Viewpoints

Addressing a century-old hypothesis – do pioneer beetles of *Ips typographus* use volatile cues to find suitable host trees?

Summary

Global warming and more frequent climate extremes have caused bark beetle outbreaks of unprecedented scale of these insects in many conifer forests world-wide. Conifers that have been weakened by drought and heat or damaged by storms are highly susceptible to bark beetle infestation. A large proportion of trees with impaired defences provides good conditions for beetle population build-up of beetles, but mechanisms driving host search of pioneer beetles are still uncertain in several species, including the Eurasian spruce bark beetle *Ips typographus*. Despite a two-century-long history of bark beetle research, we still lack a sufficient understanding of interactions between *I. typographus* and its host Norway spruce (*Picea abies*) to forecast future disturbance regimes and forest dynamics. Depending on the scale (habitat or patch) and beetle population state (endemic or epidemic), host selection is likely driven by a combination of pre and postlanding cues, including visual selection or olfactory detection (kairomones). Here, we discuss primary attraction mechanisms and how volatile emission profiles of Norway spruce may provide cues on tree vitality and suitability for attacks by *I. typographus*, in particular during the endemic phase. We identify several crucial knowledge gaps and provide a research agenda addressing the experimental challenges of such investigations.

Introduction

Bark beetles (Coleoptera; Curculionidae; Scolytinae) are among the most common and threatening forest pests in Eurasia (Lieutier *et al.*, 2004) and North America (Raffa *et al.*, 2016) and have killed millions of hectares of conifer forests during recent decades (Huang *et al.*, 2020a). Outbreaks of the Eurasian spruce bark beetle *Ips typographus* L. have major impacts on the functioning of forest ecosystems and on forest economy (Hlásny *et al.*, 2021a). Currently, it is difficult to reliably predict the occurrence and intensity of attacks as some relevant factors that drive beetle population dynamics, for instance during host selection (definition see Box 1), are not yet fully understood (Biedermann *et al.*, 2019). The selection of suitable hosts during the population build-up phase is crucial for the survival of entire subpopulations of bark beetles (Wood, 1982). While beetle broods develop better in tissues of high nutritional quality (Raffa *et al.*, 2016) from healthy trees, hosts with strong defences can also hamper both successful attack and egg deposition. Accordingly, pioneer beetles generally succeed better in infesting stressed or storm-felled than healthy trees with full defences, at least at low attack densities (Netherer *et al.*, 2022). It is currently strongly debated how *I. typographus* identifies the vigour of potential hosts and whether a tree's physiological state influences host selection by beetles (Netherer *et al.*, 2021). Host selection mechanisms may change with spatial scale of host search (long vs short distance) or beetle population densities and depend not only on the physiological condition of a tree. When populations change from endemic to epidemic conditions (definitions see Box 1), beetles are known to infest well-defended trees likewise. Yet, it has been suggested that pioneer beetles may be attracted towards volatile emissions from host trees during the dispersal phase, which may provide information on the physiological state of a tree, such as its defensive capacity (Rodriguez & Redman, 2008; Schiebe *et al.*, 2019). Such cues could additionally be amended by visual hints like colour and shape of trees (Campbell & Borden, 2006b). However, to what extent, and under which circumstances, the various cues are most determinate for identifying host suitability is currently not known for *I. typographus*.

Initial scientific investigations concerning the life cycle of *I. typographus* and its interactions with host trees date back to the mid-18th century when it was already recognised that bark beetles succeed better in colonising cut or wind-felled trees rather than healthy and vigorous trees (Gmelin, 1787). It was also observed that beetles were initially attracted to diseased trees or those affected by extreme weather events like windthrow (Ratzeburg, 1839). Meyen and Esenbeck hypothesised that weakened or stressed trees may emit 'an odour […], which is recognised by the insects from a distance' already almost 200 yr ago (Meyen & Von Esenbeck, 1841,

Box 1 Glossary

Primary attraction: initial attraction of a pioneer beetle towards a tree during the dispersal phase in response to olfactory and other cues.

Secondary attraction: aggregation of male and female beetles in response to pheromones produced by conspecifics that already located a suitable host.

Endemic: during the endemic phase, beetle abundance is low and relatively constant.

Epidemic: epidemic conditions are characterised by very high beetle population densities.

Host selection: multistep process of beetles locating suitable breeding material ultimately resulting in host acceptance, including primary attraction, postlanding cues as well as avoidance of unsuitable hosts.

p. 43). Despite numerous advances that have been achieved in the field since then, rigorous evidence for olfactory attraction to suitable host trees by *I. typographus* has not been produced yet. By contrast, several studies have been carried out on North America beetle species of the *Dendroctonus* genus. For example, treatments that increased susceptibility to *D. brevicomis* did not increase landing rates on *Pinus ponderosa* (Moeck *et al.*, 1981). Likewise, pioneer *D. ponderosae* landed equally on trees that were ultimately entered or not entered under natural conditions (Hynum & Berryman, 1980; Raffa & Berryman, 1980).

In this article, we address this century-old hypothesis and discuss potential mechanisms of primary attraction, that is initial attraction of pioneer *I. typographus* beetles towards potential hosts during early-season swarming (definition see Box 1). We also discuss how visual and olfactory cues might interact and complement each other and beetles might use these cues to assess the suitability of a host. We also address the importance of spatial scale (long-distance and short-distance cues) and population densities during the selection process. Our article focusses on *I. typographus*, as it has caused large-scale tree mortality during the past years and a better understanding is required to assess future forest risks. We argue that a better fundamental comprehension of interactions between host trees and *I. typographus* in the critical phase of population build-up can provide a foundation for mechanistically anchored predictions of future forest dynamics in the face of climatic shifts (Huang *et al.*, 2020a). We provide a research agenda for some of the most pressing outstanding questions along with practical advice for approaching the often technically challenging investigations.

Ips typographus ecology and population dynamics

In spring, during the dispersal phase, pioneer beetles emerge from overwintering sites when the temperature reaches 16–20°C (Christiansen & Bakke, 1989; Lobinger, 1994). Whereas for many bark beetle genera (e.g. *Dendroctonus*) female beetles take on the role as pioneers, for *I. typographus* solely male beetles swarm in search of forest stands with suitable host species (Fig. 1, long distance). If they consider the host to be appropriate, pioneers bore into the bark and establish a nuptial chamber in the phloem. In case the beetles decide not to infest the tree, or are hindered, by for instance resin exudation, they abandon the tree and continue their search (Wood, 1982). Once pioneer beetles have selected a suitable host, they start colonising the tree and simultaneously emit aggregation pheromones comprising two obligatory and synergistic compounds, (−)-*cis*-verbenol and 2-methyl-3-buten-2-ol (Bakke *et al.*, 1977; Keeling *et al.*, 2020), which attract both female and male conspecifics (secondary attraction (definition see Box 1), Fig. 1 inset b). Upon entering the bark, beetles also introduce their symbiotic ophiostomatoid fungi, which may assist beetles to deplete tree defences by metabolising tree defence compounds and support beetle development by concentrating essential nutrients close to the beetle feeding site (Zhao *et al.*, 2019; Kandasamy *et al.*, 2021). During the colonisation phase, females construct maternal galleries in which they deposit their eggs and inoculate symbiotic microbes, for instance ophiostomatoid fungi, yeasts and bacteria (Wood, 1982). Beyond a certain density of colonisation, beetles release anti-aggregation pheromones such as (−)-verbenone (Byers, 1989), which divert further attacks by conspecifics to other bark areas or to different trees to constrain resource competition during mass attack (Christiansen & Bakke, 1989; Schlyter *et al.*, 1989). After hatching, larvae feed on the phloem and associated ophiostomatoid fungi (Fig. 1, inset d) and develop into immature adults. Depending on environmental stimuli and diapause phenotype (univoltine/one generation per year vs multivoltine/several generations per year; Schebeck *et al.*, 2022), developing beetles emerge after maturation feeding to establish another generation of offspring. High population growth rates of *I. typographus* are further promoted by the re-emergence of parental beetles to produce sister broods (Wermelinger, 2004).

Host preference during endemic phases

Although healthy trees provide a more nutritious habitat for beetle development, it is also more difficult to overcome their defences (Raffa *et al.*, 2016). Hence, under endemic conditions during initial attack, *I. typographus* preferentially targets trees that are physiologically weak with impaired chemical defences, yet vital enough to provide nutrient-rich tissue for brood development (Wallin & Raffa, 2004; Boone *et al.*, 2011; Kausrud *et al.*, 2011). At low population densities, stressed trees (windthrown, cut, drought-affected) are the easiest hosts to overwhelm (Rudinsky, 1962), but are also relatively rare, which leads to high beetle mortality during the dispersion phase (Raffa *et al.*, 2016; Baier *et al.*, 2019). The resulting balance between availability of compatible brood trees and density of attacking beetles controls the population growth. Thus, a targeted search for suitable hosts guided by kairomones like monoterpenes (i.e. primary attraction) to improve survival rates of pioneer beetles (Campbell & Borden, 2006a; Schiebe *et al.*, 2019) can be seen as a biologically relevant mechanism for *I. typographus* fitness. Beetles must identify suitable host trees in a matrix of vigorous trees and in an atmosphere that is rich in diverse conifer volatiles (Raffa *et al.*, 2016). Primary attraction cues which are emitted by hosts may assist them to evaluate the physiological state of the host trees even before landing and thus reduce beetle mortality during the dispersal phase (Baier *et al.*, 2019).

Host preference during epidemic phases

Disturbance events that cause physiological stress in trees such as drought, excessive heat, lightning strikes or windthrow increase the abundance of suitable host trees and improve the conditions for population growth (Boone *et al.*, 2011; Kausrud *et al.*, 2012; Hlásny *et al.*, 2021b). Hence, a greater availability of acutely stressed trees entails a higher number of successful attacks (Netherer *et al.*, 2015), and the resulting increasing colonisation rates allow for rapid development of further generations. Given that two to three generations can develop in one growing season under favourable climatic conditions, a rapid change from the endemic to the epidemic phase can occur (Eriksson *et al.*, 2005; Jönsson *et al.*, 2011).

Similar to the endemic phase, pioneer beetles most likely use olfactory cues to detect weak host trees. However, during epidemic

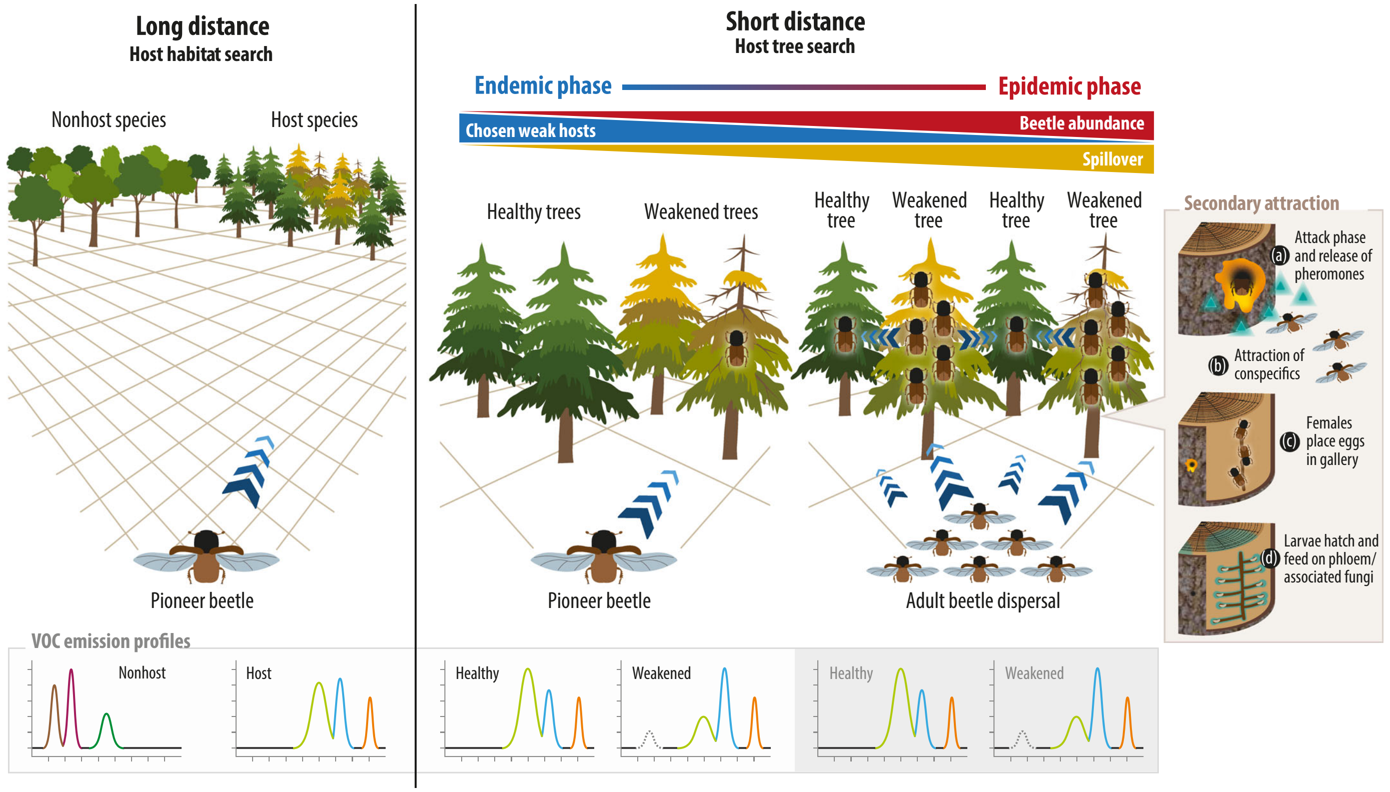

Fig. 1 Hypotheses of *Ips typographus* attraction to its host, Norway spruce (*Picea abies*). Long distance/host habitat search (host vs nonhost species) and short distance/host tree search (healthy/nonsuited trees vs weakened/suitable trees) selection are based on different visual cues (e.g. colour and silhouette of trees) and volatile organic compounds (VOC) emission profiles of the individual trees. Long-distance cues may comprise distinct compounds (e.g. monoterpene mixtures), while for short-distance selection, relative emission rates of host species-specific compounds may vary (note colour coding) and indicate tree vitality. Certain compounds may only be emitted by weak trees (dotted peak). The endemic phase is characterised by low beetle abundance and beetles succeed better in infesting weak trees with impaired defences. During the epidemic phase, beetle abundances are extremely high and a spillover can occur. Weak trees are infested to such an extent that, due to abundance of beetles and lack of space on bark for attack, beetles spill over to the adjacent trees and thus also infest viral trees. Here, besides volatiles, postlanding cues might become of higher importance in assessing host vitality. Note that secondary attraction is mediated by the release of aggregation pheromones ((−)-cis-verbenol and 2-methyl-3-buten-2-ol) from pioneer beetles after initial attack (a), inciting large numbers of conspecifics to engage in mass attack to overcome tree defences (b). After mating, females deposit their eggs and inoculate symbiotic microbes in the gallery of the phloem (c), which is also used as a food source by hatching larvae (d).

phases, beetles also infest vigorous trees, which is potentially caused by a spillover effect (Fig. 1, spillover). After abundant aggregation within weak trees, beyond a certain threshold, beetles may spillover to adjacent, potentially healthy trees. This way, neighbouring trees that have not been selected by pioneer beetles will be colonised as well, however, without selection based on their physiological properties (Geiszler & Gara, 1978). This effect may be more prominent during epidemic than endemic phases, because overall beetle density is lower during endemic phases. These spillover events also affect nonhost species such as *Pinus* spp., as has been observed in mixed stands with high beetle densities of *Pityogenes chalcographus* (Berthelot *et al.*, 2021).

For some *Dendroctonus* species, a strong density-dependent host selection behaviour has been observed. With increasing population size, *D. ponderosae* do not have to rely on stressed trees and can shift attacks to hosts that are more promising for better development of offspring (Howe *et al.*, 2022). *Dendroctonus rufipennis* from epidemic populations would colonise both weak and vigorous trees while those from endemic populations only infest weakened hosts, potentially with low defences (Wallin & Raffa, 2004). Interestingly, maternal host choice of *D. ponderosae* affected the host preferences of the next generation. Offspring of beetles that lived under endemic conditions preferred trees with low defences, while beetles originating from epidemic conditions mainly attacked well-defended trees (Burke & Carroll, 2017). Such a change in host preference between endemic and epidemic phases is not known for *I. typographus*; however, the threshold of a successful attack is assumed to be a function of host tree resistance and population density (Christiansen *et al.*, 1987).

Potential mechanisms of host selection by pioneer bark beetles

Various mechanisms, including not only visual cues (e.g. Campbell & Borden, 2006a), attractive and nonattractive olfactory stimuli (e.g. Baier *et al.*, 1997; Schiebe *et al.*, 2019) but also random landing, in which host suitability is assessed upon contact with the host substrate (e.g. Byers, 1989), have been hypothesised to play a role in host selection of bark beetles. These mechanisms are not mutually exclusive, and a combination of mechanisms could come into effect under different environmental conditions and with changing population dynamics (Person, 1931; Wood, 1982;

Byers, 1996; Campbell & Borden, 2006b; Saint-Germain *et al.*, 2007). In other wood-boring insects, host selection may involve olfactory and visual cues depending on the spatial scale of the search where beetles might use olfactory cues at the habitat scale or over longer distances while shifting to random landing over short distances or at the patch scale (Saint-Germain *et al.*, 2007). However, it is not known whether certain selection strategies become more precedent at different stages of the selection sequence or change with spatial scale for *I. typographus*.

The definition of random landing is not consistent in the literature, and generally, there seems to be some disagreement regarding the scale at which it may become important. From a general perspective, the term 'random landing' is somewhat misleading as it does not refer to a random or unguided search. Random landing may still require an attraction to host odours, and it has been shown for several bark beetle species (Saint-Germain *et al.*, 2007). However, the host acceptance is multifaceted and multistaged in this process and beetles can evaluate the host's suitability only postlanding and at close distance via haptic, gustatory or olfactory senses. On the contrary, primary attraction offers pioneer beetles an indication of where suitable hosts are located by evaluating cues emanating from the suitable host before landing on them. Postlanding cues may still be required for host acceptance when attacking vigorous trees, and hence, this is likely a more dominant mechanism during epidemics. During endemics, however, it is more likely that beetles assess the suitability of a host before landing from a long distance to avoid higher mortality due to longer exposure to, for example predators (Gries *et al.*, 1989).

Visual cues

While visual cues have not been investigated as thoroughly as olfactory cues, there is some evidence that they do matter in bark beetle host orientation (Campbell & Borden, 2006a). It has been shown for other species, including *D. ponderosae* and ambrosia beetles, that they use particular visual characteristics such as colour to avoid nonhost trees (Campbell & Borden, 2006b, 2009). Some *Ips* species are more attracted by stems with dark colours (Goyer *et al.*, 2004), while they seem to avoid white stems (Dubbel *et al.*, 1985). Additionally, it was demonstrated for *D. ponderosae* that adults show a higher attraction towards upright silhouettes. This may be a hint that besides colour, the shape is also perceived by beetles (Shepherd, 1966; Strom *et al.*, 1999), which might also be relevant for *I. typographus*.

Yet, the visual capacity of *I. typographus* and other bark beetles is rather limited and it is unlikely that visual cues alone would allow distinguishing between different coniferous species that are of similar appearance (Campbell & Borden, 2005). Instead, a combination of visual and olfactory cues may serve as a stimulus for effective host recognition (Campbell & Borden, 2006a,b; Byers, 2007).

Olfactory cues (volatile emissions)

Long-range cues Airborne odours emanating from host trees likely play an important role in directing bark beetles to forest stands with high abundance of host species and suitable individual trees during habitat and host search (Fig. 1). To find a habitat with host species, pioneering individuals of *I. typographus* are thought to respond to both host monoterpenes and nonhost volatiles (NHVs), including C_6 green leaf volatile alcohols, directing them towards spruce-dominated areas and away from deciduous trees (Schlyter & Birgersson, 1999). *Ips typographus* has numerous olfactory sensory neurons (OSNs) specifically tuned to host monoterpenes, NHVs and odours from microbial symbionts or from con- and heterospecific bark beetles (with the two latter being more important for secondary attraction; Tømmerås, 1985; Andersson *et al.*, 2009; Kandasamy *et al.*, 2019, 2021; Schiebe *et al.*, 2019). The behavioural effect of NHVs on I. *typographus* has been tested in combination with aggregation pheromones, suggesting inhibitory effects on secondary attraction (Zhang & Schlyter, 2003; Unelius *et al.*, 2014). Additionally, experiments in which NHVs in combination with anti-attractant verbenone were applied without aggregation pheromones on the trees to show decreased attack rates in treated zones, and attacks were diverted to neighbouring untreated zones (Jakus *et al.*, 2003; Schiebe *et al.*, 2011). However, since NHVs were tested together with verbenone (which is not involved in primary attraction), the potential effects of NHVs on *I. typographus* primary attraction remain unclear.

Attraction to individual host monoterpenes so far has not been demonstrated in flying *I. typographus* in natural habitats. This may not be surprising as is difficult to locate a particular source of VOCs in forest environments. Volatile concentrations in open forest spaces can be indeed higher than in the vicinity of individual trees (Stříbrská *et al.*, 2022), and the movements of volatile plumes are generally very complex to trace under natural forest conditions (Fares *et al.*, 1980). Additionally, many of the monoterpenes are also released from conifers other than spruce, as well as from individuals of the host tree species not in the diameter range of trees attacked by beetles. Hence, the informational value of individual host monoterpenes may be limited. Rather, one may expect that mixtures of hydrocarbon and oxygenated monoterpenes in specific ratios are more likely to guide the beetles to their host (Bruce *et al.*, 2005). In this regard, important unresolved questions are whether acutely stressed trees differ in terpenoid blends from fully vigorous trees and whether such emission profiles could be attractive to *I. typographus*.

Short-range cues Various stress factors alter the biochemical pathways in Norway spruce bark and needles and can cause qualitative and quantitative differences in secondary metabolite concentrations, which in turn can make host trees more attractive for colonisation. Several studies have reported primary attraction of *I. typographus* to host tree logs, trap trees and felled or windthrown trees based on olfactory cues yet without beetle pheromones (Rudinsky *et al.*, 1971; Austarå *et al.*, 1986; Lindelöw *et al.*, 1992; Jakuš & Blaženec, 2011). Notably, the attraction of pioneer beetles to windthrown trees was stronger when trees had aged on the ground for a few months, potentially because the VOC profile of the bark of felled trees also changes strongly over time (Schiebe *et al.*, 2019; Hroššo *et al.*, 2020). The total emission of volatiles in the midcrown area, where *I. typographus* usually initiates colonisation, was higher in felled trees compared with nonattacked standing trees (Schiebe *et al.*, 2019), while qualitative changes in the chemical profile of the bark of felled trees involve the accumulation of oxygenated monoterpenes and volatile aromatics over time (Kalinová *et al.*, 2014; Schiebe *et al.*, 2019). Taken together, this context-dependent variability in VOC emissions may very well be utilised by *I. typographus* for finding suitable hosts, thus reducing energy expenditure and mortality that may occur during lengthy nontargeted host search.

The volatile profile of Norway spruce needles is distinct from that of bark and is dominated mainly by oxygenated monoterpenes (Schönwitz *et al.*, 1990). Recently, OSNs specific for tree stress-related oxygenated monoterpenes were identified in *I. typographus*, indicating that such volatiles provide important cues to bark beetles (Schiebe *et al.*, 2019; Kandasamy *et al.*, 2021). Attractive cues from stressed trees may emanate also from needles and not only from the bark (Šotola *et al.*, 2021). Monoterpenes are released by all conifer tree species within the forest habitat; thus, emissions of minor oxygenated monoterpenes may convey reliable information to pioneer beetles about host suitability at the individual tree level. Low levels of oxygenated monoterpenes have been reported for bark of stressed trees before colonisation by bark beetles. Stress-induced changes in the bark of trees often switch the lifestyle of tree microbial epiphytes and endophytes to their parasitic or saprophytic phase (Rodriguez & Redman, 2008) and could lead to the production of oxygenated monoterpenes and other compounds, which are otherwise absent in vigorous trees. Notably, in certain doses several oxygenated monoterpenes like camphor and *trans*-4-thujanol that were identified in the bark of stressed host trees are attractive to *I. typographus* adults at short distance in laboratory bioassays when aggregation pheromones were absent (Kandasamy *et al.*, 2021). However, bioassays using high doses (> 200 µg) also showed that *trans*-4-thujanol was avoided by *I. typographus* (Blažytė-Čereškienė *et al.*, 2015; Kandasamy *et al.*, 2021) but high concentrations of oxygenated monoterpenes occurring after beetle attack are derived mainly from the metabolism of host terpenes by symbiotic microbes (Kandasamy *et al.*, 2021). Changes in the composition of host monoterpene concentrations in the bark and emissions from stressed trees, that is differential increase or decrease in individual volatile fluxes, could mediate their attractiveness and subsequent acceptance by bark beetles. Increased trap catches were observed during secondary attraction when (−)-α-pinene was added to pheromone-baited traps (Erbilgin *et al.*, 2007; Fang *et al.*, 2020); however, traps baited in (−)-α-pinene without aggregation pheromones do not result in any catches of *I. typographus*, suggesting no primary attraction to this single compound. Other monoterpenes such as limonene, myrcene, 3-carene and 1,8-cineole were shown to be toxic in laboratory bioassays and to reduce trap catch rates when combined with aggregation pheromones, suggesting inhibitory effects on secondary attraction (Andersson *et al.*, 2010; Fang *et al.*, 2020). Highly attractive trees emit higher levels of (−)-α-pinene and lower levels of (−)-limonene than unattractive trees (Zhao *et al.*, 2010). Bark beetles have likely evolved to avoid trees with high bark concentrations as emissions of these compounds might kill them (Everaerts *et al.*, 1988; Chiu *et al.*, 2017). However, effects of these toxic compounds on postlanding behaviour and primary attraction remain to be investigated in field experiments. Nevertheless, these studies collectively suggest that pioneers may evaluate the physiological status of potential host trees by assessing levels of a variety of conifer volatile compounds, and some of them are present only in very low concentrations.

Research agenda and methods for investigating bark beetle attractants

Despite the long history of research on bark beetle–tree interactions, there are still several knowledge gaps that limit our understanding of population dynamics of *I. typographus* and susceptibility of Norway spruce forest ecosystems to biotic disturbance. We list here some key knowledge gaps and research questions and indicate suitable approaches to address them (Table 1). Answering these questions will help understanding whether and how *I. typographus* may distinguish acutely stressed trees from highly vigorous ones and therefore increase its attack success.

Tree volatile emission and defence capacity

Although there is some evidence that volatile compounds play a role during host selection by *I. typographus* (Baier *et al.*, 1997; Schiebe *et al.*, 2019) and that pioneer beetles prefer acutely stressed trees for colonisation (Netherer *et al.*, 2015), data on differences in volatile emission profiles between stressed and unstressed trees are still missing (Table 1a). Measurements of volatile compounds can be done on trees in established drought experiments or on pull-down trees as a simulated windthrow. Such measurements are technically challenging as the forest atmosphere contains many volatile substances, but the use of dynamic stem chambers allows sampling only of those volatiles emitted by tree stems. Care should be taken during installation as to minimise physical damage of the bark by friction (Tholl *et al.*, 2006; Schiebe *et al.*, 2019), which may influence volatile emissions from the living tissues below the bark. VOCs accumulated in the headspace of the chambers can then be collected using absorption tubes containing polymer traps, Tedlar bags or canisters for later gas chromatography and mass spectrometry (GC–MS). Portable GC devices are convenient for *in situ* measurement and concurrent assessments. Concentrations of nonstructural carbohydrates and/or nonvolatile secondary metabolites like phenolics in tree stem tissues (Huang *et al.*, 2020b), which are indicative of relating to tree vitality and defence capacity (Table 1b).

Attraction and deterrence by NHVs have only been tested in combination with aggregation or anti-aggregation pheromones that are only relevant during secondary attraction. To test a potential inhibitory effect of NHVs on primary attraction, choice assays in the field, especially in mixed species stands and in the laboratory with varying combinations of NHVs, without pheromone or host monoterpenes addition, can shed light on the inhibitory effect of NHVs on host preference (Table 1c).

Beetle volatile perception and response

Once the differences in the emission profiles of vigorous/nonattractive and acutely stressed/attractive trees have been

Table 1 Knowledge gaps and proposed approaches to resolve them.

	Organism	Knowledge gap/research question	Parameters to assess	Methodological approach
(a)	T	Do VOC emission mixtures change with tree vigour?	VOC profiles	Tree vigour treatment (e.g. pull-down) adsorption tubes or a mobile GC–MS[1]
(b)	T	Is defence capacity correlated with distinct volatile profiles?	VOC profiles, defence compounds	GC–MS, LC–MS of terpenoid and phenolics
(c)	I	Do NHVs reduce primary attraction?	Attraction of beetles to NHVs and host volatiles	Choice experiments in field and laboratory
(d)	B	Which individual compounds found in (b) can be perceived by beetles?	Antennal sensilla response activity	Antennal sensilla assays[2]
(e)	B	Which individual compounds or compounds mixed identified in (d) have a high beetle attraction potential?	Attraction of beetles to individual compounds and compound mixtures	Choice experiments[2]
(f)	I	Do visual, olfactory and gustatory cues complement each other in host selection?	Host tree selection	Choice experiment using traps with different combinations of colours[3] and volatile cues in the laboratory and the field (collection traps); laboratory bioassays (Petri dish choice experiments)[4]
(g)	I	Do host choice mechanisms change with scale? (long and short distance)	Responsiveness of beetle towards emission profiles from different distances	Choice experiment drones to characterise volatile profiles

The column ‘Organism’ displays which organism is of interest in this research question.
B, beetle (*Ips typographus*); GC–MS, gas chromatography–mass spectrometry; I, interaction between beetle and tree; LC–MS, liquid chromatography–mass spectrometry; NHVs, nonhost volatiles; T, tree (*Picea abies*); VOCs, volatile organic compounds.

[1] For example, https://www.inficon.com/en/products/chemical-detection-and-monitoring.

[2] Kandasamy *et al*. (2019).

[3] Netherer *et al*. (2022).

[4] Jönsson *et al*. (2012).

established, it needs to be examined whether and which of the compounds the beetles can detect and use to evaluate the physiological status/suitability of trees. Electrophysiological studies on antennal sensilla can indicate the responsiveness of beetles towards active odorants (Table 1c). Single sensillum recording technique has proven highly successful for identifying response profiles of numerous classes of olfactory sensory neurons in *I. typographus*, (Tømmerås, 1985; Andersson *et al.*, 2009; Kandasamy *et al.*, 2019). Compounds that stimulate neuronal responses are tested in both laboratory and field selection bioassays for their potential to exert attraction (Table 1d; Kandasamy *et al.*, 2019).

Influence of scale and population dynamics

Host selection might be influenced by a variety of visual, olfactory and gustatory cues (Table 1e), which are differentially relevant at the various temporal and spatial scales. For instance, distance to host trees/forest stands, that is host search on landscape or habitat scale, likely has a strong effect on the perception of trees by pioneer beetles (Table 1f). A very promising sampling method, for evaluating differences in volatile blends and concentrations on different scales, is drones with implemented VOC samplers (Batista *et al.*, 2019; McKinney *et al.*, 2019). Measurements with drones provide volatile patterns of entire tree stands, including emissions from both bark and foliage. While models that consider tree health and population dynamics exist (Jönsson *et al.*, 2011; Wildemeersch *et al.*, 2019), primary attraction and its implications for host selection are not yet incorporated. Such models can then be used to test the effect of population size on selection criteria, and vice versa.

Conclusion

Our presented research agenda focusses on knowledge gaps concerning direct interactions between *I. typographus* pioneer beetles and *P. abies* trees. Several other biotic (e.g. predators or other herbivores, and fungal diseases), abiotic (e.g. soil water potential or light intensity) and anthropological factors (e.g. proximity of agricultural or industrial sites) will also influence these interactions and interdisciplinary approaches involving for instance tree and beetle’s ecophysiology, behavioural entomology, forest ecology, biochemistry, sensory biology and chemical ecology are needed. Here, we defined first logical steps, but we are aware that further field and laboratory experiments to investigate processes at small and large scale are required. Further improvements in sampling methods with drones, better beetle trapping methods and multifactorial behavioural bioassays will help paving the road towards a better understanding of the tree–beetle relationship. Given the enormous damages bark beetles are causing in many forests across the globe, fast progress is crucial.

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Competing interests

None declared.

Author contributions

LMAL and HH developed the concept of the paper, drafted several sections (Introduction, *Ips typographus* ecology and population dynamics, Potential mechanisms of host selection by pioneer bark beetles, and Tree volatile emission and defence capacity) and revised contributions by co-authors. DK and MNA drafted section Olfactory cues (volatile emissions). SN, EGA, and JH contributed to the conceptual ideas. All authors revised and commented on the manuscript.

ORCID

Eliane Gomes Alves https://orcid.org/0000-0001-5245-1952
Martin N. Andersson https://orcid.org/0000-0001-9807-8524
Henrik Hartmann https://orcid.org/0000-0002-9926-5484
Jianbei Huang https://orcid.org/0000-0001-5286-5645
Dineshkumar Kandasamy https://orcid.org/0000-0002-5450-3231
Linda M. A. Lehmanski https://orcid.org/0000-0002-1399-7538
Sigrid Netherer https://orcid.org/0000-0003-1801-7372

Linda M. A. Lehmanski[1]*, Dineshkumar Kandasamy[2,3], Martin N. Andersson[2,3], Sigrid Netherer[4], Eliane Gomes Alves[1], Jianbei Huang[1] and Henrik Hartmann[1,5]

[1]Department of Biogeochemical Processes, Max Planck Institute for Biogeochemistry, Jena 07745, Germany;
[2]Department of Biology, Lund University, Lund 22362, Sweden;
[3]Max Planck Center for Next Generation Insect Chemical Ecology (nGICE), Department of Biology, Lund University, Lund 22362, Sweden;
[4]Institute of Forest Entomology, Forest Pathology and Forest Protection, Department of Forest and Soil Sciences, University of Natural Resources and Life Sciences, BOKU, Vienna 1190, Austria;
[5]Institute for Forest Protection, Julius Kühn-Institute Federal Research Centre for Cultivated Plants, Quedlinburg 06484, Germany

(*Author for correspondence: email llehmanski@bgc-jena.mpg.de)

References

Andersson MN, Larsson MC, Blaženec M, Jakuš R, Zhang Q-H, Schlyter F. 2010. Peripheral modulation of pheromone response by inhibitory host compound in a beetle. *Journal of Experimental Biology* **213**: 3332–3339.

Andersson MN, Larsson MC, Schlyter F. 2009. Specificity and redundancy in the olfactory system of the bark beetle *Ips typographus*: single-cell responses to ecologically relevant odors. *Journal of Insect Physiology* **55**: 556–567.

Austarå O, Bakke A, Midtgaard F. 1986. Response in *Ips typographus* to logging waste odours and synthetic pheromones. *Journal of Applied Entomology* **101**: 194–198.

Baier P, Bader R, Rosner S. 1997. Monoterpene content and monoterpene emission of Norway spruce (*Picea abies* (L.) Karst.) bark in relation to primary attraction of bark beetles (Col., Scolytidae). *Physiology and Genetics of Tree-Phytophage Interactions–International Symposium* **90**: 249–259.

Baier P, Hoch G, Kirisits T, Netherer S. 2019. In: Hoch G, Schopf A, Wizer G, eds. *Der Buchdrucker Biologie, Ökologie, Management.* Vienna, Austria: BFW Bundesforschungszentrum für Wald.

Bakke A, Austarå O, Pettersen H. 1977. Seasonal flight activity and attack pattern of *Ips typographus* in Norway under epidemic condition. *Meddelelser Fra Norsk Institutt for Skogforskning* **33**: 257–268.

Batista CE, Ye J, Ribeiro IO, Guimarães PC, Medeiros ASS, Barbosa RG, Oliveira RL, Duvoisin S, Jardine KJ, Gu D *et al.* 2019. Intermediate-scale horizontal isoprene concentrations in the near-canopy forest atmosphere and implications for emission heterogeneity. *Proceedings of the National Academy of Sciences, USA* **116**: 19318–19323.

Berthelot S, Frühbrodt T, Hajek P, Nock CA, Dormann CF, Bauhus J, Fründ J. 2021. Tree diversity reduces the risk of bark beetle infestation for preferred conifer species, but increases the risk for less preferred hosts. *Journal of Ecology* **109**: 2649–2661.

Biedermann PHW, Müller J, Grégoire J-C, Gruppe A, Hagge J, Hammerbacher A, Hofstetter RW, Kandasamy D, Kolarik M, Kostovcik M *et al.* 2019. Bark beetle population dynamics in the Anthropocene: challenges and solutions. *Trends in Ecology & Evolution* **34**: 914–924.

Blažytė-Čereškienė L, Apšegaitė V, Radžiutė S, Mozūraitis R, Būda V, Pečiulytė D. 2015. Electrophysiological and behavioural responses of *Ips typographus* (L.) to trans-4-thujanol–a host tree volatile compound. *Annals of Forest Science* **73**: 247–256.

Boone CK, Aukema BH, Bohlmann J, Carroll AL, Raffa KF. 2011. Efficacy of tree defence physiology varies with bark beetle population density: a basis for positive feedback in eruptive species. *Canadian Journal of Forest Research* **41**: 1174–1188.

Bruce TJA, Wadhams LJ, Woodcock CM. 2005. Insect host location: a volatile situation. *Trends in Plant Science* **10**: 269–274.

Burke JL, Carroll AL. 2017. Breeding matters: natal experience influences population state-dependent host acceptance by an eruptive insect herbivore. *PLoS ONE* **12**: e0172448.

Byers JA. 1989. Chemical ecology of bark beetles. *Experientia* **45**: 271–283.

Byers JA. 1996. An encounter rate model of bark beetle populations searching at random for susceptible host trees. *Ecological Modelling* **91**: 57–66.

Byers JA. 2007. Chemical ecology of bark beetles in a complex olfactory landscape. In: Lieutier F, ed. *Bark and wood boring insects in living trees in Europe: a synthesis.* Boston, MA, USA & London, UK: Kluwer Academic, 89–134.

Campbell SA, Borden JH. 2005. Bark reflectance spectra of conifers and angiosperms: implications for bark and timber beetle host selection (Coleoptara: Scolytidae). *The Canadian Entomologist* **137**: 719–722.

Campbell SA, Borden JH. 2006a. Close-range, in-flight integration of olfactory and visual information by a host-seeking bark beetle. *Entomologia Experimentalis et Applicata* **120**: 91–98.

Campbell SA, Borden JH. 2006b. Integration of visual and olfactory cues of hosts and non-hosts by three bark beetles (Coleoptera: Scolytidae). *Ecological Entomology* **31**: 437–449.

Campbell SA, Borden JH. 2009. Additive and synergistic integration of multimodal cues of both hosts and non-hosts during host selection by woodboring insects. *Oikos* **118**: 553–563.

Chiu CC, Keeling CI, Bohlmann J. 2017. Toxicity of pine monoterpenes to mountain pine beetle. *Scientific Reports* 7: 8858.

Christiansen E, Bakke A. 1989. The spruce bark beetle of Eurasia. In: Berryman AA, ed. *Dynamics of forest insect populations: patterns, causes, implications.* New York, NY, USA: Plenum Press, 479–503.

Christiansen E, Warning RH, Berryman AA. 1987. Resistance of conifers to bark beetle attack: searching for general relationships. *Forest Ecology and Management* **22**: 89–106.

Dubbel V, Kerck K, Sohrt M, Mangold S. 1985. Influence of trap color on the efficiency of bark beetle pheromone traps. *Journal of Applied Entomology* **99**: 1–5.

Erbilgin N, Krokene P, Kvamme T, Christiansen E. 2007. A host monoterpene influences *Ips typographus* (Coleoptera: Curculionidae, Scolytinae) responses to its aggregation pheromone. *Agricultural and Forest Entomology* **9**: 135–140.

Eriksson M, Pouttu A, Roininen H. 2005. The influence of windthrow area and timber characteristics on colonization of wind-felled spruces by *Ips typographus* (L.). *Forest Ecology and Management* **216**: 105–116.

Everaerts C, Gregoire J-C, Merlin J. 1988. The toxicity of Norway spruce monoterpenes to two bark beetle species and their associates. In: Mattson WJ, Levieux J, Bernard-Dagan C, eds. *Mechanisms of woody plant defences against insects: search for pattern.* New York, NY, USA: Springer, 335–344.

Fang J, Zhang S, Liu F, Cheng B, Zhang Z, Zhang Q-H, Kong X. 2020. Functional investigation of monoterpenes for improved understanding of the relationship between hosts and bark beetles. *Journal of Applied Entomology* **145**: 303–311.

Fares Y, Sharpe PJH, Magnuson CE. 1980. Pheromone dispersion in forests. *Journal of Theoretical Biology* **84**: 335–359.

Geiszler R, Gara RI. 1978. Mountain pine beetle attack dynamics in lodgepole pine. In: *Theory and practice of mountain pine beetle management in lodgepole pine forests: symposium proceedings.* Pullman, WA, USA: Washington State University, 182–187.

Gmelin JF. 1787. *Abhandlung über die Wurmtrocknis.* Leipzig, Germany: Verlag der Crusiussischen Buchhandlung.

Goyer RA, Lenhard GJ, Strom BL. 2004. The influence of silhouette colour and orientation on arrival and emergence of *Ips* pine engravers and their predators in loblolly pine. *Forest Ecology and Management* **191**: 147–155.

Gries G, Nolte R, Sanders W. 1989. Computer simulated host selection in *Ips typographus. Entomologia Experimentalis et Applicata* **53**: 211–217.

Hlásny T, König L, Krokene P, Lindner M, Montagné-Huck C, Müller J, Qin H, Raffa KF, Schelhaas M-J, Svoboda M *et al.* 2021a. Bark beetle outbreaks in Europe: state of knowledge and ways forward for management. *Current Forestry Reports* 7: 138–165.

Hlásny T, Zimová S, Bentz B. 2021b. Scientific response to intensifying bark beetle outbreaks in Europe and North America. *Forest Ecology and Management* **499**: 119599.

Howe M, Raffa KF, Aukema BH, Gratton C, Carroll AL. 2022. Numbers matter: how irruptive bark beetles initiate transition to self-sustaining behavior during landscape-altering outbreaks. *Oecologia* **198**: 681–698.

Hroššo B, Mezei P, Potterf M, Majdák A, Blaženec M, Korolyova N, Jakuš R. 2020. Drivers of spruce bark beetle (*Ips typographus*) infestations on downed trees after severe windthrow. *Forests* **11**: 1290.

Huang J, Kautz M, Trowbridge AM, Hammerbacher A, Raffa KF, Adams HD, Goodsman DW, Xu C, Meddens AJH, Kandasamy D *et al.* 2020a. Tree defence and bark beetles in a drying world: carbon partitioning, functioning and modelling. *New Phytologist* **225**: 26–36.

Huang J, Rücker A, Schmidt A, Gleixner G, Gershenzon J, Trumbore S, Hartmann H. 2020b. Production of constitutive and induced secondary metabolites is coordinated with growth and storage in Norway spruce saplings. *Tree Physiology* **40**: 928–942.

Hynum BG, Berryman AA. 1980. *Dendroctonus ponderosae* (Coleoptera: Scolytidae): pre-aggregation landing and gallery initiation on lodgepole pine. *The Canadian Entomologist* **112**: 185–191.

Jakuš R, Blaženec M. 2011. Response of walking spruce bark beetles *Ips typographus* to host odours. *Folia Oecologica* **38**: 38–45.

Jakus R, Schlyter F, Zhang Q-H, Blazenec M, Vavercak R, Grodzki W, Brutovsky D, Lajzova E, Turcani M, Bengtsson M *et al.* 2003. Overview of development of an anti-attractant based technology for spruce protection against *Ips typographus*: from past failures to future success. *Anzeiger Fur Schödlingskunde* **76**: 89–99.

Jönsson AM, Harding S, Krokene P, Lange H, Lindelöw Å, Økland B, Ravn HP, Schroeder LM. 2011. Modelling the potential impact of global warming on *Ips typographus* voltinism and reproductive diapause. *Climatic Change* **109**: 695–718.

Jönsson AM, Schroeder LM, Lagergren F, Anderbrant O, Smith B. 2012. Guess the impact of *Ips typographus*–an ecosystem modelling approach for simulating spruce bark beetle outbreaks. *Agricultural and Forest Meteorology* **166–167**: 188–200.

Kalinová B, Břízová R, Knížek M, Turčáni M, Hoskovec M. 2014. Volatiles from spruce trap-trees detected by *Ips typographus* bark beetles: chemical and electrophysiological analyses. *Arthropod–Plant Interactions* **8**: 305–316.

Kandasamy D, Gershenzon J, Andersson MN, Hammerbacher A. 2019. Volatile organic compounds influence the interaction of the Eurasian spruce bark beetle (*Ips typographus*) with its fungal symbionts. *The ISME Journal* **13**: 1788–1800.

Kandasamy D, Zaman R, Nakamura Y, Zhao T, Hartmann H, Andersson MN, Hammerbacher A, Gershenzon J. 2021. Bark beetles locate fungal symbionts by detecting volatile fungal metabolites of host tree resin monoterpenes. *BioRxiv.* doi: 10.1101/2021.07.03.450988.

Kausrud K, Økland B, Skarpaas O, Grégoire J-C, Erbilgin N, Stenseth NC. 2012. Population dynamics in changing environments: the case of an eruptive forest pest species. *Biological Reviews* **87**: 34–51.

Kausrud KL, Grégoire J-C, Skarpaas O, Erbilgin N, Gilbert M, Økland B, NC S. 2011. Trees wanted–dead or alive! Host selection and population dynamics in tree-killing bark beetles. *PLoS ONE* **6**: e18274.

Keeling CI, Tittiger C, MacLean M, Blomquist GJ. 2020. Pheromone production in bark beetles. In: Blomquist GJ, Vogt R, eds. *Insect pheromone biochemistry and molecular biology, 2nd* edn. Amsterdam, the Netherlands: Elsevier, 123–162.

Lieutier F, Day KR, Battisti A, Grégoire J-C, Evans HF, eds. 2004. *Bark and wood boring insects in living trees in Europe: a synthesis.* Boston, MA, USA & London, UK: Kluwer Academic Publishers.

Lindelöw Å, Risberg B, Sjödin K. 1992. Attraction during flight of scolytids and other bark- and wood-dwelling beetles to volatiles from fresh and stored spruce wood. *Canadian Journal of Forest Research* **22**: 224–228.

Lobinger G. 1994. Die Lufttemperatur als limitierender Faktor für die Schwärmaktivität zweier rindenbrütender Borkenkäferarten, *Ips typographus* L. und *Pityogenes chalcographus* L. (Col., Scolytidae). *Anzeiger Fuer Schaedlingskunde Pflanzenschutz Umweltschutz* **67**: 14–17.

McKinney KA, Wang D, Ye J, de Fouchier J-B, Guimarães PC, Batista CE, Souza RAF, Alves EG, Gu D, Guenther AB *et al.* 2019. A sampler for atmospheric volatile organic compounds by copter unmanned aerial vehicles. *Atmospheric Measurement Techniques* **12**: 3123–3135.

Meyen FJF, Von Esenbeck CGN. 1841. *Pflanzen–Pathologie: Lehre von dem kranken Leben und Bilden der Pflanzen.* Berlin, Germany: Hause und Spener.

Moeck HA, Wood DL, Lindahl KQ. 1981. Host selection behavior of bark beetles (Coleoptera: Scolytidae) attacking *Pinus ponderosa*, with special emphasis on the western pine beetle *Dendroctonus brevicomis. Journal of Chemical Ecology* 7: 49–83.

Netherer S, Kandasamy D, Jirosová A, Kalinová B, Schebeck M, Schlyter F. 2021. Interactions among Norway spruce, the bark beetle *Ips typographus* and its fungal symbionts in times of drought. *Journal of Pest Science* **94**: 591–614.

Netherer S, Matthews B, Katzensteiner K, Blackwell E, Henschke P, Hietz P, Pennerstorfer J, Rosner S, Kikuta S, Schume H *et al.* 2015. Do water-limiting conditions predispose Norway spruce to bark beetle attack? *New Phytologist* **205**: 1128–1141.

Netherer S, Schebeck M, Morgante G, Rentsch V, Kirisits T. 2022. European spruce bark beetle, *Ips typographus* (L.) males are attracted to bark cores of drought-stressed Norway spruce trees with impaired defenses in Petri dish choice experiments. *Forests* **13**: 537.

Person HL. 1931. Theory in explanation of the selection of certain trees by the western pine beetle. *Journal of Forestry* **29**: 696–699.

Raffa KF, Andersson MN, Schlyter F. 2016. Host selection by bark beetles: playing the odds in a high-stakes game. In: Tittiger C, Blomquist GJ, eds. *Advances in insect physiology, vol. 50.* Oxford, UK: Academic Press, 1–74.

Raffa KF, Berryman AA. 1980. Flight response and host selection by bark beetles. In: Berryman AA, Safranyik K, eds. *Proceedings of the second IUFRO conference on dispersal of forest insects: evaluation, theory and management implications.* Pullman, WA, USA: Washington State University, 213–233.

Ratzeburg JTC. 1839. *Die Forstinsecten.* Berlin, Germany: Nicolai'sche Buchhandlung.

Rodriguez R, Redman R. 2008. More than 400 million years of evolution and some plants still can't make it on their own: plant stress tolerance via fungal symbiosis. *Journal of Experimental Botany* **59**: 1109–1114.

Rudinsky JA. 1962. Ecology of Scolytidae. *Annual Review of Entomology* **7**: 327–348.

Rudinsky JA, Novák VSP, Švihra P. 1971. Pheromone and terpene attraction in the bark Beetle *Ips typographus* L. *Experientia* **27**: 161–162.

Saint-Germain M, Buddle CM, Drapeau P. 2007. Primary attraction and random landing in host-selection by wood-feeding insects: a matter of scale? *Agricultural and Forest Entomology* **9**: 227–235.

Schebeck M, Dobart N, Ragland GJ, Schopf A, Stauffer C. 2022. Facultative and obligate diapause phenotypes in populations of the European spruce bark beetle *Ips typographus*. *Journal of Pest Science* **95**: 889–899.

Schiebe C, Blaženec M, Jakuš R, Unelius CR, Schlyter F. 2011. Semiochemical diversity diverts bark beetle attacks from Norway spruce edges: NHV interfere with bark beetles' host finding. *Journal of Applied Entomology* **135**: 726–737.

Schiebe C, Unelius CR, Ganji S, Binyameen M, Birgersson G, Schlyter F. 2019. Styrene, (+)-trans-(1R,4S,5S)-4-Thujanol and oxygenated monoterpenes related to host stress elicit strong electrophysiological responses in the bark beetle *Ips typographus*. *Journal of Chemical Ecology* **45**: 474–489.

Schlyter F, Birgersson G. 1999. Forest beetles. In: Hardie RJ, Minks AK, eds. *Pheromones of non-lepidopteran insects associated with agricultural plants*. Wallingford, UK: CAB International, 113–148.

Schlyter F, Birgersson G, Leufvén A. 1989. Inhibition of attraction to aggregation pheromone by verbenone and ipsenol–density regulation mechanisms in bark beetle *Ips typographus*. *Journal of Chemical Ecology* **15**: 2263–2277.

Schönwitz R, Lohwasser K, Kloos M, Ziegler H. 1990. Seasonal variation in the monoterpenes in needles of *Picea abies* (L.) Karst. *Trees* **4**: 34–40.

Shepherd RF. 1966. Factors influencing the orientation and rates of activity of *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). *The Canadian Entomologist* **98**: 507–518.

Šotola V, Holuša J, Kuželka K, Kula E. 2021. Felled and lure trap trees with uncut branches are only weakly attractive to the Double-spined bark beetle, *Ips Duplicatus*. *Forests* **12**: 941.

Stříbrská B, Hradecký J, Čepl J, Tomášková I, Jakuš R, Modlinger R, Netherer S, Jirošová A. 2022. Forest margins provide favourable microclimatic niches to swarming bark beetles, but Norway spruce trees were not attacked by *Ips typographus* shortly after edge creation in a field experiment. *Forest Ecology and Management* **506**: 119950.

Strom BL, Roton LM, Goyer RA, Meeker JR. 1999. Visual and semiochemical disruption of host finding in the southern pine beetle. *Ecological Applications* **9**: 1028–1038.

Tholl D, Boland W, Hansel A, Loreto F, Röse USR, Schnitzler J-P. 2006. Practical approaches to plant volatile analysis. *The Plant Journal* **45**: 540–560.

Tømmerås BÅ. 1985. Specialization of the olfactory receptor cells in the bark beetle *Ips typographus* and its predator *Thanasimus formicarius* to bark beetle pheromones and host tree volatiles. *Journal of Comparative Physiology A* **157**: 335–341.

Unelius CR, Schiebe C, Bohman B, Andersson MN, Schlyter F. 2014. Non-host volatile blend optimization for forest protection against the European spruce bark beetle, *Ips typographus*. *PLoS ONE* **9**: e85381.

Wallin KF, Raffa KF. 2004. Feedback between individual host selection behavior and population dynamics in an eruptive herbivore. *Ecological Monographs* **74**: 101–116.

Wermelinger B. 2004. Ecology and management of the spruce bark beetle *Ips typographus*–a review of recent research. *Forest Ecology and Management* **202**: 67–82.

Wildemeersch M, Franklin O, Seidl R, Rogelj J, Moorthy I, Thurner S. 2019. Modelling the multi-scaled nature of pest outbreaks. *Ecological Modelling* **409**: 108745.

Wood DL. 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization of bark beetles. *Annual Review of Entomology* **27**: 411–446.

Zhang Q-H, Schlyter F. 2003. Redundancy, synergism, and active inhibitory range of non-host volatiles in reducing pheromone attraction in European spruce bark beetle *Ips typographus*. *Oikos* **101**: 299–310.

Zhao T, Kandasamy D, Krokene P, Chen J, Gershenzon J, Hammerbacher A. 2019. Fungal associates of the tree-killing bark beetle, *Ips typographus*, vary in virulence, ability to degrade conifer phenolics and influence bark beetle tunneling behavior. *Fungal Ecology* **38**: 71–79.

Zhao T, Krokene P, Björklund N, Långström B, Solheim H, Christiansen E, Borg-Karlson A-K. 2010. The influence of *Ceratocystis polonica* inoculation and methyl jasmonate application on terpene chemistry of Norway spruce, *Picea abies*. *Phytochemistry* **71**: 1332–1341.

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