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Verbenone (SPLAT® Verb) delays *Ips typographus* (L.) infestation and reduces infestation risk and severity in windthrown Norway spruce in Southwest Germany

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ABSTRACT

Outbreaks of European spruce bark beetle, *Ips typographus*, often follow storms, and can result in losses of Norway spruce, *Picea abies*, that largely exceed those caused by storms alone. Management actions to reduce *P. abies* losses attributed to *I. typographus* mainly consist of salvage and sanitation logging of windthrown *P. abies*, which are sometimes limited by logistic capacities and constraints. Recent outbreaks across Europe have destroyed large areas of *P. abies* forests, and are expected to further intensify as a consequence of climate change, so that additional tools are needed for integrated bark beetle management. In a 4-yr study, we applied (–)-verbenone (SPLAT® Verb, ISCA Inc., Riverside, CA, U.S.), a common bark-beetle inhibitor, to natural and artificially generated windthrows of *P. abies* (5–6 trees) to examine its efficacy for reducing infestation by *I. typographus* in spring. In two of four years, SPLAT® Verb caused delay of infestation of ~3 wks, which may provide a relevant gain of time for logging operations. Infestation probability and density were reduced by up to 78% and 76%, respectively. Treatment effectivity increased with dose per volume of windthrown *P. abies* and seemed to decrease with greater infestation pressure. Elevated concentrations of verbenone in the active airspace of forests could only be detected in close proximity (<50 cm) of SPLAT® Verb application points (dollops). We propose a decision pathway for management of windthrown *P. abies* that includes verbenone as an environmentally friendly tool within the integrated management of *I. typographus* in Central Europe.

1. Introduction

Bark beetles (Curculionidae: Scolytinae) are the most harmful group of forest pests in Europe (Wermelinger, 2021) of which European spruce bark beetle, *Ips typographus* L., causes by far the largest amount of tree mortality (Gregoiré and Evans, 2004). Its primary host is Norway spruce, *Picea abies* (L.) H. Karst., which accounts for more than a quarter of the current growing stock in Europe (Hlásny et al. 2021). In recent years, notable outbreaks of *I. typographus* have occurred in central Europe and future outbreaks are projected to intensify in coming decades due to warming and drought (Biedermann et al. 2019; Seidl et al. 2014), likely compromising the ability of forest managers to mitigate the negative effects of *I. typographus* in some forests (Dobor et al., 2020; Fettig, 2022).

Like most aggressive bark beetles, *I. typographus* deploys aggregation pheromones in addition to cues originating from host and non-host trees to find suitable hosts (Borden, 1997; Lehmanski et al. 2023). Male *I. typographus* initiate host colonization and emit an aggregation pheromone consisting of *cis*-verbenol, 2-methyl-3-buten-2-ol, as well as specific concentrations of ipsdienol (Bakke, 1976; Bakke et al. 1977; Vité and Francke, 1985). Attraction to the host tree is synergized by host volatiles (Erbilgin et al. 2007). During outbreaks the gregarious behaviour allows *I. typographus* to mass attack standing host trees overcoming their defences (Raffa, 2001).

Ips typographus outbreaks alternate with phases of low population abundance in cycles of several years or decades (Hlásny et al. 2021;

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Weed et al. 2015). Outbreaks are typically facilitated by sudden changes in abiotic conditions favourable to *I. typographus*, offering a surplus of suitable breeding habitats (Dobor et al. 2020; Marini et al. 2017; Thalenhorst, 1958). Besides snow breakage (Wermelinger, 2004), storms are the most important driver of outbreaks as they often produce large numbers of windthrown *P. abies* (e.g., Inouye, 1962; Komonen et al. 2011; Potterf et al. 2019; Ravn, 1985; Stadelmann et al. 2013; Wichmann and Ravn, 2001). These easily colonisable trees of weakened defences allow *I. typographus* to reproduce at comparatively low colonisation densities, thus enhancing their productivity (Komonen et al. 2011). If windthrown *P. abies* remain on site, colonization and reproduction can occur several months up to two years after the storm event, depending on prevailing climatic conditions (Göthlin et al. 2000; Louis et al. 2014). Drought facilitates further population growth if surrounding live *P. abies* areas are stressed to levels so that they are still attractive and more easily overwhelmed by *I. typographus* (Netherer et al. 2015; Marini et al. 2017).

In the case of windthrown *P. abies*, management tactics consist of removing windthrown trees prior to colonization by *I. typographus* (salvage logging) and removing infested windthrown trees before the next *I. typographus* generation emerges (sanitation logging) (Fettig and Hilszczański, 2015; Wermelinger, 2004). In practice, this can be challenging because there is usually little time to implement these measures, and technical as well as logistic capacities are often limited (Stadelmann et al. 2013). This is particularly the case at lower elevations (ca. <800 m) or latitudes where *I. typographus* may complete up to 3 generations yr^{-1} (i.e., development is faster due to warmer temperatures in these areas; Baier et al. (2007); Kogler and Rauch (2023)), in steep or difficult terrain (Deganutti et al. 2023), and in the case of large numbers of windthrown *P. abies* which are often distributed in small patches over extensive areas. Under these conditions, salvage and sanitation logging is difficult to achieve and requires prioritization of treating some areas over others (Deganutti et al. 2023; Dobor et al. 2020), thus leaving groups of windthrown *P. abies* susceptible to colonization by *I. typographus*. Furthermore, salvage and sanitation logging may not be permissible in protected areas (Hlásny et al. 2021). Within integrated bark beetle management (Sweeney et al. 2023), it would therefore be desirable to possess an environmentally friendly tool to reduce the risk of infestation of windthrown *P. abies* in addition to salvage and sanitation logging (Fettig, 2022; Fettig and Hilszczański, 2015) and thus reduce, or at least delay, the risk of transition from low to outbreak population levels of *I. typographus*.

Verbenone (4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one) is an aggregation inhibitor of many bark beetle species (Frühbrodt et al. 2024). It naturally occurs in and around colonizing *I. typographus* (Birgersson and Bergström, 1989; Birgersson et al. 1984; Frühbrodt et al. 2023; Leufvén and Birgersson, 1987) and is synthesized from the aggregation pheromone component *cis*-verbenol, primarily by associated microorganisms (Hunt and Borden, 1990; Leufvén et al. 1984). Verbenone has been shown to reduce attraction of *I. typographus* to baited traps (Bakke, 1981; Niemeyer et al. 1995; Schlyter et al. 1989; Vité and Baader, 1990; Zhang, 2003), stored logs (Bakke, 1987; Schlyter et al. 1988), and live, standing *P. abies* (Jakuš et al. 2003; Vité and Baader, 1990). Several verbenone-based products are registered for use in North America to reduce infestation of live, standing conifers from several species of bark beetles, primarily *Dendroctonus* spp. (Seybold et al. 2018).

We conducted a 4-yr study to examine the potential of verbenone for protecting small patches of windthrown *P. abies* (5–6 trees) from colonization by *I. typographus*. We used verbenone in the formulation SPLAT® Verb (10.0% (–)-verbenone by weight; EPA Reg. No. 80286−20, ISCA Inc., Riverside, California, U.S.) which has been repeatedly shown to prevent mass attacks of *Pinus* spp. by mountain pine beetle, *Dendroctonus ponderosae* Hopkins, in western North America (Fettig, 2016; Fettig et al., 2015, 2020; Progar, 2021), as well as those of other bark beetle pests in forests and agricultural systems (Audley et al., 2020; Byers et al., 2021; Hughes et al., 2017; Mafra-Neto, 2022). Rather than a single release device (e.g., pouches), SPLAT® Verb is a flowable emulsion that allows the user to adjust the size of each application point (i.e., deployed with a caulking gun and hereafter referred to as "dollop") according to desired distributions in the field. Our objectives were to determine i) whether applications of SPLAT® Verb affect the onset of *I. typographus* infestation, in so far as verbenone ii) reduces the probability, as well as iii) the intensity of infestation, and whether iv) this ultimately affects reproduction of *I. typographus*. We also conducted volatile sampling to track the release and distribution of verbenone in the active airspace of forests and discuss spatial dimensions regarding the release distribution of verbenone from SPLAT® Verb when attempting to protect a small area of windthrown *P. abies* from colonization by *I. typographus*.

2. Material and methods

Four field experiments were conducted in the southern Black Forest (Southwest Germany, elevation: 800–1,000 m above sea level [a.s.l.]) during 2020–2023 comprising a pilot study following a natural windthrow event in 2020 and three simulated windthrows in 2021, 2022, and 2023 (Table 1). During each year, 6–9 groups of 4–6 *P. abies* were either treated with SPLAT® Verb or left as untreated positive controls (see 2.1–2.4). The release rate of verbenone from SPLAT® Verb as determined from active headspace sampling under standardized conditions in the laboratory at 22°C was 27 ± 6.2 μg d^{-1} cm^{-1} from a 1.2 cm thick dollop, which corresponds to ~1.3 ± 0.28 mg d^{-1} for the 75 g applications in our experiments (see 2.3–2.4). However, under field conditions with larger temperature fluctuations and wind, the release rate from 17.5 g dollops (i.e., 0.25X the full dose) determined from direct extraction from previously exposed dollops was 28.6 mg d^{-1} (14.7 – 56.0 mg d^{-1}) during a 30-d period (Fettig et al. 2015). Subsequent infestation of windthrown *P. abies* by *I. typographus* was recorded weekly, and the established gallery systems were analysed at the end of each experiment (see 2.5).

At least one weather station was installed near each study site (<1 km; ADL-MX, Mayer-NT, Zwönitz, Germany) to record wind speed and direction, precipitation, relative air humidity, and temperature in 5-min intervals. Mean temperatures during the experiments were 10, 11, 12, and 11 °C in 2020–2023, respectively. Precipitation amounted to 70, 381, 203, and 114 mm, respectively. Mean annual temperature at a nearby weather station (Lenzkirch-Ruhbühl, Germany; 854 m a.s.l.; 47°51'34.9" N, 8°13'50.7" E; period: 1981–2010) was 7 °C, with mean annual precipitation of 1306 mm (data from Deutscher Wetterdienst, online at opendata.dwd.de, last accessed 5 January 2024).

2.1. 2020 pilot study

In 2020 seven groups of 4–6 adjacent and naturally windthrown *P. abies* (dbh: 38 ± 8 cm; following storm "Sabine", 9–11 February 2020) were defined as study plots near Berau, Germany (5 plots = windthrows, ~800 m a.s.l.) and Bernau, Germany (2 plots; ~900 m a.s.l.) with ≥60 m between plots (Table 1). All windthrown trees had root contact with the soil and had green crowns when the experiment was initiated. The forest in Berau was a 25-ha isolated stand dominated by young (~60-year-old) *P. abies*, intermixed with silver fir (*Abies alba* Mill.), beech (*Fagus sylvatica* L.), and oak (*Quercus* spp.; Table 1). Windthrows occurred along the edges of stands of relatively open structure. The forest in Bernau was dominated by (~90-year-old) *P. abies*, with a low proportion of *A. alba*. Windthrows occurred in the interior of the forest. SPLAT® Verb (Batch #2458907) was applied to the stem of windthrown *P. abies* in four of the plots, while remaining plots served as untreated controls. Within a pair of two adjacent plots, treatments were assigned randomly. In treatment plots, each tree received four ~20 g dollops of SPLAT® Verb apically and as evenly spaced as possible along the stem. Some *I. typographus* had already swarmed prior to initiation of the experiment on 11–13 April 2020. However, all windthrown trees were thoroughly checked for

Table 1
Site characteristics, study plots, and SPLAT® Verb applications for each experiment in Southwest Germany.

Year and study design	Number of plots (treated: untreated control)	Stand characteristic	Coordinates	Amount of SPLAT® Verb (verbenone: 10%)	Application mode	Local *I. typographus* population according to infestation pressure
2020, "Pilot study" on natural windthrows	4:3	74–87% *Picea abies* (~ 60–90 years old), 6–21% *Abies alba*, 5–6% *Fagus sylvatica*	47°42'22.7"N 8°15'02.9"E; 47°46'20.5"N 8°04'26.7"E	4 × ~20 g tree^{-1} equidistant throughout tree length	directly to stem	high
2021, trees were pulled down with mechanical winch	3:3	80% *Picea abies* (~ 70 years old), 13% *Abies alba*, <5% *Fagus sylvatica*, *Pinus sylvestris*; some plots had few surrounding standing trees left due to intensive bark beetle damage and sanitation logging in the adjacent stand	47°44'23.1"N 8°16'28.7"E	4 × ~20 g tree^{-1}, every 4 m; 7.1 ± 0.7 kg ha^{-1}	directly to stem	intermediate
2022, trees were pulled down with mechanical winch	4:4(:1)*	as in 2021	47°44'23.1"N 8°16'28.7"E	4–6 × 75 g plot^{-1} *1 plot: 4 × 20 g tree^{-1}; 7.0 ± 2.2 kg ha^{-1}	on wooden poles in 15 × 15 m grid; *1 plot directly to stem	low
2023, trees were pulled down with mechanical winch	4:5	78–90% *Picea abies* (~ 90–100 years old), 6–16% *Abies alba*, <5% *Pinus sylvestris*, *Fagus sylvatica*	47°48'11.5"N 8°15'28.2"E; 47°48'50.2"N 8°11'43.9"E	4–6 × 75 g plot^{-1}; 4.5 ± 0.4 kg ha^{-1}	on wooden poles in 15 × 15 m grid	high

I. typographus infestation, and no signs of infestation were observed before the application of SPLAT® Verb. Two plots and one additional *P. abies* from another plot were accidently removed by forest workers before the end of the experiment.

2.2. 2021 study

In 2021, six groups of 5–6 *P. abies* (diameter at half tree length: 22 ± 4 cm) were pulled to the forest floor (hereafter "down") by a mechanical winch (8 April 2021) assuring that they maintained root contact and with caution to minimize bark damage. These trees (hereafter "windthrown") were situated at the edge or inside (wherever small groups of trees remained) a clear cut resulting from previous *I. typographus* infestation near Buggenried, Germany (~800 m a.s.l.; Table 1) and neighbouring ~70-year-old *P. abies* forest (~80% *P. abies*, Table 1). Plots were ≥50 m apart. On 14 April 2021, before initiation of *I. typographus* flight for this year, the stems of half of the plots were treated with four ~20 g dollops of SPLAT® Verb (Batch #2459270) each. SPLAT® Verb was reapplied on 1 June 2021. In both cases, the first dollop was placed at 2.6 m from the stem base of each windthrown *P. abies* with remaining dollops placed every 4 m along the stem. The three remaining plots served as untreated controls.

2.3. 2022 study

In 2022, nine groups of *P. abies* (dbh: 31 ± 5 cm) were pulled down by a mechanical winch (17 March 2022) at the same site used in 2021 near Buggenried, Germany. Plots were ≥50 m apart. In three of the plots, the smallest possible 15 ×15-m grid was established inside each plot, starting with four grid points. More grid points were added only when parts of a tree were >7.5 m away from the initial four grid points. This resulted in 4–6 grid points plot^{-1}. A wooden pole was installed at each grid point with a 20-cm horizontal bar screwed to the pole ~1.6 m above the ground at which 75 g of SPLAT® Verb (Batch #2458907) were deployed on 26 March 2022. Deployment of SPLAT® Verb occurred shortly after initial captures of *I. typographus* were detected in pheromone-baited monitoring traps placed at lower elevation. SPLAT® Verb was reapplied on 2 May 2022. A small horizontal board was attached ~20 cm above the SPLAT® Verb for rain protection. Another plot was treated with SPLAT® Verb using methods employed in 2021 (see 2.2.) while the four remaining plots served as untreated controls.

2.4. 2023 study

In 2023, a total of nine groups of *P. abies* (dbh: 40 ± 4 cm) were pulled down by a mechanical winch (5 April 2023) in two *P. abies*-dominated stands (Table 1; Faulenfürst, Germany: ~1000 m a.s.l.; Rothaus, Germany: ~1,000 m a.s.l.). Plots were ≥50 m apart. SPLAT® Verb was deployed on 18 April 2023 using the same methods as in 2022 (see 2.3).

2.5. Weekly infestation monitoring of bark sampling windows and assessment of I. typographus galleries

Ips typographus infestation over time and at the end of the experiments was assessed based on 20 × 20-cm bark sampling windows (hereafter "sampling windows") that were defined at regular intervals apically on the stem of each windthrown tree (Komonen et al. 2011). In 2020, all stems received 6 sampling windows, equidistantly distributed within the range starting at ~0.5–1 m from the stem base until reaching a stem diameter of <0.20 m. In 2021–2023 all stems received 4–6 sampling windows positioned every 4 m starting at 0.6 m from the stem base until reaching a stem diameter of ≤0.18 m. All experimental trees were checked weekly for signs of infestation (i.e., boring dust, entrance holes, sites with resin) by *I. typographus* and other bark beetle species (only *Pityogenes chalcographus* occurred; differentiation made according to entrance hole size and amount of boring dust). Sampling intervals were adapted as necessary to avoid sampling on days with high precipitation (boring dust is washed away, and visibility on bark surfaces is poor). In 2020 and 2021 all signs of *I. typographus* infestation were counted cumulatively every week (e.g., an entrance hole that appeared in the first week was counted anew in all subsequent samples) while in 2022–2023 signs of *I. typographus* infestation were permanently marked with acrylic paint (boesner ACRYL STUDIO, boesner, Witten, Germany), and only signs that had not been recorded previously were counted in subsequent samples. The exact position (precision: 2–5 cm) of each sampling window in 2021–2023 was recorded with a GNSS device (Geomax Zenith 35Pro, Gottlieb Nestle GmbH, Dornstetten, Germany). Aerial images were obtained via drone (flight height: ~90 m) to verify the correct location of GPS-points and to measure the plot area in QGIS (version 3.12.2-București).

Experiments were concluded shortly after (2020) or before (2021–2023) the next generation of *I. typographus* started to emerge from windthrown trees (28–29 May 2020, 1–2 July 2021, 21 June 2022,

13–14 June 2023). Sampling windows were cut from the trees with a 1–2 cm buffer and stacked into a wooden press for transportation to the laboratory and subsequent storage at −4°C. In the laboratory, the sampling windows were digitalized (scan or photograph) and analysed via ImageJ (Rasband, 1997), and by marking signs of infestations on the original sample with pins. For each sampling window, the number of male nuptial chambers, female galleries, and pupal chambers was recorded. Female galleries were counted separately depending on whether they connected to a nuptial chamber inside a given sampling window or whether they loosely reached inside the window. Sex ratio was determined by dividing the number of connected maternal galleries per window by the number of nuptial chambers in the same window.

2.6. Volatile sampling

2.6.1. Vertical and horizontal distribution of verbenone, 2021

Air concentrations of verbenone were determined in a forest stand near Faulenfürst, Germany (as in 2.4). For this purpose, a 12-m high tower was installed in proximity to 75 g of SPLAT® Verb which was applied as described in 2.3 and 2.4. Air samples were collected at different distances vertically and horizontally, i.e., at 0.25, 0.5, 1, 2, 3, 6, and 12 m above the SPLAT® Verb dollop to determine the vertical distribution, and at 0.25, 0.5, 1, 2, 3, 4, 7, 10, and 14 m from the SPLAT® Verb dollop (1.6 m above ground level) to determine the horizontal distribution. A sample was also collected directly at the SPLAT® Verb dollop. Sampling was conducted between 23 July–26 August 2021 with air sampling pumps (220–1000 TC, PocketPump, SKC Inc. PA 15330, USA) connected to glass sampling tubes (Gerstel, Mülheim a.d.R., Germany) filled with Tenax (Sigma Aldrich, Munich, Germany) as an adsorbent. The flow rate was adjusted to 200 mL min^{-1} and sampling occurred for 5 h (10:00–15:00 CEST), hence, in total 60 L of ambient air passed through each adsorber. The glass tubes were transported to the laboratory and stored at 4 °C until analyzed by gas chromatography–mass spectrometry (GC-MS) to determine verbenone concentrations (see 2.6.4.).

2.6.2. Verbenone abundance near the source, at SPLAT® Verb-treated trees, and at untreated control trees in 2021

Verbenone abundance within plots were determined on 7 days (2, 15–18, 24–25 June 2021) with self-made passive samplers at different distances from the SPLAT® Verb applied to each tree. Each passive sampler consists of four pieces of 1-cm long polydimethylsiloxane (PDMS) tubing (Carl Roth GmbH Co. KG, Karlsruhe, Germany; internal and external diameters 1.0 and 1.8 mm, respectively). The PDMS pieces were cleaned in acetonitrile: methanol solution (4:1, v/v) for 8 h before being heated to 230 °C for 12 h under constant nitrogen flow (Kallenbach et al. 2014) and then deployed in the field at 12:00 CEST. Five passive samplers were stapled evenly on a string between the third and fourth sampling window (1 m distance, ~2 cm above the stem). The central sampler was placed directly above the SPLAT® Verb dollop between the two sampling windows. Verbenone was simultaneously measured at three positions (2 m distance between) on two trees in one untreated control plot. The PDMS pieces of each loop were harvested about 12:00 CEST the following day (i.e., 24-h exposure time), sealed immediately in a glass vial (Agilent Technologies, Böblingen, Germany), and stored at −20°C until GC-MS analysis (see 2.6.4.).

2.6.3. Verbenone abundance near the source, at SPLAT® Verb-treated trees, and at untreated control trees in 2022

Verbenone abundances at each SPLAT® Verb dollop as well as at the sampling windows of each windthrown tree were determined as described in 2.6.2. One passive sampler was placed directly above (~2 cm high) the dollop at each pole and ~2 cm above each sampling windows, respectively (see 2.5). Passive samplers were also installed near the first sampling window per tree on 1–2 untreated control plots per sampling day. Sampling was conducted on 12 May, and 19–20 May 2022 with an exposure time of 24 h, respectively. The passive samplers were harvested on the next day, sealed immediately in glass vials (Agilent Technologies), and stored at −20°C until GC-MS analysis (see 2.6.4.).

2.6.4. Verbenone analysis

For GC-MS analyses the PDMS pieces were transferred into thermodesorption tubes (Gerstel). The PDMS (see 2.6.2, 2.6.3) and Tenax (see 2.6.1) samples were analysed on a gas chromatograph (GC, model 7890, Agilent, Santa Clara, California, U.S.) connected to a mass-selective detector (MSD, 5975 C, Agilent) and equipped with a thermodesorption/cold injection system (TDU-CIS4, Gerstel, Mülheim an der Ruhr, Germany). The mass-selective detector was run in SIM mode detecting *m/z* 55, 67, 77, 79, 93, 107, 109, 121, 122, 134, 135, 136, 150, and 152 with GC-MS conditions described previously (Byron et al. 2022; Frühbrodt et al. 2023). Briefly, volatiles were released from the PDMS/Tenax adsorbent by heating them up to 220°C in the TDU. Thermodesorbed volatiles were directly channelled into the CIS4 where they were cryotrapped at −40°C. The CIS4 was then heated to 240°C, releasing the volatiles onto the separation column (DB-5 ms UI, 60 m × 0.25 mm × 0.25 µm film thickness, Agilent). Helium was used as a carrier gas at a flow of 1 mL min^{-1}. The MSD ran at 70 eV at an ion source temperature of 230°C and a quadrupole temperature of 150°C. For the data analysis the MassHunter Software (Version B.07.00, Agilent) was used. Verbenone was identified and quantified (in ng d^{-1} for PDMS samples) according to a standard of ((1 *S*)-(−)-verbenone, > 94%) (Sigma-Aldrich, Munich, Germany) analysed in the same manner. For the vertical and horizontal distribution experiment (see 2.6.1), verbenone concentration was expressed in ng L^{-1} air.

2.7. Statistical analyses

Data storage and initial data preparation was done in MS Excel (Microsoft Corporation 2016). All subsequent data analyses were done in R (version 4.1.3, R Core Team, 2018) using R studio (RStudio Team, 2022). Infestation of sampling windows was expressed as a binary response (infestation: y/n), and as the actual count (separate analysis for the number of established nuptial chambers, maternal galleries, and pupal chambers, respectively). Generalized linear mixed models (GLMM) were fitted assuming a binomial distribution ('infestation probability') or poisson, negative-binomial or tweedy - depending on the dispersion - for modelling the number of nuptial chambers, and of pupal chambers per sampling window (Bolker et al. 2009; glmmTMB: Brooks et al. 2017). The treatment effect on the sex ratio was analysed with linear mixed models (LMM) (lme4: Bates et al. 2015; lmerTest: Kuznetsova et al. 2017). Structural parameters inherent to the experimental design (plot, tree ID nested therein, as well as sampling window ID, and date for measurements repeated over time) were included as random effects. Treatment, time ("day after start of experiment" as a continuous variable) and other relevant predictors (infestation with *P. chalcographus*, tree diameter and/or bark structure, and position of the sampling window) were included as fixed effects. Model diagnostic was performed using the DHARMa-package (Hartig, 2022). Models were built by first defining the random effect structure according to the experimental design but accepting a simpler structure for the sake of model convergence (Barr et al. 2013), followed by a top-down approach for the fixed effects that always included treatment and time or treatment alone as the minimum set of predictors even when their effect was not significant. The model with the lowest AIC and non-conspicuous patterns in the residuals was selected. Model predictions were calculated as marginal means (i.e., only the variable of interest was varied, while all other parameters were set to their mean or an intermediate category) with the predict-function (R Core Team, 2018) or ggpredict (Lüdecke, 2018). Visualisations during data exploration and final figures were done with the ggplot-package (Wickham, 2016). The treatment efficacy was expressed as the reduction according to Abbott (1925):

Reduction = $(1 - TC^{-1}) \times 100\%$, with T and C being the modelled means of the response variable for SPLAT® Verb and untreated control group, respectively. For example, if the infestation probability was 100% in the untreated control group and 0% in the treatment group, the treatment would reduce the infestation probability by 100% (i.e., a 100% reduction or complete protection); if the infestation probability in the SPLAT® Verb treatment was also 100%, then there would be a reduction of infestation probability by 0% (i.e., a 0% reduction or no treatment effect).

In a second step of analysis (post-hoc) only observations from the treatment group in 2021–2023 (excluding the pilot study in 2020) were used to investigate differences in treatment effects across years. Infestation probability, as well as infestation density (number of nuptial chambers), were modelled as described for the main analysis above. The year was added as a random effect where applicable. The shortest distance of each sampling window to a SPLAT® Verb dollop was calculated (nncross-function from the spatstat-package; Baddely et al. 2015). The application rate of SPLAT® Verb per stem volume of *P. abies* (m^3), per area (ha), as well as total *P. abies* wood volume per plot and per *P. abies* volume were also tested as predictors. Stem volume was calculated with the formula $V = \pi 4^{-1} \times D^2 \times L$, where D is the diameter at half tree length (it was assumed that $D = 2 \times$ dbh) without correction for bark thickness, and L is the total tree length. Due to non-balanced data structure which resulted in model convergence issues and non-homogenous distribution of the residuals, the binomial models had to be fitted separately (Zuur et al. 2010) for data where SPLAT® Verb was applied directly to the stem (in 2021 and one plot in 2022) and where SPLAT Verb was applied in a grid (2022 and 2023). Because of the overall low infestation rate in 2021, infestation density was only modelled for the grid application data (2022, 2023), and the analysis needed to be conducted separately for each year.

Verbenone amounts and concentrations were log-transformed and analysed via LMMs (as above) or, in case of conspicuous residual patterns, analysed via GLMM of the beta-family (as above). Post-hoc tests were done with the emmeans-function (Lenth 2023), applying a Tukey HSD test with Bonferroni correction for multiple comparisons.

3. Results

During the four experiments ~27 m^2 of *P. abies* bark (698 sampling windows) were examined in detail. In the untreated controls, 221 of 341 sampling windows were infested with *I. typographus*, while only 167 of 357 sampling windows were infested in the SPLAT® Verb treatments. The incidence of infestation was thus reduced by 29% with SPLAT® Verb when data were pooled for all years. The overall mean infestation density (i.e., all nuptial chambers counted divided by all sampling

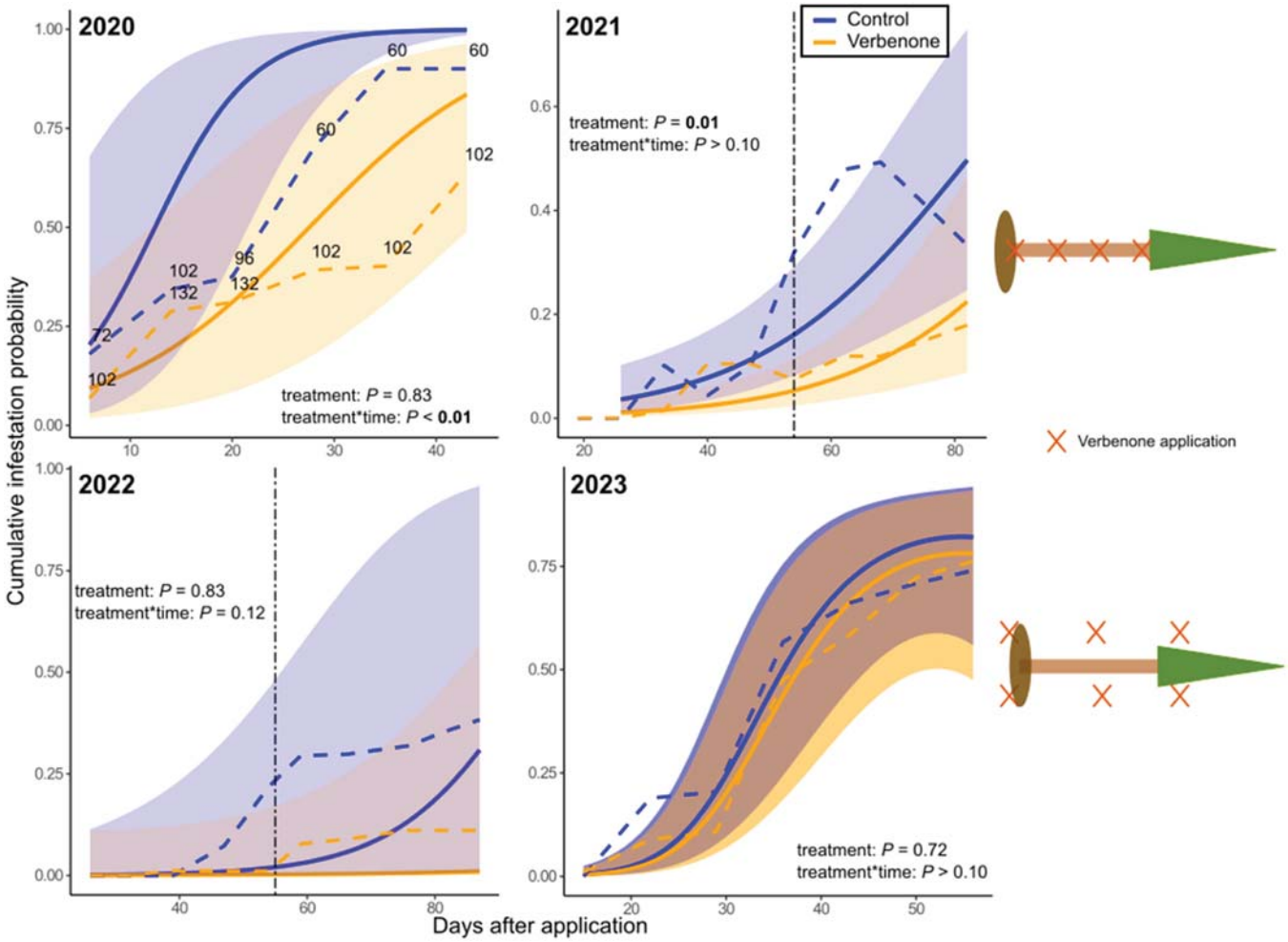

Fig. 1. Cumulative *Ips typographus* infestation probability (modeled: solid line with shaded area as 95% confidence interval, observed frequency: dashed line) on the level of sampling windows over time for untreated control trees (blue) and SPLAT® Verb-treated trees (orange) in Southwest Germany. SPLAT® Verb was applied directly to the stems of windthrown *P. abies* in 2020–2021, and in a grid around windthrown *Picea abies* in 2022–2023. Note that the axes differ in all plots according to the different phenology across years. SPLAT® Verb was reapplied in 2021 and 2022 due to an unexpected long period of cool temperatures (vertical dashed line). In 2020, some of the trees were accidentally removed before the end of the experiment (sample size given for each data point). In all other years, the sample size was constant throughout each experiment.

windows in a treatment) was 0.80 and 0.54 nuptial chambers dm^{-2} bark area in the untreated control and SPLAT® Verb group, respectively (i.e., an overall reduction by 33%). However, the treatment effect and the overall attack dynamic differed greatly among years (Fig. 1).

3.1. Infestation probability over time

SPLAT® Verb significantly reduced the risk of infestation by *I. typographus* over time in 2020 and 2021 ($P \leq 0.01$) when SPLAT® Verb was deployed directly to the stem. This tendency was also found in 2022 ($P = 0.12$, application in grid) when within treatment variability among plots was large and overall infestation risk and density were low, resulting in quite large confidence intervals at the population level. In 2020, a 50%-infestation risk threshold was reached on average 19 d later in the SPLAT® Verb treatment than in the untreated control. In 2021 a 10%-infestation risk threshold was reached 21 d later in the SPLAT® Verb treatment, and in 2022 the estimated mean infestation probability over time remained below 10% in the SPLAT® Verb treatment. In 2023, infestation probability over time did not differ between treatments ($P = 0.72$).

At the end of the experiment in 2020 and according to the analysis of gallery systems in the laboratory, 87% of the sampling windows in the untreated control had signs of *I. typographus* infestation, while only 73% of sampling windows in the SPLAT® Verb treatment were infested. In 2021, 2022, and 2023 this was 62% vs. 14%, 39% vs. 13%, and 76% vs. 72%, respectively. These differences were significant in 2020 and 2021 ($P \leq 0.05$), with a modelled reduction by 5% and 78%, respectively. In 2022, there was also a tendency toward reduced infestation in the SPLAT® Verb treatment (by 95%; $P = 0.14$). There was no significant difference in 2023 ($P = 0.83$).

3.2. Infestation density – treatment effect on male I. typographus nuptial chambers

The estimated reduction of infestation density in the SPLAT® Verb treatment according to the model was on average 48% in 2020 ($P < 0.01$), and 76% in 2021 ($P = 0.01$) (Fig. 2, Table S1). In 2022, there was a tendency towards reduced infestation densities in the SPLAT® Verb treatment (by 90%; $P = 0.16$), while there was no significant difference in 2023 ($P = 0.62$).

3.3. Sex ratio – treatment effect on females

Sex ratio (i.e., as determined by the number of connected maternal galleries per number of nuptial galleries in the same sampling window) was not affected by treatment in any year (Fig. S1, Table S1), except in 2020 when there was a tendency for more females per male in the untreated control group ($P = 0.09$), but the effect size was negligible (6% reduction; Table S1). On average, there were close to two females per male in all years (range of means: from 1.63 ± 0.45 to 1.92 ± 1.24; Table S1).

3.4. Density of pupal chambers – treatment effect on Ips typographus reproduction

The number of pupal chambers at the end of the experiment (i.e., at

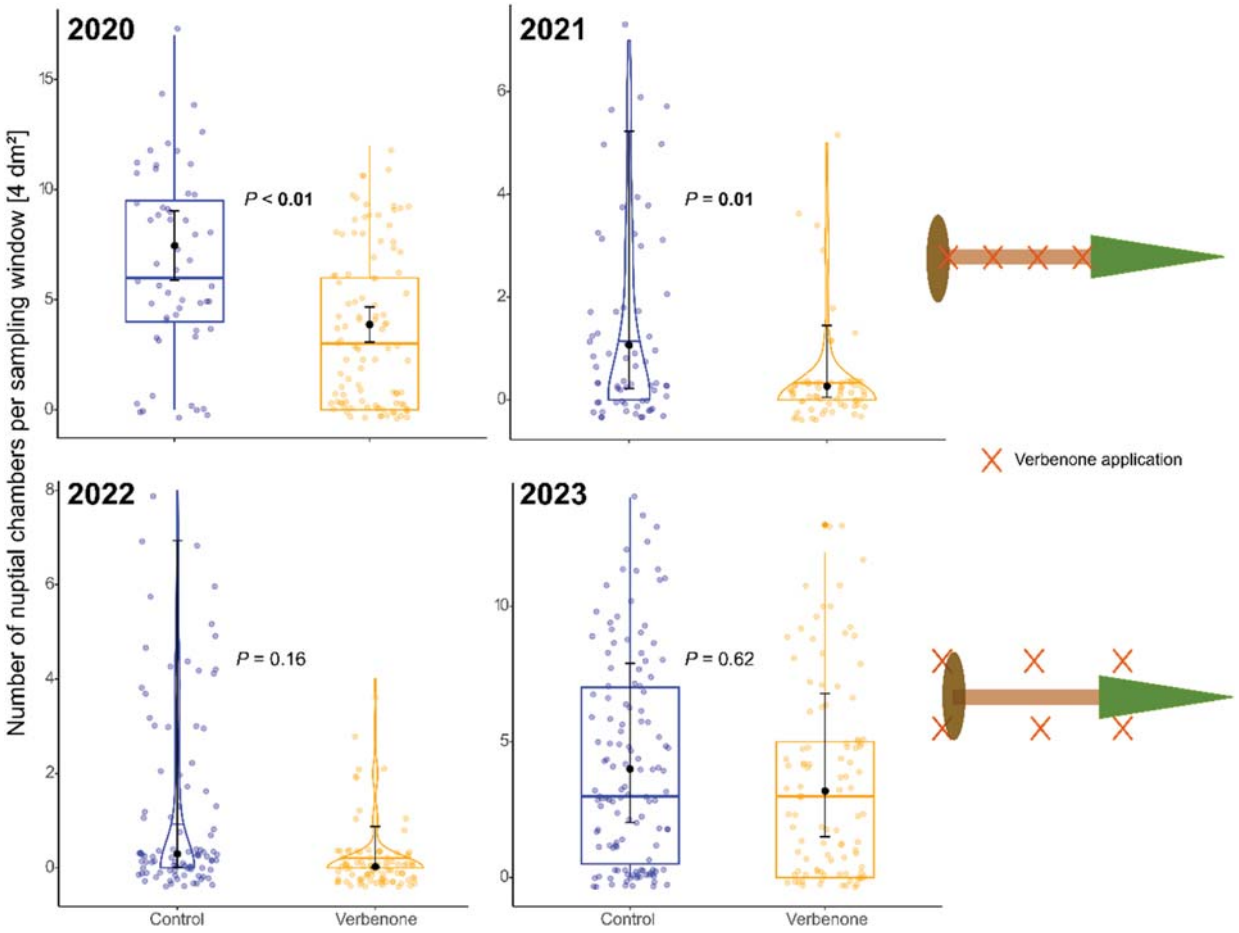

Fig. 2. Number of *Ips typographus* nuptial chambers per sampling window (modeled: black dot with 95% confidence intervals, observed data as jitter and boxplot or violin-plot in case boxplots were not informative) for untreated control trees (blue) and SPLAT® Verb-treated trees (orange) in Southwest Germany. SPLAT® Verb was applied directly to the stems of windthrown *Picea abies* in 2020–2021, and in a grid around windthrown *P. abies* in 2022–2023. Note that scales of Y-axes differ.

the time when the first brood had fully developed) was significantly ($P << 0.01$ in all cases) and weakly to moderately correlated (Kendall's τ: 0.33, 0.60, 0.65 and 0.53 in 2020, 2021, 2022, and 2023, respectively) with the number of nuptial chambers per sampling window in all years. There was a significant 99% reduction in 2021 ($P = 0.03$), while in 2020 and in 2022 a 63–71% reduction was not significant ($P \geq 0.25$; Fig. 3; Table S1). No difference was observed in 2023 (-3% reduction; $P = 0.64$).

3.5. Post-hoc analysis of infestation in treated plots

In a second step of the analysis, the influence of other factors on treatment effects across years was investigated. Because our experimental design was primarily focussed on examining the effect of SPLAT® Verb against the untreated control at the level of a windthrow, the amount of SPLAT® Verb applied per tree volume was correlated with plot size, as well as the amount applied per area (Pearson's $r = -0.85$ and 0.68, respectively). Thus, not all terms could be included as predictors in the model. We decided that the amount of SPLAT® Verb applied per unit (m^3) stem volume (i.e., the volume of windthrown trees in a windthrow) is the most relevant parameter in practical terms and hence used it as a predictor. When SPLAT® Verb was applied directly to the stem (in 2021 and one plot in 2022), the occurrence of infestation by *I. typographus* was not explained by the distance of a sampling window from the nearest SPLAT® Verb dollop ($P = 0.74$), nor by the amount of SPLAT® Verb applied per plot ($P = 0.66$). Contrarily, when SPLAT® Verb was applied in a grid (2022 and 2023), the amount of SPLAT® Verb applied per unit stem volume affected the probability of infestation: an increase from 0.03 to 0.10 kg m^{-3} lowered the infestation probability by 96% ($P < 0.01$, Fig. 4). Distance to the nearest dollop did not affect infestation probability ($P = 0.95$).

Infestation density in the grid application in 2022 was not affected by the distance to the nearest SPLAT® Verb dollop ($P = 0.66$) or by the amount applied per timber volume ($P = 0.21$). For the 2023 data, the amount of SPLAT® Verb per tree volume was categorized because of the uneven distribution of values within the range. There was a significant effect for the highest application rate (poisson-glmm, $P = 0.05$). The pairwise test then suggested a non-significant 78% reduction (Tukey HSD with Bonferroni correction for three tests, $P = 0.14$) when the application rate is doubled from 0.03 to 0.06 kg m^{-3} (Fig. 4).

3.6. Spatial distribution of verbenone from SPLAT® Verb applications (2021)

Results from the active sampling of volatiles in the active airspace of the forest suggest a strong decline in verbenone concentrations from ~4 ng L^{-1} to <1 ng L^{-1} within only 0.5 m of a SPLAT® Verb dollop (Fig. S2). Concentrations then remained constantly low until the furthest distance sampled (14 m). The vertical distribution of verbenone concentrations yielded a surprisingly similar trend, with a strong decline

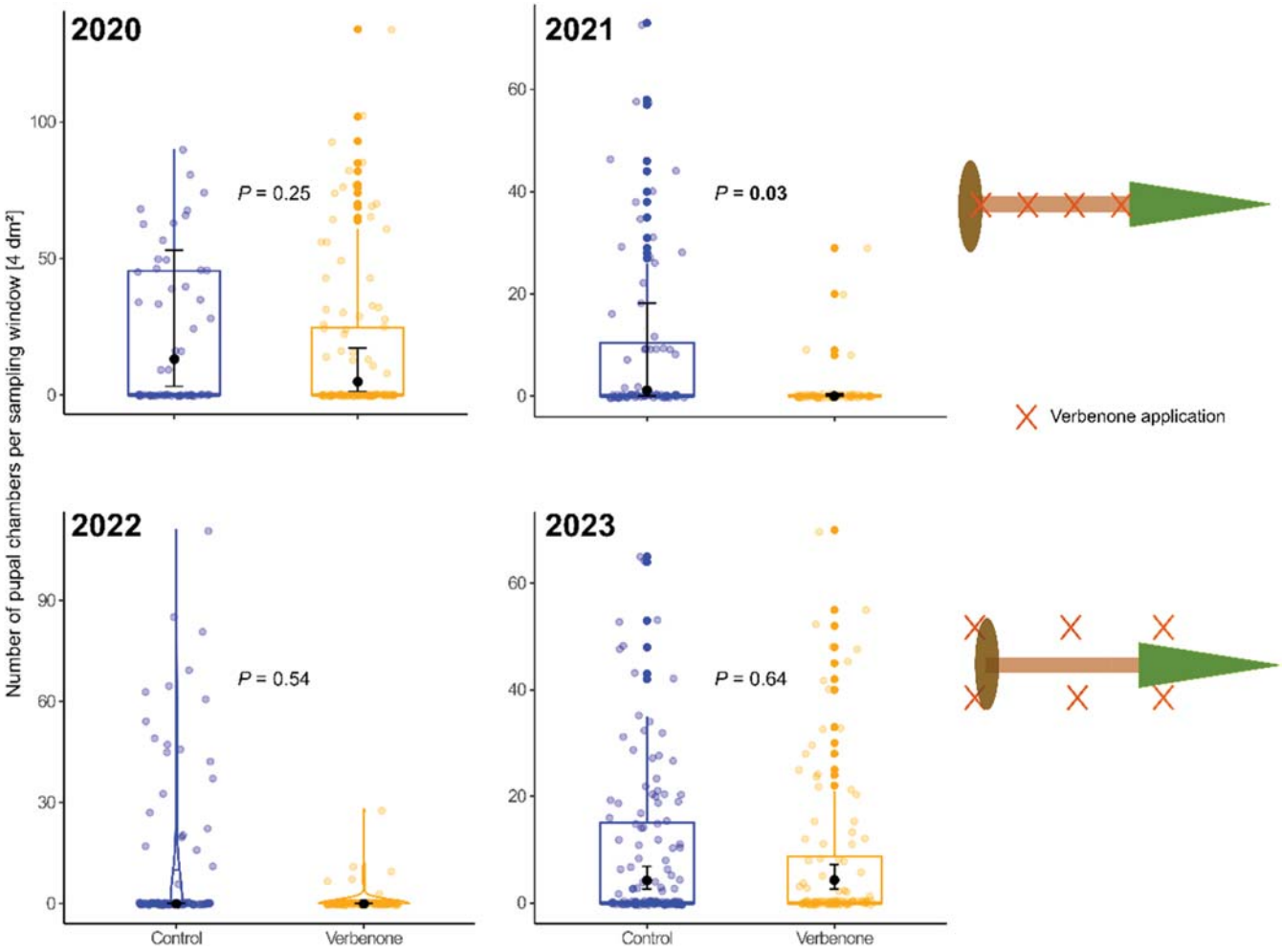

Fig. 3. Number of *Ips typographus* pupal chambers per sampling window (modelled: black dot with 95% confidence intervals, observed data as jitter and boxplot or violin-plot in case boxplots were not informative) for untreated control trees (blue) and SPLAT® Verb-treated trees (orange) in Southwest Germany. SPLAT® Verb was applied directly to the stems of windthrown *Picea abies* in 2020–2021, and in a grid around windthrown *P. abies* in 2022–2023. Note that scales of Y-axes differ.

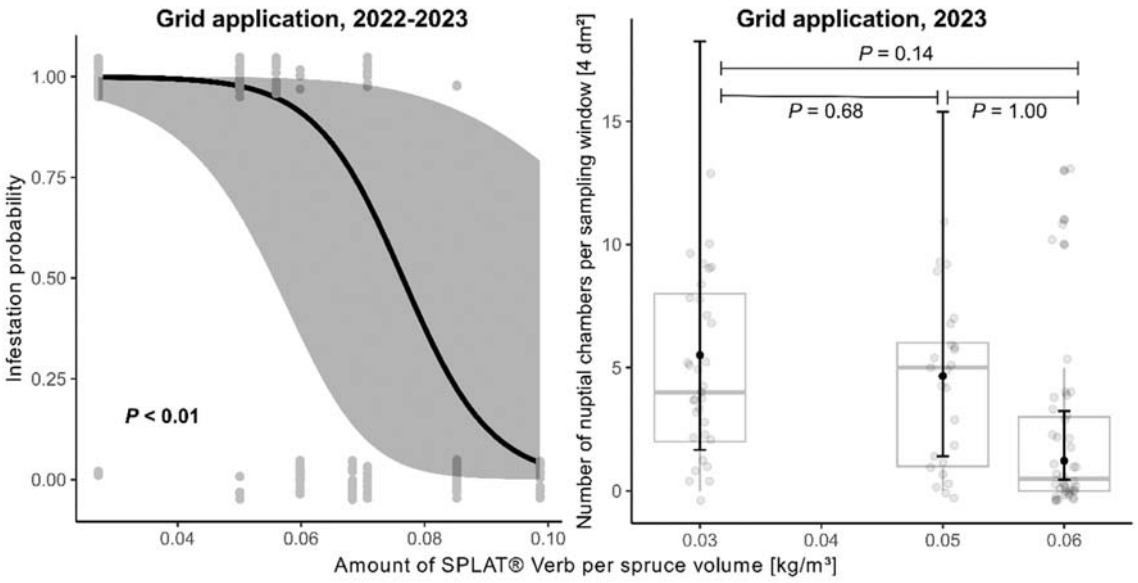

Fig. 4. Effect of the SPLAT® Verb application rate per tree volume on *Ips typographus* infestation probability (left), and infestation density (right) for the grid-application on windthrown *Picea abies* in Southwest Germany. Note that for reasons of the data structure, a separate analysis had to be conducted for the infestation density model in 2022 and 2023. Shown are the original data points with a jitter (grey dots), along with the modelled population averages (black solid line or point) and the 95% confidence interval (shaded area or error bars). Note that scales of X-axes differ.

within the first 0.5 m above the dollop (Fig. S2). Mean temperatures during the 5-h sampling intervals ranged from 14 ± 1 °C (mean ± SD) to 22 ± 1 °C; mean relative air humidity ranged from 50 ± 5% to 88 ± 9; an mean wind speeds ranged from 0.4 ± 0.3 to 0.9 ± 0.4 m s^{-1}. No precipitation occurred during the 5-h sampling intervals. No parameter was significantly correlated with verbenone concentration (Kendall's τ; $P > 0.24$).

In 2021, the passive sampling of volatiles in the active airspace of the forest showed that the amounts of verbenone were 1.8X higher (17 ± 38 vs. 9 ± 17 ng 24 h^{-1}) at sampling windows on SPLAT® Verb-treated trees compared to the untreated controls, but this difference was not significant (linear mixed model with log-transformed response, P =

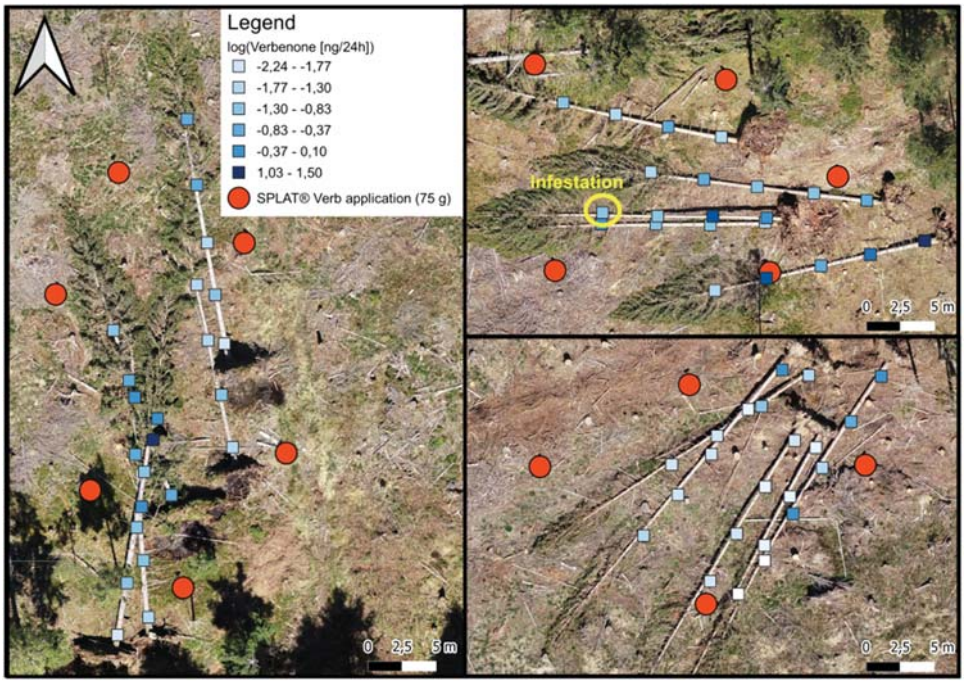

Fig. 5. Log-verbenone amounts (average over three volatile samplings as log[ng 24 h^{-1}]) at the sampling windows (blue squares; light blue: low amounts, dark blue: high amounts) resulting from grid-application of verbenone from SPLAT® Verb (red circles: point sources of SPLAT® Verb) in 2022 in Southwest Germany. Shown are three of four treatment plots on which volatile sampling of the active airspace was conducted. Note that the verbenone amounts measured directly above the SPLAT® Verb-dollops were on average 1,000X higher than at the sampling windows, and that the distance to the nearest source was not significantly associated with verbenone amounts (see 3.7). The latter is also clearly visible in the aerial images: light blue colored sampling windows are found in direct proximity of dollops. At the same time, verbenone amounts may accumulate in denser part of the crown (left and upper right), even though this tendency is not very strong (e.g. bottom right). During the time of volatile sampling, only one sampling window had signs of *I. typographus* infestation (yellow circle, upper right).

1.00, Fig. S3). Verbenone amounts measured directly above the ~20 g dollops were almost 10X higher than in 1–2 m from the dollop and this difference was significant (174 ± 298 vs. 18 ± 42; generalized linear mixed model with beta-family and log-link function, Tukeys-HSD post-hoc test, $P < 0.01$, Fig. S3). There was no significant difference in verbenone amounts at 1 and 2 m ($P > 0.95$ in all pairwise-comparisons). Mean temperatures during the 24-h sampling intervals ranged from 14 ± 2 °C (mean ± SD) to 22 ± 4 °C; mean relative air humidity ranged from 52 ± 13% to 94 ± 9; and mean wind speeds ranged from 0.8 ± 0.6 to 1.0 ± 0.6 m s^{-1}. Precipitation occurred during two sampling intervals with 21 and 1 mm. Relative air humidity was significantly and negatively correlated with verbenone amounts (Kendall's $\tau = -0.50$, $P < 0.01$). Accordingly, overall verbenone amounts were on average around 1.4X and 2.1X greater during the sample periods without precipitation compared to the two sample periods with precipitation for the untreated control and treatment plots, respectively.

3.7. Spatial verbenone distribution in grid-application (2022)

In 2022, the passive sampling of volatiles in the active airspace of the forest showed that verbenone amounts were on average almost 1,000X higher immediately above SPLAT® Verb dollops than at the sampling windows inside SPLAT® Verb-treated plots (1,724 ± 2,229 vs. 2 ± 7 ng 24 h^{-1}; average distance to nearest dollop: 4.5 ± 2.6 m). Within treated plots, distance (range: 0.5–8.7 m) to the nearest SPLAT® Verb dollop had no effect on verbenone amounts (linear mixed model with log-transformed response, $P = 0.36$, Fig. 5). From the spatial distribution, it appears that verbenone may be accumulating in areas of high crown cover (either crowns of downed trees or near the stand edge), but on occasion higher verbenone amounts were also observed in more open areas of the windthrows (Fig. 5). Verbenone amounts near the sampling windows were on average >2X higher in SPLAT® Verb-treated plots compared to the untreated controls (2 ± 7 vs. 1 ± 2 ng 24 h^{-1}), however due to the large variation, this difference was not significant ($P = 0.37$, there was a significant interaction of day 2 and treatment, $P = 0.02$, when the treatment effect was less pronounced than on day 1 and 3). Mean temperatures during the 24-h sampling intervals was 19 ± 4 °C (mean ± SD) for all days; mean relative air humidity ranged from 51 ± 8% to 70 ± 18; and mean wind speeds ranged from 1.1 ± 0.9 to 2.0 ± 1.2 m s^{-1}. No precipitation occurred during the 24-h sampling intervals.

4. Discussion

Storms play an important role in the epidemiology of *P. abies* forests by triggering *I. typographus* outbreaks (Forster, 1993; Gilbert et al. 2005; Økland et al. 2016; Ravn, 1985; Stadelmann et al. 2013) that often lead to timber losses exceeding the amount of the windthrown trees multiple times (Kärvemo et al. 2014; Økland et al. 2016). Climate change is projected to intensify the interaction of storms and subsequent *I. typographus* outbreaks (Seidl and Rammer, 2017), which may result in *I. typographus* populations that are extremely challenging to manage by salvage and sanitation logging alone (Dobor et al., 2020; Fettig, 2022). Given these projections together with formal directives from the European Union that require plant protection and bark beetle management to be implemented based on the principles of integrated pest management (European Parliament, 2009), there is an urgent need to develop complementary and environmentally friendly tools and strategies for managing *I. typographus* populations in the future.

4.1. Effects of verbenone (SPLAT® Verb) on the aggregation potential of I. typographus

In our 4-yr study, we found that verbenone (SPLAT® Verb) reduces the infestation risk of windthrown *P. abies* by *I. typographus*. We observed a global 29% reduction in infestation probability and 33% reduction in infestation density. It is notable that under low to moderate infestation pressure (i.e., infestation probability in untreated controls ≤60%) the reduction was up to 78%, and 76%, respectively. Numerous studies on many different bark beetle species likewise suggest that applications of verbenone rarely yield complete inhibition (Frühbrodt et al. 2024). While other studies have previously shown that verbenone alone or in combination with other inhibitors can protect stored logs from *I. typographus* infestation (Bakke, 1987; Schlyter et al. 1988), to our knowledge there is only one other study that examines the efficacy of verbenone for protecting windthrown trees: Jakuš et al. (2003) reported several unsuccessful approaches to protect single naturally windthrown *P. abies* with verbenone alone or in combination with *trans*-conophthorin in Slovakia. As also discussed below, possible explanations for the lack of a treatment efficacy in their study are the distribution of dispensers (single point sources per tree), and the high local infestation pressure (all untreated control trees were heavily infested; Jakuš et al. 2003).

Contrary to previous findings (Bakke, 1981; Schlyter et al. 1989; Unelius et al. 2014; Zhang and Schlyter, 2003), we did not find a sex-specific effect. Stronger inhibition of males has been reported in baited traps treated with verbenone (Bakke, 1981; Schlyter et al. 1989; Unelius et al. 2014; Zhang and Schlyter, 2003). The effect is usually more pronounced when verbenone is combined with other inhibitors (Schlyter et al. 1989; Unelius et al. 2014; Zhang and Schlyter, 2003). On the other hand (and similar to our results), no sex specific response was found on stored logs when using verbenone alone or in combination with other inhibitors (Bakke, 1987; Schlyter et al. 1988). It is therefore possible that i) a stronger male response depends on the presence of specific additional compounds (such as non-host volatiles, see Zhang and Schlyter, 2003) or ii) that males are indeed inhibited more strongly by verbenone alone, but that downstream mate selection behaviour stabilises the sex ratio on trees (males control females entering their nuptial chamber; see Schopf et al. 2019). The latter is consequently not detectable with data obtained from baited traps.

Given the reduction in attraction of male and female *I. typographus* to windthrown *P. abies* in response to verbenone, one would also expect an overall reduction in the number of offspring produced. Unfortunately, we were unable to directly assess the emergence of the next *I. typographus* generation. Instead, we used the number of pupal chambers as a proxy for offspring development. The latter was indeed considerably lower (24–93% reduction in observed data) for the verbenone treatment in three of four years, but this difference was only significant in one year. While counting pupal chambers (instead of emerging beetles) is efficient, it also has disadvantages. For example, when gallery systems are densely pack, it is difficult to keep individual larval galleries separated and to distinguish individual chambers. Furthermore, it is impossible to predict whether an individual would also have successfully molted from pupa, exhibited maturation feeding, and dispersed. Since we had to terminate our experiments prior to beetle emergence so that timely sanitation could be implemented for the purposes of forest protection, not all eggs had the chance to fully develop and therefore some offspring were not represented in our data (pupal chamber counts). Intraspecific competition during maturation feeding may cause some additional mortality, as offspring beetles are lighter and emerge earlier from the brood systems of high density (Anderbrant et al. 1985). In all four years, 61 ± 5% of the sampling windows in the untreated control that were infested with *I. typographus* already had pupal chambers at the end of the experiments, while only 49 ± 3% of the infested windows in the verbenone group had pupal chambers. Intraspecific competition among larvae can greatly increase their mortality, and even decrease the fitness of subsequent beetle generations (Anderbrant et al. 1985; Raffa, 2001). Consequently, an artificially reduced infestation density could theoretically lead to greater success in reproduction and ultimately foil a potential treatment effect. The density optimum for *I. typographus* is estimated to be ~4 males dm^{-2} (Byers, 1984; Toffin et al. 2018) or 5–15 females dm^{-2} (Anderbrant, 1990; Anderbrant et al. 1985), corresponding to ~2.5–8 males dm^{-2} assuming

a sex ratio near 2:1 (f:m) as observed in our study and other *I. typographus* populations (Kirkendall, 1989). A density of ≥4 males dm^{-2} almost never occurred in our study (Fig. 2). Together with the overall trend that the number of pupal chambers was considerably lower in the verbenone group (except in the last year), we therefore assume that verbenone reduced the infestation density from densities below the optimum in the majority of cases, so that a positive treatment effect also results in fewer offspring. Reduced infestation densities in turn delay the formation of sister-broods (i.e., females completing oviposition, re-emerging, and replenishing their energy reserves; Anderbrant, 1989), as well as offspring dispersal (Anderbrant et al. 1985). Consequently, the application of verbenone may additionally lower and slow the risk of further spread of subsequent infestations. On the other hand, individuals from lower brood densities may be more vital, and have greater reproductive success (Anderbrant et al. 1985).

Previous studies suggest the active inhibitory range (see Zhang and Schlyter, 2003 for definition) of other formulations of verbenone is <5 m for *I. typographus* (Niemeyer et al. 1995; Zhang and Schlyter, 2003). However, catches in pheromone-baited traps were significantly reduced up to 14 m from 75 g-dollops of SPLAT® Verb (Löcken et al., unpublished). Interestingly, in our study distances of up to 10 m from the nearest SPLAT® Verb dollop had similar infestation probabilities and densities, despite on average ~1,000X lower amounts of verbenone near the stem surface compared to immediately above the dollop. Odour plumes do not distribute homogenously around a release point, but rather scatter in small bulks of high amounts amidst spaces of neutral air (Thistle et al. 2004). This is reflected in our data by the larger variation in verbenone amounts near SPLAT® Verb-treated compared to untreated control trees (~2–3X greater standard deviation). Of note, verbenone is also produced naturally by several pathways including auto-oxidation of α-pinene to *trans*-verbenol and then to verbenone under normal field conditions explaining its occurrence in untreated control plots (Bhattacharyya et al. 1960; Hunt and Borden, 1990; Hunt et al. 1989). Microstructures likely affected the distribution of verbenone, e.g., greater amounts tended to occur near the stand edge, or in denser parts of the crown independent of distance to the nearest SPLAT® Verb dollop (Fig. 5). Intact leaves can adsorb and desorb volatiles and thus buffer their concentrations in air (Himanen et al. 2010; Wall and Perry, 1983). Furthermore, the release of volatiles from passive dispensers varies with meteorological conditions such as temperature and wind speed (Nielsen et al. 2019, Thistle et al. 2004). Surprisingly, mean temperature was not significantly associated with verbenone amounts, probably due to the low range of different temperature conditions covered with our data, and the integration over 5–24 h sampling intervals. Greater relative air humidity in combination with precipitation during the sampling intervals was associated with lower verbenone amounts, and the effect was of comparable magnitude in treatment and untreated control plots. It can be assumed that *I. typographus* flight is positively linked to verbenone emissions from passive samplers, e.g. flight activity is greatly reduced at wind speeds above 1 ms^{-1} and is positively correlated with temperature (Botterweg, 1982). Although we could not detect significant differences in verbenone amounts between the untreated control and the SPLAT® Verb-group, there was a significant treatment effect on *I. typographus* colonization (or at least a strong tendency) in three of four years of study (Figs. 1–2). Furthermore, we detected large amounts of verbenone in direct proximity to the SPLAT® Verb dollops. Hence, *I. typographus* must be able to perceive sufficient concentrations of verbenone in the active airspace to alter their behaviour at this scale. Insect flight orientation is complex and is not a mere response to a concentration gradient of an odour but rather a continuous interplay of optomotor upwind-flight and re-tracking of odour plumes (Cardé 2021).

4.2. Other factors affecting the efficacy of verbenone from SPLAT® Verb

Interpretations of post-hoc analyses on the pooled data of three to four years of experiments indicate two trends: i) there was an overall and marked difference in infestation pressure by year (i.e., the infestation probability in untreated controls ranged between 39–87%). This is likely driven by variation in the local *I. typographus* population, but the relative attractiveness of windthrows (e.g., timber volume per plot was 1.5–1.9X higher in 2020 and 2023 compared to the other years due to site characteristics) could also be a contributing factor. The combination of both factors is likely the reason for increased infestation risk in untreated control and verbenone-treated plots in respective years; ii) as a consequence of different timber volumes, the application rate of SPLAT® Verb, which was standardized by tree (2020–2021) or area estimated in the field (2022–2023), but not explicitly by timber volume, varied from 0.03–0.17 kg m^{-3} (one outlier with 0.17 kg m^{-3}). This enabled us to investigate the effect of application rate per tree volume, which had an important effect: while an application rate of only 0.03 kg m^{-3} resulted in almost 100% infestation probability, an intermediate rate of 0.08 kg m^{-3} lowered the infestation risk to 38%, and 0.10 kg m^{-3} lowered the infestation risk to only 4% (Fig. 4). Similarly, infestation density was reduced from 1.38 nuptial chambers dm^{-2} to 0.31 nuptial chambers dm^{-2} by increasing the application rate from 0.03 to 0.06 kg m^{-3} (Fig. 4). In general, higher doses of verbenone have also been associated with higher levels of inhibition in other bark beetle species (Frühbrodt et al. 2024). Due to the unplanned variation of application rate per tree volume (which is common among studies evaluating the efficacy of verbenone and other semiochemicals for tree protection), application rate per tree volume was strongly and positively correlate with the application rate per area of windthrow, and negatively correlated with plot size. We recommend that future studies standardize application rate based on the volume of windthrown trees being treated.

As stated above, infestation pressure differed noticeably among years. The highest levels of tree protection were achieved in years of comparatively low infestation pressure (≤60% infestation probability in untreated controls). The post-hoc analysis suggests that there is at least a tendency for declining treatment efficacy when infestation pressure is high (Fig. S4, $P = 0.21$). Previous studies likewise observed that the inhibitory effect of verbenone is lower when infestation pressure is higher, even though this could not formally be tested (Bakke, 1987; Bentz et al. 2005; Foote et al. 2020; Progar et al. 2013). We encourage future studies to investigate this relationship, acknowledging this will be challenging due to the large area required to obtain sufficient sample sizes of varying infestation pressures under similar abiotic and forest conditions.

None of the factors discussed above fully explains the difference in treatment success between 2020 (when applications of verbenone resulted in a significant delay and reduction of *I. typographus* infestation), and 2023 (when no treatment effect was observed). Both infestation pressure (infestation rate in untreated controls: 87% vs. 76% in 2020 and 2023, respectively), and application rate per volume (0.06 ± 0.03 vs. 0.05 ± 0.01 kg m^{-3}, respectively) were similar between 2020 and 2023. Our volatile measurements revealed that while large amounts of verbenone were present immediately above SPLAT® Verb dollops, verbenone amounts near the stems were not significantly different between treatments. It is possible that under otherwise comparable conditions, higher densities of smaller dollops may be more effective for protecting windthrows than lower densities of larger dollops (~20 g deployed directly to the stem vs. 75 g deployed in a 15-m grid in 2020 and 2023, respectively; but see Andersson et al. 2011). This may have to do with the fact that *I. typographus* can discern attractive and inhibitory cues when their respective sources are more than ~0.5–1.0 m apart (Andersson et al. 2011), even though this likely also depends on the respective concentration ratios. A similar case has been argued regarding the efficacy of verbenone (SPLAT® Verb) for reducing *Pinus* spp. mortality attributed to *D. ponderosae* in western North America (Fettig et al. 2015).

4.3. Potential management implications: application of verbenone during phases of low to moderate infestation pressure on small windthrows

Based on our findings, we outline two post-windthrow management scenarios in which the application of verbenone may complement existing management options (Hlásny et al. 2021, Fig. 6). The first addresses the potential use in managed forests where timber production is the goal. From the perspective of forest protection, under ideal circumstances, windthrown *P. abies* are removed from the forest before being colonized by *I. typographus* (salvage logging) or at the latest before the next generation of *I. typographus* emerges from windthrown trees (sanitation logging) (Stadelmann et al. 2013; Wermelinger, 2004). Models suggest that ≥80% of management efficiency must be achieved to reduce the likelihood of spreading the infestation to surrounding areas (Dobor et al. 2020; Fahse and Heurich, 2011; Pietzsch et al. 2023), which is often difficult due to logistic constraints, especially when the amount of windthrow is high (Hartebrodt and Delb, 2020; Kogler and Rauch, 2023; Odenthal-Kahabka, 2004; Stadelmann et al. 2013; Wermelinger, 2021). In these situations, the use of verbenone may complement salvage and sanitation logging (Fig. 6) by delaying colonization of small windthrows (Fig. 1, Lobinger, 2006). In practical terms, this relaxes some logistical constraints and allows for better allocation of resources following large storm events (Schröter et al. 2004). Depending on temperature, *I. typographus* requires at least ~6 wks (only during summer conditions in Central Europe) or longer to complete development (Doležal and Sehnal, 2007; Hofmann et al. 2024), which means that the time span for salvage and sanitation operations could be increased by up to 50% with verbenone. The delay of infestation by ~3 weeks (Fig. 1) corresponds well with the amount of time typically needed for transportation of salvaged wood after cutting, which ranges from 10 to 104 days in Europe (summarized by Kogler and Rauch, 2023) with the upper range being clearly too lengthy for effective pest control. Small, scattered windthrows are usually prioritized for salvage and sanitation (BAFU, 2008a, b; Odenthal-Kahabka, 2004; Schröter et al. 2004; WF and LFI, 2018) as emergent beetles readily colonize adjacent, live *P. abies* (Kärvemo et al. 2014; Potterf and Bone, 2017) due to locally limited numbers of windthrown trees. Our post-hoc analyses suggest that the protective effect of verbenone may extend to larger windthrows than evaluated in our studies.

The second management scenario refers to areas where salvage and

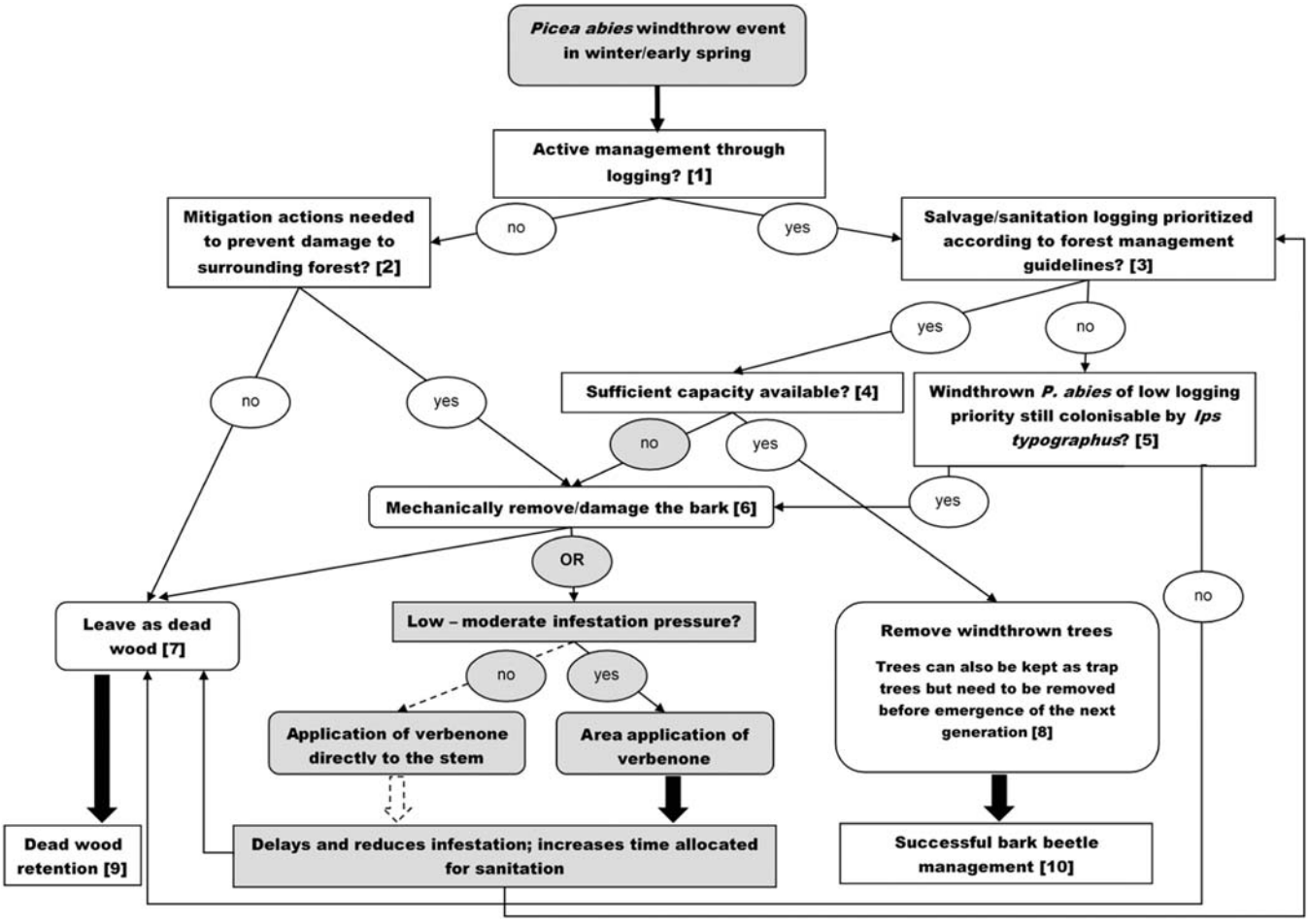

Fig. 6. Potential management options after a windthrow event in *Picea abies* forests based on current literature and management guidelines (white boxes; see references below) including potential application scenarios for verbenone to delay and reduce infestation of windthrown *P. abies* by *Ips typographus* (grey boxes) within an integrated bark beetle management approach. The application of verbenone will not replace existing management practices but may complement them to achieve management goals that lie between the two opposing objectives of nature conservation (i.e., dead wood retention) and timber production (Hlásny et al. 2021). Our results suggest that verbenone can delay and reduce the infestation of small windthrows under low to moderate infestation pressures (solid arrows) but may not be effective under high infestation pressures (dashed arrows). Further study of optimal doses of verbenone per volume of *P. abies* timber, as well as spatial distributions of verbenone applications within windthrows are necessary. References: 1: Hlásny et al. (2021), 2: Hlásny et al. (2021); 3: e.g. BAFU (2008a, b); CGAAER, 2018; Schröter et al. (2004); WF and LFI, 2018 4: Schröter et al. (2004); 5: BAFU (2008b); Schröter et al. (2004); 6: Delb et al. (2021); Hagge et al. (2019); Thorn et al. (2016); Zarges et al. (2023); 7: Bouget and Duelli (2004); Hagge et al. (2019), 8: Odenthal-Kahabka, 2004; Schroeder and Lindelöw, 2002; Schröter et al. (2004); Wermelinger, 2004; Wichmann and Ravn (2001); 9: Bouget and Duelli (2004); Hlásny et al. (2021); 10: Dobor et al. 2020; Fahse and Heurich, 2011; Pietzsch et al. 2023; Wermelinger, 2004.

sanitation logging are not permitted (e.g., protected areas; Fig. 6), and where the retention of dead wood is a primary objective (Hagge et al. 2019 Hlásny et al. 2021). In this case, verbenone may be an interesting option for managing *I. typographus* also due to its low toxicity (River-a-Dávila et al. 2021). It is likely that verbenone is less effective than mechanically damaging the bark (i.e., either complete debarking or damaging the bark by scratching or gouging), which destroys brood habitat and brood if done before beetles have attained the adult stage; i.e. preventive and therapeutic (Delb et al. 2021; Hagge et al. 2019; Thorn et al. 2016). Verbenone, on the contrary, is mostly effective as a preventive measure. However, if maintaining biodiversity is a goal, verbenone may be the preferred option, since mechanically damaging the bark also negatively affects saproxylic organisms and bark beetle antagonists (Thorn et al. 2016; Weslien et al. 2024). Moreover, mechanically damaging the bark is laborious, dangerous, and costly (Thorn et al. 2016; Zarges et al. 2023) while applying verbenone is physically simple and may be facilitated with airborne technologies in the future (similar to Onufrieva et al. 2010).

In addition to treating windthrows, future efforts warrant evaluating verbenone for reducing colonization and mortality of live *P. abies* in Europe as occurs with verbenone and *Pinus* spp. in North America (Fettig et al. 2015; Mafra-Neto et al. 2014).

5. Conclusions

Verbenone (SPLAT® Verb) does not completely inhibit the infestation of *I. typographus* on windthrown *P. abies* but lowers the aggregation potential at low to intermediate infestation pressures or at high infestation pressure when applied at high spatial densities. Verbenone also delays infestation of windthrown *P. abies* by ~3 wks, allowing managers additional time to plan and coordinate salvage and sanitation operations. The lower infestation risk and intensity likely results in lower reproductive success of *I. typographus*. Thus, whenever windthrown *P. abies* cannot be salvaged in time, SPLAT® Verb may serve as a mild tool (i.e., environmentally friendly, low toxicity, no mechanical impact on the forest and soil, but on average lower efficacy as conventional insecticides) within the integrated management of *I. typographus*. This approach expands the range of bark beetle management tools in the context of integrated forest plant protection, while salvage and sanitation operations remain the most important measures (Fettig and Hilszczański, 2015; Wermelinger, 2004).

The results of our work highlight the necessity of future studies on i) optimal application rates, ii) treatment of larger windthrow areas (≥1.0 ha), iii) the economic costs vs. benefits compared to alternative management tools and strategies, iv) alternative application methods of verbenone (e.g., air borne, spraying), and v) combining verbenone with other inhibitors (Deganutti et al. 2023; Unelius et al. 2014; Zhang and Schlyter, 2004) to protect both windthrown and adjacent live, standing *P. abies*.

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CRediT authorship contribution statement

Helge Löcken: Writing – review & editing, Methodology, Conceptualization. **Baoguo Du:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **Christopher J. Fettig:** Writing – review & editing, Writing – original draft, Conceptualization. **Peter H.W. Biedermann:** Writing – review & editing, Supervision. **Jürgen Kreuzwieser:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Tim Burzlaff:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Horst Delb:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Tobias Frühbrodt:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare no relevant financial or non-financial interests to disclose that might be perceived as affecting the objectivity of this study. The authors declare no conflicts of interests.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121856.

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