested trees would have been detected correctly, and very likely also timely, by looking only for this single symptom. The importance of boring dust can be assumed to decrease when less intense monitoring would be applied, because of an increased likelihood of disappearance due to rain or wind. In contrast to boring dust, entrance holes are small and thus hard to detect visually, partial defoliation or discoloration might occur also independently from bark beetles, e.g. triggered by drought, and resin flow might indicate unsuccessful attacks or tree decay due to other reasons. Unfortunately, none of the early-stage infestation symptoms can be detected reliably by current sensor-based approaches. Remotely detectable symptoms (defoliation, discoloration) as well as extensive, well perceptible bark loss are in turn less suitable indicators due to its late-stage appearance (Fig. 1). Often the next bark beetle generation has already emerged at this point in time, so that recognition of these symptoms will likely not enable timely sanitation. A delayed detection may then only serve to support locating undiscovered previous breeding sites by applying terrestrial monitoring in their vicinity in order to detect recent infestations (Kautz et al. 2011). An overall advantage of terrestrial monitoring over alternatives (e.g. sensor-based approaches) is its integration of the whole range of infestation symptoms appearing at the tree's bottom, stem and crown. Except for boring dust and entrance holes, detection rate significantly decreases when considering only one or two symptoms instead of six (Fig. 4, Online Resource S7).

Although we focussed on terrestrial surveys in our study, findings also suggest a substantially reduced potential for crown-based early-detection approaches such as through satellite or aerial imagery. For instance, only 40% of infested trees showed visual crown degradation (i.e. sparse or clear evidence of discoloration and/or defoliation) at the time of detection. This amount is likely to have been overestimated, as defoliation has been assessed relatively to a completely closed crown and without referring to a pre-infestation stage which might have been degraded already (Huo et al. 2021). Relative importance of crown symptoms showed an increasing trend towards the end of the season, hence suggesting higher potential of crown-based approaches for detecting hibernation trees. This finding is consistent with data from recent satellite-based approaches that prove accurate detections of current-year infestations are hardly possible before autumn (MODIS/ RapidEye: Latifi et al. 2018; Sentinel 1/2: Bárta et al. 2021; Huo et al. 2021). High resolution UAV- and airborne-based systems may detect infested trees earlier than satellite-based approaches, nonetheless, they also show a substantial delay regarding terrestrial detectability (Bárta et al. 2022). While remote sensing approaches comprise optical and radar systems facilitating detection of infested trees beyond the visible range (e.g. subtle decreases in chlorophyll and water content of the needles), terrestrial monitoring may be more advantageous for detecting early crown discoloration which typically begins in the lower crown and progresses to the tree top (Bárta et al. 2021). Noteworthy in this context is also that the remotely sensed detection of 'green-attacked trees' (e.g. Abdullah et al. 2019) doesn't necessarily correspond to an earlyattack stage regarding the brood development within the tree (Fig. 1). Hence, although being classified as 'greenattacked trees', such trees are likely in a late-attack stage and thus less conducive to sanitation (i.e. emergence of the next generation has already likely occurred).

Intensive terrestrial monitoring for infested trees should be applied in Central Europe in June-October with areas in lower and warmer regions initiated in May. Highest efficacy can be achieved in July–September, as boring dust is most obvious during this time (Fig. 4). Interestingly, infestations caused by hibernating beetles in the spring were less frequently observed than later in the season (Fig. 3). This might be due to lower attack densities, and/or the limited detectability of infestations in spring. Possible reasons for the first theory are that spring swarming occurs more scattered due to different hibernation sites (trees and soil litter; Dworschak et al. 2014) and shorter periods of suitable weather for swarming. In addition, trees are more resistant to I. typographus infestation in spring due to a reduced likelihood of drought stress (Netherer et al. 2015). In combination, this might result in reduced success of attacks and increased dispersal mortality. A limited detectability in spring is likely caused by the absence of crown discoloration due to tree's sufficient water supply and by the reduced amount of boring dust in spring (Fig. 4). The latter suggests a reduced colonization density, which in turn might also be consequence of a more scattered swarming and of noticeable overwintering mortality (Faccoli 2002). Timely detection of infested trees would nevertheless be most beneficial during spring and early summer, as the population may grow exponentially exhibiting two or even three generations within a season.

Since *I. typographus* monitoring and management is typically constrained by limited personnel and logistic capacities during summer, the extension of such measures into autumn and winter months provides an opportunity to (at

least partly) keep pace with an ongoing outbreak. Furthermore, winter management may have reduced negative effects on antagonists (Wermelinger et al. 2012). Managing hibernation trees is most important in regions where I. typographus populations predominately hibernate in trees, i.e. in regions with bi- or multivoltine populations (Dworschak et al. 2014). Our results suggest that monitoring of hibernation trees would be most efficient from August to mid-September as beetles are still establishing broods and are thereby producing boring dust (Fig. 4). Later in the season there is a trade-off between increased detectability by latestage symptoms (discoloration and defoliation) and reducing efficacy by enhanced bark loss. The drop of bark patches leads to a passive transfer of hibernating *I. typographus* to the soil litter (Dworschak et al. 2014), thereby reducing the amount of *I. typographus* removed by sanitation felling. Consequently, sanitation felling should preferably be done soon in autumn (before November), before bark will get loose and drop either passively or during sanitation felling.

Detection accuracy of infested trees was very high in our study. However, accuracy metrics only consider detection within the season of infestation occurrence, but not timeliness regarding beetle emergence. For this reason, accuracy might be overestimated as we cannot prove that beetles had not already emerged from correctly detected infested trees during the season (affecting TPR), or underestimated as hibernation trees omitted during the late season, but detected in April of the following year, could still be sanitized prior to beetle emergence (affecting FNR). An accurate quantification of the delay between occurrence of successful attacks and detection of an infestation during our study is hindered by the unknown timing of attack. Nevertheless, our results suggest that by applying an intensive bi-weekly monitoring sanitation efficiency would be sufficient (> 80%; Fahse and Heurich 2011; Dobor et al. 2020) to widely suppress the spread of infestations. The less frequent the monitoring is carried out, the more delayed the detection of infested trees, and consequently the lower the sanitation rate and the management success.

An increased management efficiency, that is indispensable in light of climate change-induced higher outbreak frequency and intensity (Seidl et al. 2017), would require an intensified effort in terrestrial monitoring as the crucial first step. Sniffer dogs trained to detect boring dust may prove to be supportive during monitoring surveys (Johansson et al. 2019), particularly in environments featuring rough or steep terrain. Complementary to this, dynamic maps quantifying the infestation risk, or displaying previously occurred infestations, may optimize the use of limited survey resources in space and time. An improved infestation detection should be accompanied by further measures to accelerate the subsequent management process chain, including app-based information systems and strengthened infrastructure and resources (personnel, transport, storage, markets). In the long term, large parts of Central European spruce forests will ultimately require conversion in order to reduce disturbance risk and increase resilience. This can be achieved, for example, by diversifying tree species and age classes, reducing rotation periods and locally replacing spruce by more climate-adapted tree species (Hlásny et al. 2019; Fettig et al. 2022).

To summarize, this study provides novel evidence on patterns and drivers associated with the detectability of *I. typographus* infestations, thereby elucidating the potential and limitations for their monitoring and management. We consider the obtained findings and derived implications to be representative for most spruce-dominated regions of Central Europe. However, given the lack of similar studies, we encourage further investigation. Future studies should optimally include a verification of the brood status within the tree (development stage, proportion of beetles emerged) at the time of detection to better evaluate timeliness. Moreover, alternative monitoring approaches (e.g. satellite-, airborneand UAV-based) need to be measured against the benchmarks for terrestrial monitoring, as this would facilitate evaluating their future potential.

Authors contributions

MK and HD conceived and designed the research. MK, FJP, LH and SK recorded data and employed the analyses. MK wrote the first draft of the manuscript. All authors contributed to revisions and approved the final manuscript.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10340-022-01490-8.

Acknowledgements The authors acknowledge the BFNP administration for their kind permission to employ research activities within the National Park, and the BFNP administration as well as ForstBW for providing infestation data from managed forests. We would also like to thank Jan Wußler for photo courtesy (Figure 2a), and Christopher J. Fettig for proofreading the manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL. The study was funded by the German Federal Ministry of Food and Agriculture (FNR-FKZ: 22000516).

Availability of data and material The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interest to disclose.

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