



Interactions among Norway spruce, the bark beetle *Ips typographus* and its fungal symbionts in times of drought

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Abstract

Resilience and functionality of European Norway spruce forests are increasingly threatened by mass outbreaks of the bark beetle *Ips typographus* promoted by heat, wind throw and drought. Here, we review current knowledge on Norway spruce and *I. typographus* interactions from the perspective of drought-stressed trees, host selection, colonisation behaviour of beetles, with multi-level effects of symbiotic ophiostomatoid fungi. By including chemo-ecological, molecular and behavioural perspectives, we provide a comprehensive picture on this complex, multitrophic system in the light of climate change. Trees invest carbon into specialised metabolism to produce defence compounds against biotic invaders; processes that are strongly affected by physiological stress such as drought. Spruce bark contains numerous terpenoid and phenolic substances, which are important for bark beetle aggregation and attack success. Abiotic stressors such as increased temperatures and drought affect composition, amounts and emission rates of volatile compounds. Thus, drought events may influence olfactory responses of *I. typographus*, and further the pheromone communication enabling mass attack. In addition, *I. typographus* is associated with numerous ophiostomatoid fungal symbionts with multiple effects on beetle life history. Symbiotic fungi degrade spruce toxins, help to exhaust tree defences, produce beetle semiochemicals, and possibly provide nutrition. As the various fungal associates have different temperature optima, they can influence the performance of *I. typographus* differently under changing environmental conditions. Finally, we discuss why effects of drought on tree-killing by bark beetles are still poorly understood and provide an outlook on future research on this eruptive species using both, field and laboratory experiments.

Keywords *Picea abies* · Spruce bark beetle · Ophiostomatoid fungi · Drought · Tree defence · Specialised metabolites

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Key message

- Drought-induced mass outbreaks of the bark beetle *Ips typographus* cause extensive tree mortality in European Norway spruce forests.
- Altered tree chemistry due to heat and drought affects composition, amounts, and emission rates of specialised metabolites including defence compounds.
- Specialised metabolites have positive and negative impacts on bark beetle host aggregation and acceptance on spatial and temporal scales.
- Drought can affect the performance of *I. typographus* and also its symbiotic ophiostomatoid fungi that detoxify tree defence compounds and produce beetle semiochemicals.

Introduction

The Eurasian spruce bark beetle, *Ips typographus* (L.) (Coleoptera: Curculionidae: Scolytinae), is the most destructive forest pest of Norway spruce, *Picea abies* (L.) Karst. (Pinales: Pinaceae). It is one of the few bark beetle species worldwide that can undergo eruptive population outbreaks and lead to extensive forest mortality (Bentz et al. 2019; Kausrud et al. 2012). Rapid population growth commonly follows abiotic disturbance events, such as wind throw, snow break, high temperatures and drought (Jakoby et al. 2019; Marini et al. 2017; Seidl et al. 2016; Stadelmann et al. 2014). Climate change has caused an increased frequency and severity of hot and dry periods, thereby altering the distribution of trees and their susceptibility to diverse abiotic and biotic stressors (Allen et al. 2010; Jactel et al. 2012; Rouault et al. 2006). A number of recent articles have addressed the effects of abiotic factors on tree mortality and defence (Berini et al. 2018; Hartmann et al. 2018; Holopainen et al. 2018) and drought-related interactions between bark beetles and trees, especially *Dendroctonus* species attacking *Pinus* hosts in North America (Kolb et al. 2016, 2019; Sambaraju et al. 2019). Knowledge of climate change effects on Norway spruce defence chemistry, *I. typographus* population dynamics and interactions with associated organisms such as ophiostomatoid fungi (Kandasamy et al. 2019; Kirisits 2004; Zhao et al. 2019b) is crucial to understand the life history processes of this insect and also provides the basis for reliable predictions of mass outbreaks (Biedermann et al. 2019; Huang et al. 2020).

Here, we review chemo-ecological, molecular and behavioural aspects of this multitrophic system from the

perspectives of bark beetles, symbiotic fungi and Norway spruce. In drought-stressed conifers, the decline of photosynthetic activity due to closure of stomata results in reduced availability of carbon for primary and secondary metabolism. In particular, drought stress affects the investment of carbon into plant growth and the maintenance of life-sustaining mechanisms such as respiration and defence (Adams et al. 2013; McDowell et al. 2008). Drought stress can have negative, neutral or even positive effects on constitutive (preformed) and induced tree defences, depending on the intensity and frequency of the triggering event and recovery times (Ayres and Lombardero 2000; Eyles et al. 2010; Koricheva et al. 1998; Niinemets 2010). Apart from acute stress events, stress history and tree genotype mediate drought effects on tree resistance and defence (Lopez-Goldar et al. 2018). Resin flow, for example, which most effectively protects Pinaceae against biotic invaders, is highly variable among trees and was shown to increase with mild to moderate drought but to decrease and even stop with severe water deficiency (Gaylord et al. 2013; Lieutier 2004; Lombardero et al. 2000; Netherer et al. 2015). Moreover, drought can impair further induction of defences such as formation of traumatic resin ducts in response to physical injury, insect and/or fungus attack (Klutsch et al. 2017). Conifer resin contains mainly terpenes; their concentration and emission rates are strongly influenced by heat and drought in both positive and negative ways (Ferrenberg et al. 2017; Holopainen et al. 2018; Mattson and Haak 1987). In the following sections, we focus on biochemical processes in drought-stressed trees with particular focus on specialised (secondary) metabolite concentrations, emission of volatile organic compounds (VOC) (Table 1) and their role as essential cues for *I. typographus* host selection, aggregation and host acceptance.

The diversity of specialised metabolites comprises terpenoids, phenolics and some compounds derived from fatty acids and proteins. Proteins, for instance, are involved in many stress-related processes such as the strengthening of

Table 1 Abbreviations used in manuscript, figures and table

Abbreviation	Term
ABA	Abscisic acid
GR	Gustatory receptors
IR	Ionotropic receptors
MeJA	Methyl jasmonate
NSC	Non-structural carbohydrates
OR	Odorant receptors
OSN	Olfactory sensory neurons
PP	Polyphenolic parenchyma cells
VOC	Volatile organic compounds

plant cell walls (Fossdal et al. 2007). Concentration and composition of specialised metabolites determine the bark quality for insect and fungal performance (Erbilgin et al. 2017; Franceschi et al. 2005; Holopainen et al. 2018; Måns-son 2005). A healthy tree has constitutive defence traits in the form of terpene-rich resins stored in specialised resin ducts or canals and (poly)phenolic compounds, produced and stored in polyphenolic parenchyma (PP) cells (Franceschi et al. 2005). Constitutive phenolic diversity and specific phenolic compounds have been recognised to enhance tree resistance against ophiostomatoid fungi associated with bark beetles (Brignolas et al. 1998; Evensen et al. 2000). However, induced defence reactions involving the upregulation of specialised metabolites such as monoterpenes and phenolics in response to wounding, fungal attack or methyl jasmonate application are more reliable to indicate the potential of a tree to defend itself (Balogh et al. 2018; Martin et al. 2003; Schiebe et al. 2012; Zhao et al. 2010, 2011b). Methyl jasmonate (MeJA) is an organic compound derived from the plant hormone jasmonic acid that induces plants to produce multiple types of defence chemicals. By activating enzymes involved in terpene synthesis (Celedon and Bohlmann 2019), MeJA treatments can lead to increased toxic terpene levels in tree tissue (Zeneli et al. 2006). Such tree reactions potentially impact host acceptance and colonisation success of *I. typographus*, which we discuss in Sect. 3.

Bark defence compounds affect bark beetle host acceptance for feeding and oviposition. These compounds indicate host quality via taste of *I. typographus* or provide olfactory signals from host and non-host trees (Byers et al. 1998; Faccoli et al. 2005; Zhang and Schlyter 2004). During beetle dispersal, emergence and flight are not directly dependent on chemical cues, but mainly driven by temperature and wind conditions (Byers 2000). Flight exercise and fat loss during dispersal stimulate response of bark beetles to kairomones and pheromones (Byers et al. 1998; Graham 1959; Wijerathna and Evenden 2019), and beetles become sensitive to cues from suitable habitats or individual trees. Although host tree distribution in the landscape is unpredictable and patchy (Kausrud et al. 2011), *Ips* pioneer beetles appear to select spruce trees of suitable age, nutritional value and defence status with remarkable precision (Wood 1972). The exact mechanisms for choosing susceptible trees, such as drought-stressed or wind-thrown individuals, are as yet little known. The role of volatile cues from stressed host trees for host-seeking pioneer beetles remains elusive. Alternatively, beetles are supposed to land randomly (Byers 1989, 1999) and select hosts based on chemical stimuli acting at short distances. Navigation of conspecifics to suitable hosts are then guided by pheromones and may be further supported by volatiles released by symbiotic fungi (Kandasamy et al. 2016). Associated ophiostomatoid fungi produce pheromone components and help to exhaust tree defences.

Fungal symbionts are able to detoxify terpenes and phenolics (Lieutier et al. 2009; Wadke et al. 2016; Wang et al. 2014; Zhao et al. 2019a). Understanding these multipartite relationships is essential to predict *I. typographus* performance and is facilitated by the now available genome of this species (Powell et al. 2020).

The Norway spruce perspective

Tree metabolism under drought stress

Conifer defences have evolved under multifaceted abiotic and biotic selection pressures for millions of years. Expression of defence mechanisms differs substantially among tree species and underlies genotypic, phenotypic, as well as ontogenetic variation. Tree defence is strongly shaped by environmental conditions, such as light and temperature (Berini et al. 2018; Ferrenberg et al. 2017). Heat and drought conditions continuously reduce water tension in the xylem. Tree species with mainly isohydric behaviour, such as many Pinaceae, do not tolerate water potential to drop below a certain threshold and respond by closing their stomata to prevent water loss (Fig. 1) (Moran et al. 2017; Sevanto et al. 2014). Soil water supply and climatic parameters impact tree net-photosynthesis and consequently the supply of non-structural carbohydrates (NSC), mainly low-molecular weight sugars and starch (Adams et al. 2013; Hoch et al. 2003). NSC pools, which vary among plant tissues and fluctuate over the season, are the central energy resources of a tree for respiration, growth, reproduction, storage, as well as constitutive and induced production of specialised metabolites (Fig. 1) (Bansal and Germino 2009; Hoch et al. 2003; Körner 2003). Availability and allocation of NSC to defence change under drought conditions in a nonlinear way depending on compound class, tree characteristics, affected plant organs, presence of biotic agents, timing and intensity of stress (Huang et al. 2020). Under moderate drought, conifer trees tend to sustain or even reinforce defences against attacks (Ferrenberg et al. 2015; Jacquet et al. 2014; McDowell and Sevanto 2010; McDowell 2011). There is increasing evidence that trees shunt NSC to specialised metabolite biosynthesis and repair stress-induced damages even when they are severely stressed (Hartmann et al. 2018; Huang et al. 2019) rather than simply trading off growth against defence (Bryant et al. 1983; Herms and Mattson 1992). The ability of conifer trees to mobilise defences might be impaired by multiple stressors, in particular when biotic and abiotic factors co-occur. For example, water deficit mainly reduced accumulation of monoterpenes in necrotic lesions produced after inoculation of the fungus *Grosmannia clavigera* in *Pinus banksiana* and *Pinus contorta*, pointing to an increased susceptibility of drought-stressed seedlings and trees to biotic

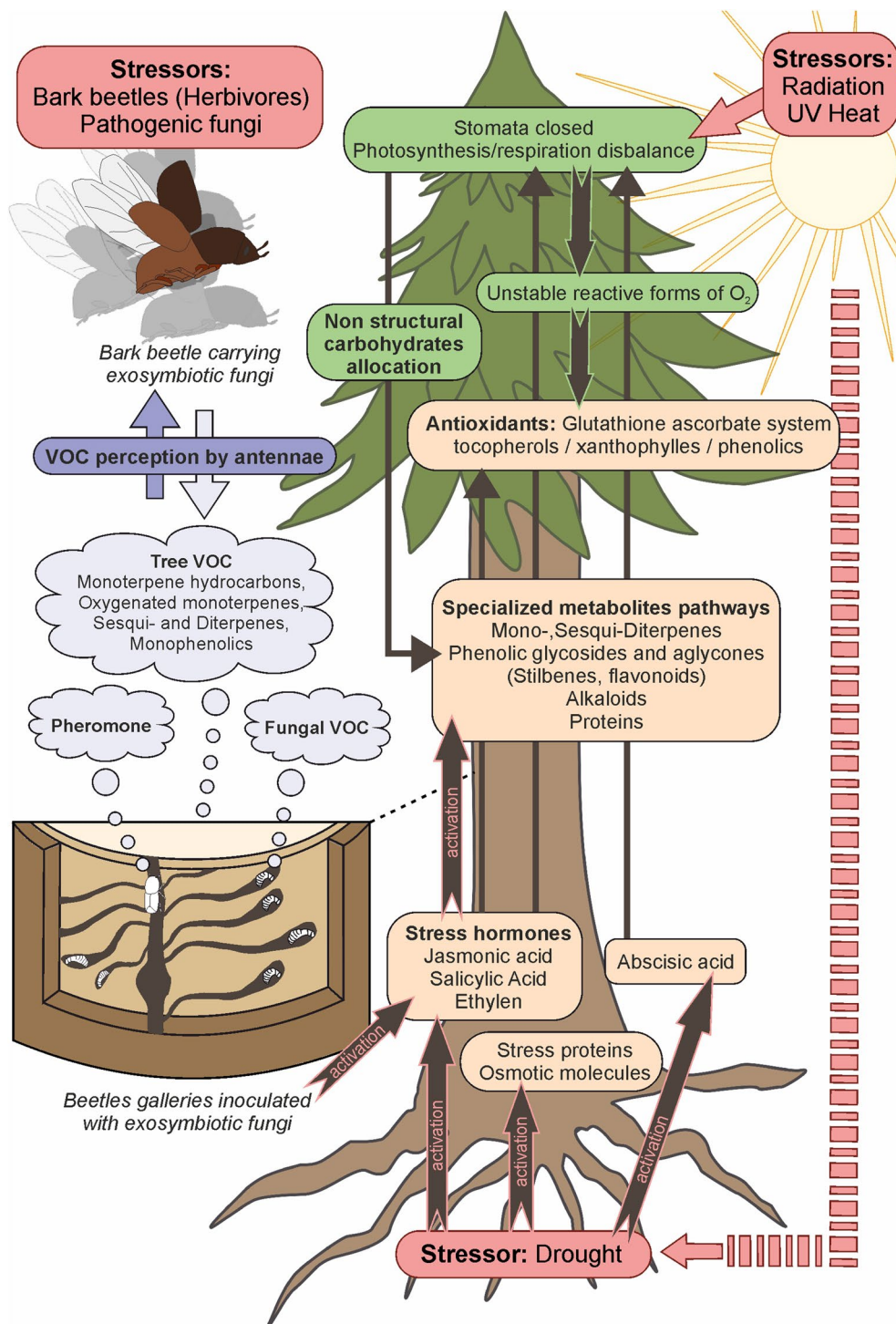


Fig. 1 Conceptual scheme of interactions among Norway spruce, *Ips typographus* and symbiotic ophiostomatoid fungi under drought conditions. Stressors such as heat and drought activate stress hormones and stress proteins and trigger the closure of stomata via activation of abscisic acid. Stomatal closure and reduced photosynthetic activity cause a cascade of biochemical reactions in the tree involving pathways for the biosynthesis of antioxidants and specialised metabolites from non-structural carbohydrates. Activation of hormones and pro-

teins as well as biochemical reactions are indicated by brown arrows. Defence compounds in the bark and volatile organic compounds (VOC) such as monoterpene hydrocarbons and oxygenated monoterpenes as well as pheromone components (fair blue clouds) are important gustatory and olfactory signals for host searching and attacking bark beetles. Associated fungi play a crucial role in detoxification of compounds and attraction of beetles to the tree

attack (Hussain et al. 2020; Klutsch et al. 2017; Lusebrink et al. 2016). In conifers, terpene synthesis and emission of volatile compounds have been documented to rise with increasing water stress, but to eventually decrease under severe drought (Holopainen et al. 2018; Lieutier 2004). Such a response underlines the relevance of terpenes as potential stress markers indicating changes in tree susceptibility to biotic attack. In conifer trees, bark contents of polyphenols have not shown such trends, while endogenous levels of phenolic compounds are increased under drought stress in other plants such as rapeseed *Brassica napus* or thyme *Thymus vulgaris* by activation of the phenylpropanoid metabolism (Sharma et al. 2019). Interestingly, due to variations in stress-mediated responses on bio-synthetic pathways and trade-offs between defence compounds, total amounts of numerous specialised compound classes in the bark (but not terpenes) often remain unaffected by drought and therefore do not reliably indicate stress (Koricheva et al. 1998).

Biochemical stress indicators in Norway spruce

From the biochemical perspective, tree response to drought stress is a complex mechanism. It involves universal signatures present in all plants, but also includes specific pathways found only in certain taxa. When trees experience a lack of soil water, expression of genes related to certain proteins and plant hormones such as abscisic acid (ABA) but also jasmonic acid, salicylic acid and ethylene is upregulated (Eldhuset et al. 2013; Jackson et al. 1995; Tan and Blake 2006) (Fig. 1). Initiation of signal cascades by shifts in gene expression patterns already happens in the early stage of a drought event promoting the closure of stomata by ABA (Moran et al. 2017). Reduced stomatal conductance results in a decrease in CO₂ in chloroplasts, triggering oxidative and photo-oxidative stress. A disturbed redox state of cells can lead to damages of cell components caused by free radicals and peroxides, i.e. the active forms of oxygen (Felicijan et al. 2015). In return, trees start to synthesise antioxidants such as tocopherols (vitamin E) and xanthophylls (carotenoids) to quench reactive oxygen species (Tausz et al. 2001). The main pathway for removal of reactive oxygen species is the ascorbate–glutathione cycle. Key compounds of this cycle are ascorbate (ascorbic acid or vitamin C), which is the most abundant water-soluble antioxidant in plant cells, and glutathione, essential for the regeneration of ascorbate (Urbanek Krajnc et al. 2014). Ascorbate and glutathione levels increase in Norway spruce needles during mild drought stress, along with a changed ratio of reduced and oxidised glutathione (Tausz et al. 2004, 2001). A rise in glutathione and cysteine levels was also observed in response to salicylic acid application on bark sections of Norway spruce. Such treatment was shown to reduce the number of spruce bark beetle entrance holes and maternal gallery lengths

compared to untreated controls by increasing expression levels of defence-related genes via systemic acquired resistance (Urbanek Krajnc et al. 2011). Apart from anti-oxidative defence and redox control, glutathione plays multiple roles in plant metabolism, promoting resistance to various pathogens (Tausz et al. 2004). Experimental infections of Norway spruce bark with ophiostomatoid fungi revealed interactions between the ascorbate–glutathione system and chemical defence via phenolic compounds. Antioxidants such as polyphenols are oxidised to phenoxyl radicals, which are then reduced by ascorbate to avoid DNA damage of trees (Hammerbacher et al. 2019; Urbanek Krajnc et al. 2014). The synthesis and storage of phenolics in PP cells, in combination with the ascorbate–glutathione cycle, have been increasingly recognised as pivotal systems for tree response to biotic and abiotic stress (Felicijan et al. 2015). The importance of particular phenol families and specific phenolic compounds for tree resistance is clearly demonstrated by their effects on *I. typographus* and associated blue-stain fungi, as described in Sects. 3, 4. Several other biochemical and tree physiological characteristics are considered to be indicators of tree stress such as contents of plant stress hormones (Fig. 1), changes in proteome, concentrations of key proteins, photosynthetic ability (chlorophyll fluorescence, stomatal conductance), fluctuations in monoterpene contents (Kainulainen et al. 1992) and emissions of volatiles (Holopainen et al. 2018).

Constitutive terpene patterns in Norway spruce

The composition of terpenoids in Norway spruce bark is strongly influenced by environmental conditions, tree genotype and tissue types (Schönwitz et al. 1990). Moreover, observed terpene blends depend on the mode of extraction with differences between volatiles that are directly absorbed from the bark surface or extracted from the phloem using organic solvents (Hietz and Baier 2005). Table 2 and associated Fig. 2 list terpenoid compounds typically found in Norway spruce and relevant information regarding tree defence, host recognition and attack success of *I. typographus* as well as interactions with fungal symbionts. Extraction of monoterpene hydrocarbons from spruce phloem has revealed considerable variability in the proportion of different compounds with α -pinene (23–39%), β -pinene (25–58%), β -phellandrene (5–19%), limonene (1.5–4%), myrcene (1.6–3.4%), Δ -3-carene (0.6–1.1%) and camphene (0.2–1.1%) predominating in the low molecular fraction. This variability is likely due to differences in the age of sampled trees (Baier et al. 2002; Borg-Karlson et al. 1993; Silvestrini et al. 2004). Furthermore, proportions of (–)-enantiomers of chiral compounds (Borg-Karlson et al. 1993; Lindström et al. 1989; Persson et al. 1996) differ with genetic origin (Kännaste et al. 2012), plant tissue (Borg-Karlson et al. 1993), as well as among and even within

Table 2 Ecologically relevant chemical compounds that mediate interactions among Norway spruce, *Ips typographus* (IT), and ophiostomatoid fungi

Compounds and their origin	Physiological changes to host tree chemicals in ^a		Bark beetle (<i>Ips typographus</i>) Ecological relevance/Tree physiological response ^c	Impact on fungal growth/ Fungal origin ^d
	Response to MeJA	Response to fungi		
<i>Tree/Monoterpene hydrocarbons</i> ^{4,10,26,27,28,29,30,32,33,38,39,43,47}				
α -Pinene	↑abs ^{27,46}	↓abs ⁴⁶	GC-EAD ^{21,33} , SSR ^{3,33}	Host recognition ^{9,1} , conifer habitat cue ^{9,41}
(-)- α -Pinene	↑abs ³² no ⁴⁶	↑abs ⁴ no ^{43,46}	GC-EAD ^{21,33} , SSR ^{1,3,33}	Pheromone precursor ³¹ Attraction (with pheromone) ¹⁵ higher proportion in surviving, lower in killed trees (?) ^{4,32,46}
β -Phellandrene	↑abs ^{27,46} ↓rel ⁴³	↑abs ⁴⁶	GC-EAD ^{2,21,33}	—
(-)- β -Pinene	↑abs ^{32,46}	↑abs ⁴ no ⁴⁶	GC-EAD ^{21,33} , SSR ^{3,33}	—
Δ 3-Carene	↑abs ^{4,46}	↑abs ^{4,28,46} ↑rel ⁴³	GC-EAD ^{21,33} , SSR ^{1,3,33}	↓abs in IT killed trees (MeJA) ³²
(-)-Limonene	↑abs ^{4,46}	no ⁴⁶	GC-EAD ^{21,33} , SSR ^{3,33}	↑abs and ↑rel in bark of less attractive and surviving trees; abs↓ and ↓rel in IT killed trees ^{32,46}
(+)-Limonene	↑abs ^{4,46}	↓abs ^{4,46}	GC-EAD ^{21,33} , SSR ^{3,33}	↓abs in IT killed trees ³²
<i>Tree/Oxygenated monoterpenes</i> ^{4,26,27,28,30,32,33,36,43,47}				
1,8-Cineole (Eucalyptol)	↑abs ^{27,32} ↑rel ^{33,43}	↑abs ⁴	GC-EAD ^{2,21,33} , SSR ^{2,3}	Antiattractant ^{2,6} , true resistance marker for tree survival ³² ↑abs emission in IT attacked trees ³³ , ↑abs in bark of IT surviving trees, ↓abs in IT killed trees ³²
Camphor	no ³³	—	GC-EAD ^{21,33} , SSR ³³	—
Pinocamphone	↑rel ³³	—	GC-EAD ^{21,33}	—
trans-Pinocarveol	—	↑abs ²⁸	—	↑abs emission in IT attacked trees ³³
α -Terpineol	↑rel ³³	↑abs ⁴ ↑rel ⁴	GC-EAD ^{2,33} , SSR ³³	—
trans-4-Thujanol (Sabinene hydrate)	—	—	GC-EAD ³³ , SSR ³³	Antiattractant ⁹ ↓abs with tree age ⁹
(-)-Terpinen-4-ol	no ³³	↑abs ²⁸	GC-EAD ^{21,33} , SSR ³³	—
Verbenone	—	—	GC-EAD ^{21,33} , SSR ^{3,33}	Antiattractant pheromone ^{6,35} , terminates aggregation of IT ^{33,35} ↑abs emission in IT attacked and decomposed wood ^{8,33}
<i>Tree/Phenolics</i> ^{11,12,16,18,19,20,21,26,30,32,33,39}				
(+)-Catechin	—	↑abs in lesions ^{11,12,16,20,26}	—	Antifeedant ¹⁷ or anti-nutritive ¹⁹ Marker of resistance to fungi (?) ^{11,12}
				Fungal growth inhibitor ¹⁶ , synergizes with taxifolin ¹⁹ Degradation by <i>Gn</i> and <i>Ge</i> ⁴⁵

Table 2 (continued)

Compounds and their origin	Physiological changes to host tree chemicals in ^a			Bark beetle (<i>Ips typographus</i>) Ecological relevance/Tree physiological response ^c	Impact on fungal growth/ Fungal origin ^d
	Response to MeJA	Response to fungi	Antennal response ^b		
Estragole (4-Allylanisole)	↑abs ³²	–	GC-EAD ^{2,33} , SSR ³³	↑abs emission in felled IT attacked trees ³³ ; ↓abs in IT killed, ↑abs in surviving trees/MeJA ³²	–
Gallocatechin	–	↑abs ²⁰	–	–	Inhibits growth and melanin biosynthesis in <i>Ep</i> ^{18,20}
<i>trans</i> -Resveratrol (Resveratrol)	–	↑abs ¹⁶	–	Antifeedant for males ¹⁷	abs in spruce clone more susceptible to <i>Ep</i> ¹⁶
Taxifolin	–	↑abs in lesions ^{16,18}	–	Antifeedant ^{17,19} and anti-nutritive ¹⁹	Fungal growth inhibitor ¹¹ ; synergises with catechin ^{18,20}
<i>Beetle pheromones</i>					
2-Methyl-3-buten-2-ol (MB)	–	–	GC-EAD ^{2,14} , SSR ³	Main pheromone component, produced by beetles <i>de novo</i> ^{5,8,34}	Produced by <i>Ge</i> and <i>Gp</i> de novo ^{42,44}
(<i>S</i>)-(-)- <i>cis</i> -Verbenol	–	–	GC-EAD ¹⁴ , SSR ³	Aggregation pheromone component produced from α-pinene ^{5,8,31,34}	ND
(<i>S</i>)-(-)-Verbenone	–	–	GC-EAD ^{21,33} , SSR ^{3,33}	Terminates aggregation on host tree ^{33,35}	Produced by IT yeasts from <i>cis</i> -verbenol ^{23,26,25}
(<i>R</i>)-(-)-Ipsdienol	–	–	GC-EAD ¹⁴ , SSR ³	Produced de novo by males after mating with females, weakly boosts the attraction of pheromone mixture MB/ <i>cis</i> -Verbenol ^{17,34}	ND
(<i>R</i>)-(+)-Ipsenol	–	–	GC-EAD, SSR ^{3,33}	Produced de novo by males after mating with females, relict of ipsdienol ^{7,34,35}	ND
<i>Non-host tree volatiles</i>					
<i>trans</i> -Conophthorin	–	–	GC-EAD, SSR ³	Angiosperm bark ⁴¹ , part of non-host volatiles anti-attractants blend ^{40,41} , antifeedant ¹⁷	Produced by <i>Gp</i> , <i>Ge</i> de novo ⁴⁴
1-Octen-3-ol	–	–	GC-EAD, SSR ³	Angiosperm bark ⁴¹ , part of non-host volatiles anti-attractants blend ^{40,41}	Produced by <i>Op</i> de novo ²²
3-Octanol	–	–	GC-EAD, SSR ³	Angiosperm bark ⁴¹ , part of non-host volatiles anti-attractants blend ^{40,41}	ND
1-Hexanol	–	–	GC-EAD, SSR ³	Angiosperm leaf ⁴¹ (green leaf volatiles) blend component; part of non-host volatiles anti-attractants blend ^{40,41}	Produced by <i>Ge</i> , <i>Ob</i> and <i>Op</i> de novo ²²
(<i>E</i>)-2-Hexenol	–	–	GC-EAD, SSR ³	Angiosperm leaf ⁴¹ (green leaf volatiles) blend component; part of non-host volatiles anti-attractants blend ^{40,41}	–

Table 2 (continued)

Compounds and their origin	Physiological changes to host tree chemicals in ^a		Bark beetle (<i>Ips typographus</i>) Ecological relevance/tree physiological response ^c	Impact on fungal growth/ Fungal origin ^d
	Response to MeJA	Response to fungi		
(Z)-3-Hexenol			Angiosperm leaf ⁴¹ (green leaf volatiles) blend component, part of non-host volatiles anti-attractants blend ^{40,41}	–
<i>Fungal compounds as bark beetle semiochemicals</i>				
exo- and endo-Brevicomine	–	–	Increased attraction to pheromone blend ³⁸	Produced by <i>Gp</i> , <i>Ge</i> , <i>Ob</i> , <i>Op</i> de novo ⁴⁴
3-Methyl-1-butanol	–	–	Component of short-range attraction blend in lab assay ²²	Produced by <i>Ep</i> , <i>Gp</i> , <i>Ge</i> , <i>Ob</i> , <i>Op</i> de novo ²²
2-Methyl-1-butanol	–	–	Component of short-range attraction blend in lab assay ²²	Produced by <i>Ep</i> , <i>Gp</i> , <i>Ge</i> , <i>Ob</i> , <i>Op</i> de novo ²²
3-Methyl-1-butyl acetate	–	–	Component of short-range attraction blend in lab assay ²²	Produced by <i>Ep</i> , <i>Gp</i> de novo ²²
2-Phenylethanol	–	–	Produced also by males ⁷ , not field active ³⁴ , component of short-range attraction in lab assay ²²	Produced by <i>Ep</i> , <i>Gp</i> , <i>Ge</i> , <i>Ob</i> , <i>Op</i> de novo ²²
2-Phenylethyl acetate	–	–	Component of short-range attraction blend in lab assay ²²	Produced by <i>Ep</i> , <i>Gp</i> de novo ²²

Compounds were grouped based on their origin (tree, beetle, non-hosts and fungi/yeasts)

Tree compounds are further divided into monoterpene hydrocarbons, oxygenated monoterpenes and phenolics

The literature references are indicated by superscript numbers in the table. References corresponding to numbers in the table are listed in the footnote

Ep: *Endoconidiophora polonica*, *Gp*: *Grosmanella penicillata*, *Ge*: *Grosmanella europaeoides*, *Ob*: *Ophiostoma bicolor*, *Op*: *Ophiostoma piceae*, ND: not detected, –: unknown or not tested

^aPhysiological changes to host tree chemicals in Norway spruce in response to MeJA application and inoculation with pathogenic fungi; arrows indicate absolute (abs) or relative (rel) decrease (↓) or increase (↑) compared to control treatments

^bPerception of chemical compounds on *Ips typographus* antennae confirmed either by electroantennography (GC-EAD) or single sensillum recording (SSR) or both

^cEcological relevance of host chemicals to bark beetles and tree's physiological response upon bark beetle infestation

^dImpact of host tree chemicals on fungal growth and fungal origin of beetle semiochemicals

References: Andersson (2012)¹; Andersson et al. (2010)²; Andersson et al. (2009)³; Baier et al. (2002)⁴; Bakke (1976)⁵; Binyameen et al. (2014)⁶; Birgersson et al. (1984)⁷; Birgersson and Bergström (1989)⁸; Blažytė-Čerėskienė et al. (2015)⁹; Borg-Karlson et al. (1993)¹⁰; Brignolas et al. (1995)¹¹; Brignolas et al. (1998)¹²; Cale et al. (2019)¹³; Dickens (1981)¹⁴; Erbilgin et al. (2007)¹⁵; Evensen et al. (2000)¹⁶; Faccoli and Schlyter (2007)¹⁷; Hammerbacher et al. (2019)¹⁸; Hammerbacher et al. (2014)¹⁹; Hammerbacher et al. (2018)²⁰; Kalinová et al. (2014)²¹; Kandasamy et al. (2019)²²; Leufvén et al. (1984)²³; Leufvén and Birgersson (1987)²⁶; Leufvén et al. (1988)²⁵; Lieutier et al. (2002)²⁷; Martin et al. (2013)²⁸; Persson et al. (1996)²⁹; Pettersson and Boland (2003)³⁰; Renwick et al. (1976)³¹; Schiebe et al. (2012)³²; Schiebe et al. (2019)³³; Schlyter et al. (1987a)³⁴; Schlyter et al. (1989)³⁵; Silvestrini et al. (2004)³⁶; Tømmerås (1985)³⁷; Tømmerås and Mustaparta (1984)³⁸; Zeneli et al. (2006)³⁹; Zhang and Schlyter (2003)⁴⁰; Zhang and Schlyter (2004)⁴¹; Zhao et al. (2015)⁴²; Zhao et al. (2011a)⁴³; Zhao et al. (2019a)⁴⁴; Zhao et al. (2019b)⁴⁵; Zhao et al. (2010)⁴⁶; Zhao et al. (2011b)⁴⁷

geographic areas (Persson et al., 1996). Sesquiterpenes such as α -longipinene, β -farnesene and germacrene D occur in much smaller fractions in spruce bark than monoterpenes (Schiebe et al. 2012; Zeneli et al. 2006; Zhao et al. 2011b). Diterpenes (resin acids, alcohols and hydrocarbons) such as sandaracopimarate, abienol and thunbergol are less volatile but have been found to correlate with tree resistance against *I. typographus* and associated fungi (Zeneli et al. 2006; Zhao et al. 2011b). Shifts in terpene blends and concentrations are strongly linked to tree stress and interactions with bark beetles and their fungal symbionts. In healthy trees, oxygenated monoterpenes are represented only in trace amounts. However, after bark beetle attack and fungal inoculation, the concentration of oxygenated monoterpenes gradually increases via detoxification of monoterpene hydrocarbons in the beetle gut and by symbiotic fungi (Kandasamy et al. 2016; Leufvén and Birgersson 1987; Petterson and Boland 2003; Schiebe et al. 2019).

Stress-induced tree responses

Changes in Norway spruce bark chemistry, including the increased oxygenation of monoterpene hydrocarbons, have been clearly linked to biotic stress caused by *I. typographus* attack and fungus inoculation, or activation of induced tree defence by MeJA treatment (Martin et al. 2003; Novak et al. 2013; Schiebe et al. 2019). Oxygenated monoterpenes in conifer bark are ecologically significant as pheromone components of numerous bark beetle species (Francke and Vité 1983; Schlyter et al. 1989). Interconversion of verbenone from verbenols by yeasts and ophiostomatoid fungi growing in bark beetle brood galleries (Birgersson and Bergström 1989; Cale et al. 2019; Davis 2015) and potential stress-related biochemical regulation of oxygenated monoterpenes by trees suggests dual roles of these compounds in beetle communication and induced tree defence (compare Sects. 3 and 4). Heavily infested trees are no more attractive for spruce bark beetles. In *I. typographus* galleries, a large number of oxygenated compounds including camphor, α -terpineol, terpinene-4-ol and borneol were found (Leufvén and Birgersson 1987). The oxygenated monoterpene *trans*-4-thujanol shows repellent effects on both sexes of *I. typographus* and strongly decreases in concentration from saplings to mature Norway spruce (Blažytė-Čereškienė et al. 2015), rendering trees of larger diameter size more susceptible to infestation (Table 2).

Linking tree disposition to bark beetle attack to specific volatiles is challenging due to high heterogeneity among tree individuals and influence of temperature, light, and humidity on volatile emission rates (Hietz and Baier 2005; Santos et al. 2006; Zhang and Schlyter 2004). Although enhanced attraction of bark beetles to increased release rates of volatiles from spruce logs cannot be entirely excluded,

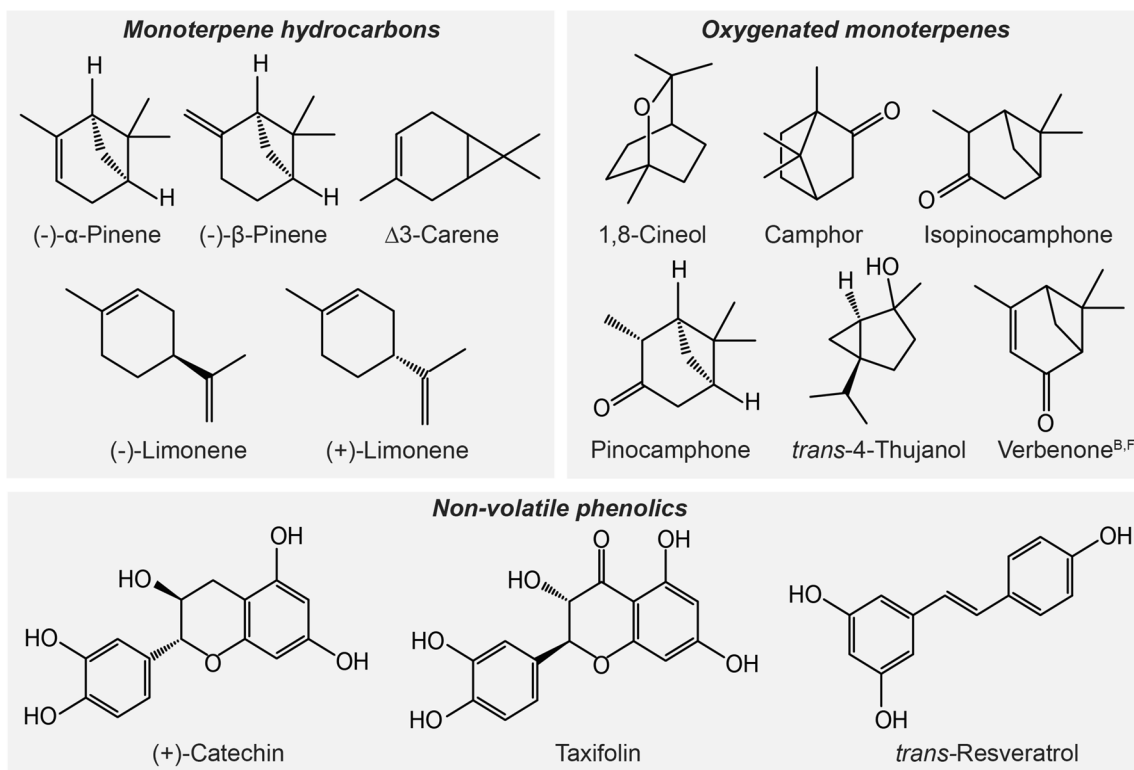
evidence from the literature is limited as effects of VOC emissions and *I. typographus* attack have been rarely studied on healthy, mature trees. Most analyses of terpene contents and/or emissions in the context of drought focus on pine needles of mainly younger trees. For example, potted *Pinus pinaster* with moderate water deficits emitted more myrcene and less β -pinene from the canopy than control plants, but bark beetles (*Tomicus destruens*) performed worse in drought-stressed plants (Branco et al. 2010). Volatile emission rates from needles of drought-stressed *Pinus halepensis* seedlings significantly exceeded those of well-watered trees, but declined with continued drought (Ormeno et al. 2007). In the same tree species, drought stress also enhanced phloem terpene concentrations (Kelsey et al. 2014; Ormeno et al. 2007). In needles of severely drought-stressed Scots pine, and Norway spruce seedlings and saplings, total and individual monoterpene contents (especially α -pinene, limonene, tricyclene and camphene), and sesquiterpene contents increased significantly, while resin acids showed a decreasing trend (Kainulainen et al. 1992; Sancho-Knapik et al. 2017; Turtola et al. 2003). Sancho-Knapik et al. (2017) recently showed that accumulation of terpenes in mildly drought-stressed *Pinus sylvestris* coincided with stomatal closure and increase in ABA. Similarly, MeJA application enhanced the expression of terpene synthases regulating de novo synthesis of terpenes in Norway spruce needles (Martin et al. 2003). While these results seem to overall corroborate that increased terpene concentrations and emissions are triggered by moderate drought, monoterpene biosynthetic capacity might be reduced under severe drought-stress as demonstrated in saplings of *Abies grandis* (Lewinsohn et al. 1993).

The *I. typographus* perspective: host selection and acceptance

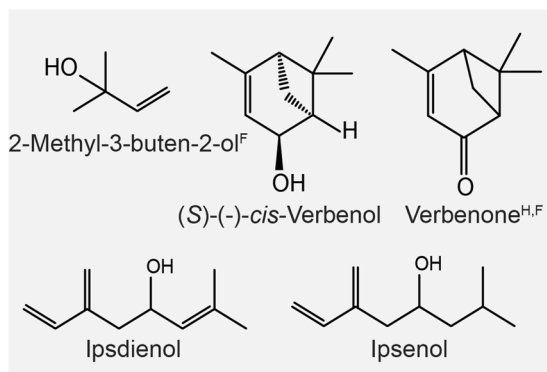
Olfaction and taste

Bark beetles live in a complex, multitrophic environment. Their ability to survive depends on their senses, which mediate intra- and interspecific interactions with plants, animals, fungi and other microorganisms. Phytophagous insects discriminate host from non-host odours based on specific blends of compounds (Bruce and Pickett 2011). The volatile mixture released from newly cut Norway spruce logs was not found to particularly attract *I. typographus* in field trapping experiments (Lindelöw et al. 1992). In addition, neither individual host compounds of Norway spruce have been shown attractive (Schlyter and Birgersson 1999), nor did host material supplemented with synthetic aggregation pheromones increase trap catches (Schlyter et al. 1987). However, *I. typographus* has numerous sensory cells, specific

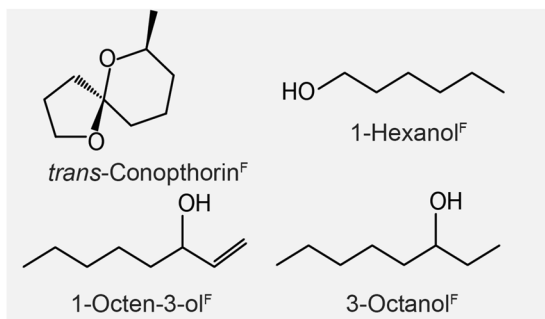
Host tree (*Picea abies*)



Bark beetle (*Ips typographus*)



Nonhost volatiles



Symbiotic fungi

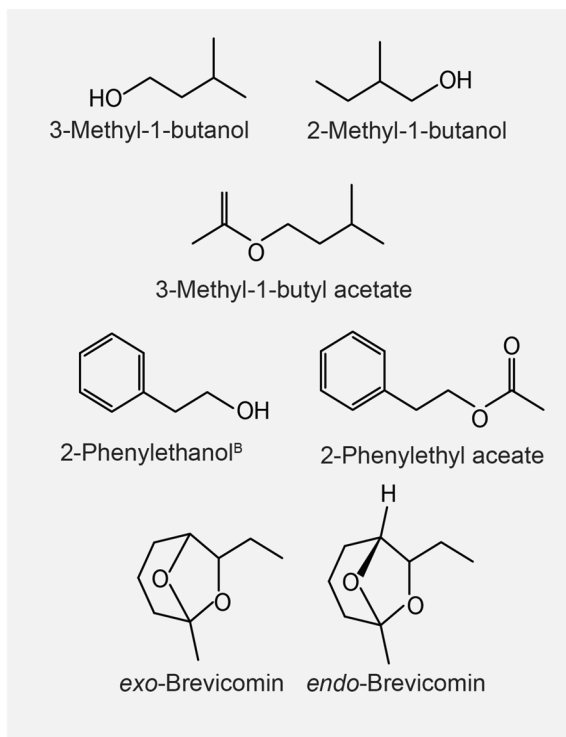


Fig. 2 Chemical structures of some selected compounds that mediate interactions among Norway spruce trees, bark beetles and fungi. The compounds are divided into four major groups based on their origin: Host tree (*Picea abies*)—monoterpene hydrocarbons, oxygenated monoterpenes and non-volatile phenolics; bark beetle (*Ips typographus*) pheromones; nonhost tree volatiles; symbiotic fungal volatiles that function as insect semiochemicals. See Table 2 for more details on the ecology of individual compounds. Several bark beetle semiochemicals have multiple origins, and other known sources are denoted as *H*: host tree or *B*: beetle or *F*: fungus in suffixes next to compound names

for monoterpene hydrocarbons (Table 2), which might help to locate odours of suitable conifer habitats (Zhang and Schlyter 2004) and aid in close-range host acceptance after landing on trees (Fig. 3) (details see Sects. 3.2, 3.3).

Among the diversity of elaborate antennal structures in insects (Hansson and Stensmyr 2011), bark beetles have olfactory sensillae located merely on the ventral side of their club-shaped antennae. Olfactory sensory neurons (OSN) within olfactory sensillae (Hallberg 1982) show high specificity to many groups of semiochemicals, reflecting the major role of olfaction in bark beetle long- and short-range orientation (Fig. 3). Chemical signals are further processed in higher brain centres and eventually evaluated as positive and negative signals, which forms the basis for orientation towards or away from sources (Andersson et al. 2015). Host discrimination by insects in general is supported by particular co-localization of certain OSN types found among sensillar functional types (Andersson et al. 2010; Hansson and Anton 2000). In *I. typographus*, the most narrowly tuned OSN specifically respond to a single compound or few closely related molecules, while response spectra of generalist OSN comprise a broader range of plant volatiles (Andersson 2012). In several electrophysiological studies, 24 classes of OSN were identified for *I. typographus* (Andersson et al. 2009; Mustaparta et al. 1984; Schiebe et al. 2019; Tømmerås 1985). OSN responding to attractive or anti-attractive pheromonal compounds are highly specific, strongly reacting to only one or a few structurally related compounds (Andersson 2012; Andersson et al. 2009). Plant odour-responding OSN show a variety of response specificities, often quite specific to key ligands (1,8-cineole OSN) or more broadly tuned such as OSN for host monoterpene hydrocarbons (Table 2) (Andersson et al. 2009; Kandasamy et al. 2019; Schiebe et al. 2019). The specificity of OSNs likely reflects strong selection pressures on host recognition in *I. typographus*, making it such an efficient tree-killing bark beetle (Andersson et al. 2013).

In two transcriptomic studies on *I. typographus* antennae (Andersson et al. 2013; Yuvaraj et al. 2020), receptors for airborne molecules form three different multigene families: 73 odorant receptors (OR), 7 ionotropic receptors (IR) and 6 gustatory receptors (GR) were identified (Andersson

et al. 2013; Yuvaraj et al. 2020). ORs detecting volatile compounds such as pheromones, plant odours and fungal volatiles have been investigated in *I. typographus* so far. IRs detecting nitrogen-containing compounds, aromatics, organic acids and temperature have not been investigated in detail yet. Only a fraction of olfactory receptors and their ligands that shape olfactory-driven behaviours in *I. typographus* are known. Recently, the first two *I. typographus* ORs tuned to single enantiomers of the bark beetle pheromone compounds ipsenol and ipsdienol have been functionally characterised (Yuvaraj et al. 2020) and their binding mechanisms described. The biological significance of the characterised ORs positions them as prime targets for pest control and use in biosensors to detect bark beetle infestations (Yuvaraj et al. 2020).

Compared to olfaction, taste perception of host phytochemicals in insects is much less explored (Pentzold et al. 2017) and knowledge is entirely lacking in bark beetles. Insects taste non-volatile plant metabolites via cuticular hairs, pegs, or pits abundant on the mouthparts, antennae, tarsi and genitalia. In bark beetles, the sense of taste might be very important during host selection (Elkinton and Wood 1980; Raffa et al. 2016) to discriminate host and non-host plants (Byers et al. 1998, 2000). Antennal transcriptomic investigations showed relatively low numbers of GR and taste-related IR in *I. typographus*. The same is true for *D. ponderosae* (Andersson et al. 2013), suggesting that taste receptors may be more expressed in mouth parts such as labella and less in antennae.

Host selection

The behavioural sequence of host selection starts with dispersal through the landscape, ending in directed search of host trees in suitable habitats and final acceptance of host tissues (Fig. 3a–d). Although *I. typographus* is able to kill whole forest stands, identification of scattered, adequate hosts is challenging for a small insect. Mortality in the dispersal phase is high, with first-day mortality rates up to 50% (Coulson et al. 1980). At the habitat level (forest stands), olfactory cues keep bark beetles away from unsuitable sites (Fig. 3b) (Zhang and Schlyter 2004). Conifer bark beetles are guided by a combination of both positive cues (aggregation pheromone, host foliage monoterpene hydrocarbons, microbial volatiles) and negative cues (heterospecific pheromones, non-host volatiles, microbial volatiles) (Erbilgin et al. 2007; Franklin et al. 2000; Kandasamy et al. 2019; Raffa et al. 2016; Schlyter and Birgersson 1999; Zhang and Schlyter 2004). *Ips typographus* beetles avoided the source of non-host volatiles (six green-leaf alcohols, two bark alcohols and a ketol) (Table 2, Fig. 3b) (Zhang and Schlyter 2004), which are inhibitory to many bark beetle species. Having likely evolved in mixed forests landscapes (Lindgren

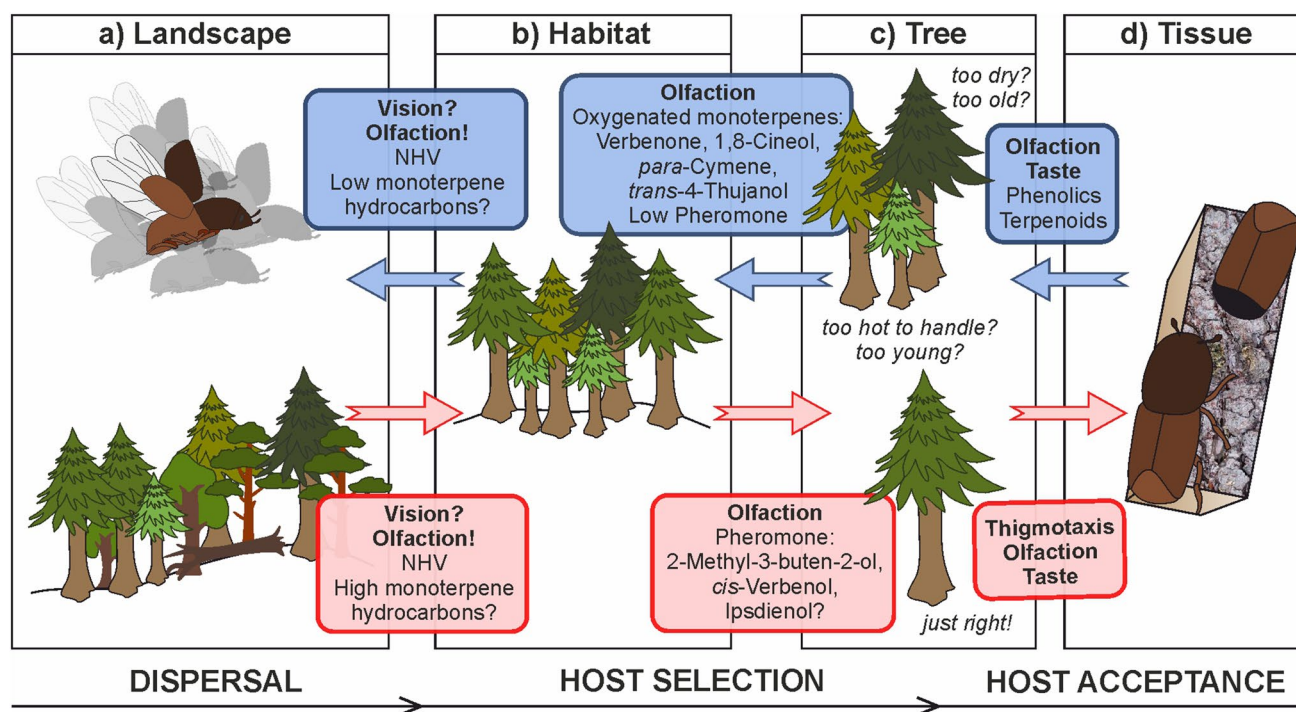


Fig. 3 Behavioural sequence for *Ips typographus* in **a** landscape (dispersal), **b** habitat and **c** tree (both host selection), and **d** tissue (host acceptance) by positive (fair blue arrows and boxes) and negative cues (red arrows and boxes). Focus is set on the pioneering male

beetles, whose rapidly produced pheromone signals guide the vast majority of both males and females to aggregate. The individual beetle follows a sequence of steps, guided by visual, chemo-sensory and thigmotactic cues

and Raffa 2013), *I. typographus* is well adapted to avoid non-host trees. It is less clear how pioneer beetles locate particular susceptible hosts in semiochemically diverse habitats without any pheromone release.

The exact mechanisms of beetle orientation to single trees and final choice of suitable hosts based on their stress levels are elusive. Beetles seem to recognise both severely/chronically stressed trees and dying trees that are heavily attacked by other beetles ("too dry, too old") as unsuitable hosts (Fig. 3c, top tree). In a field-bioassay, chronically/severely drought-stressed Norway spruce trees were less accepted for gallery initiation than vital but acutely drought-stressed ones; the cues are as yet unknown (Netherer et al. 2015). In trees at advanced stage of attack, after female egg deposition, males produce ipsdienol (*R*-(-)) and ipsenol (*R*-(+)) in their hindguts (Birgersson et al. 1984; Kohnle et al. 1991), with variable roles from attractants at low doses to repellents at higher doses (Schlyter et al. 1989). When nutritive resources are increasingly occupied by conspecific beetles and fungi, *cis*-verbenol is oxygenated to the corresponding ketone, verbenone by yeasts (Leufvén et al. 1984) and possibly by ophiostomatoid fungi (compare Sect. 4, Table 2) (Blomquist et al. 2010; Leufvén and Birgersson 1987). Increased emission of verbenone coincides with successful fungal establishment (Cale et al. 2019). Verbenone acts

as anti-attractant at different doses alone (Bakke 1981), or in synergism with non-host volatiles (Zhang and Schlyter 2003) and counteracts attractive effects of aggregation pheromones (Binyameen et al. 2014; Lindgren and Miller 2019). Similarly, oxygenated monoterpenes such as 1,8-cineole released from heavily attacked trees show anti-attractant effects (Andersson et al. 2010). The compound 1,8-cineole was found to be the best predictor of resistant trees among several other specialised metabolites. The inducibility of 1,8-cineole, in turn, strongly increased the survival of trees from colonisation attempts by beetles (Schiebe et al. 2012).

Inhibitory effects of *trans*-4-thujanol in laboratory olfactometer experiments might explain low attraction of *I. typographus* to younger Norway spruce trees where this compound is more abundant (Blažytė-Čereškienė et al. 2015). Non-stressed trees ("too hot to handle, too young") (Fig. 3c) are expected to be less susceptible and able to strongly induce defences during biotic attack as demonstrated using MeJA treatment (Zhao et al. 2011a). Intermediately stressed trees ("just right") can be successfully attacked, and further arriving beetles emit aggregation pheromones rapidly upon landing. Direct effects of drought on pheromone synthesis are not known. The pheromone consists of the two active compounds 2-methyl-3-buten-2-ol and *cis*-verbenol (Bakke 1976; Schlyter et al. 1987). Most

aggregation pheromones of *Ips* and *Dendroctonus* species are biosynthesised de novo (Byers and Birgersson 1990; Schlyter and Birgersson 1999), while some compounds are derived from host compounds (Blomquist et al. 2010; Tittiger and Blomquist 2017). Biosynthesis of *cis*-verbenol depends on the amount of (-)- α -pinene in the host bark (Lindström et al. 1989). During bark beetle attack, α -pinene is increasingly emitted from lacerated resin canals (Ghimire et al. 2016; Schiebe et al. 2019) and may attract more beetles in synergy with low amounts of pheromone (Erbilgin et al. 2007). When nuptial chambers are established by pioneer bark beetles at susceptible trees of reduced defences (Fig. 3c) maximum production of aggregation pheromone follows (Birgersson et al. 1984; Schlyter and Löfqvist 1986). Thus, α -pinene is a key compound for initial mass attack and semiochemicals production (Table 2).

***Ips typographus* host acceptance and colonisation success**

The chance of *I. typographus* to survive host colonisation attempts strongly depends on a tree's response to the attack (Figs. 1 and 3d). Experimental inoculations with ophiostomatoid fungi and MeJA treatment induce immune responses involving changes in anatomical and chemical features of living bark and wood. These studies have revealed important mechanisms of tree defence such as the priming of inducible defences of Norway spruce for an accelerated and intensified response to future bark beetle attack (Krokene 2015; Mageroy et al. 2020). Induced formation of traumatic resin ducts and accumulation of terpenes in affected tissues reduce the number of *I. typographus* attacks, parental tunnel lengths and numbers of deposited eggs, as well as the growth of ophiostomatoid fungi (Erbilgin et al. 2006; Zeneli et al. 2006; Zhao et al. 2011a). Increased terpene concentrations triggered by MeJA application were reported to reduce or even prevent bark beetle attacks when exceeding a certain threshold (Zhao et al. 2011b).

Bark beetles, in turn, have adapted to tree defences by engaging in symbiotic interactions with fungi that detoxify defence compounds and help them to colonise even healthy trees (Lindgren and Raffa 2013). Yet, certain substances such as limonene, myrcene and Δ -3-carene are particularly toxic for beetles, limiting tunnelling and oviposition (Erbilgin et al. 2017; Everaerts et al. 1988; Wallin and Raffa 2002). In *in vitro* assays, limonene inhibited the growth of *Endoconidiophora polonica*, an important blue-stain fungal associate of *I. typographus* (Novak et al. 2013). Feeding of *I. typographus* on artificial diet was reduced when adding (+)-limonene (Faccoli et al. 2005), while (-)-limonene was linked to reduced attractiveness of Norway spruce for landing beetles (Zhao et al. 2010). However, the increase in oxygenated monoterpene 1,8-cineole in bark samples

was the strongest predictor of induced defence in Norway spruce, leading to higher tree survival from natural attacks by *I. typographus* (Schiebe et al. 2012) (see previous section on anti-attractant activity and Table 2). In addition to 1,8-cineole, monoterpene hydrocarbons such as Δ -3-carene, myrcene, (-)- α -pinene, β -pinene and the diterpene thunbergol were found in increased amounts in the bark (Schiebe et al. 2012). These data support the assumption that enhanced monoterpene concentrations, as observed under moderate drought, increase tree defence against bark beetle attack. Apart from terpenoid compounds, fatty acids can be toxic to bark beetles (Erbilgin et al. 2017; Ishangulyyeva et al. 2016). Fatty acids are major components of lipids and involved in the synthesis of plant hormones. However, it is not known if *I. typographus* and its symbiotic fungi are influenced by fatty acids, and how fatty acid contents in bark are affected by drought.

A number of recent studies focused on the particular role of phenolic compounds in tree defence and effects on beetle-fungus interactions (Hammerbacher et al. 2019, 2014). Phenolics accumulate in hypersensitive wound reaction zones caused by pathogen attack (Christiansen et al. 1987; Krokene et al. 2001). Spruce phenolics are stored in PP cells (Franceschi et al. 2005), and the presence of phenylalanine ammonia lyase in these structures suggests that they are directly synthesised in these cells in response to biotic attack (Li et al. 2012). Phenylalanine ammonia lyase is an important enzyme of the phenylpropanoid pathway and catalyses the first step in the synthesis of polyphenolic stilbenes and flavonoids (Metsämuuronen and Sirén 2019). Stilbenes are known to protect the heartwood of pines from microbial decay and have nematocidal and fungicidal effects (Chong et al. 2009; Witzell and Martín 2008). The stilbenoids resveratrol and its glycosides piceid, astringin and isorhapontin are mainly present in Norway spruce phloem (Hammerbacher et al. 2011; Metsämuuronen and Sirén 2019). Resveratrol glycosides have been shown to accumulate in response to fungal infection and have antifungal activity (Evensen et al. 2000; Hammerbacher et al. 2011). Despite high stilbene levels, spruce trees suffer from fungal colonisation and fatal bark beetle infestation (Brignolas et al. 1995; Schiebe et al. 2012). This is attributed to the “fungus effect” (Brignolas et al. 1998) resulting in decreased stilbene glycosides around fungal infections (Viiri et al. 2001) due to degradation of phenolic glycosides to aglycones and use of these compounds for fungal metabolism (Hammerbacher et al. 2013). Highly virulent ophiostomatoid fungi are most efficient in degrading stilbenes and flavonoids (compare Sect. 4). The key virulence factor, catechol dioxygenase catalysing the first step in phenolic degradation, however, cannot degrade flavonols and dihydroflavonols (Hammerbacher et al. 2019; Wadke et al. 2016).

Activation of the flavonoid pathway, mainly the synthesis of proanthocyanidins, such as the flavan-3-ol monomers (+)-catechin and (+)-gallocatechin as well as condensed tannins, has been consistently linked to increased tree resistance to biotic attack (Brignolas et al. 1998; Hammerbacher et al. 2014, 2018; Lieutier et al. 2003) (Table 2). Flavan-3-ols and their metabolic precursor taxifolin showed anti-fungal effects in a synergistic way (Hammerbacher et al. 2019). Moreover, catechin- and taxifolin-enriched diet significantly reduced tunnel lengths and weight gain of *I. typographus* males in feeding bioassays (Faccoli and Schlyter 2007; Hammerbacher et al. 2019). Metabolites of taxifolin, i.e. laricitrin and its precursor myricetin, as well as the phenylpropane estragole (4-allylanisole) were induced significantly stronger in Norway spruce trees that eventually survived *I. typographus* attack (Schiebe et al. 2012). Furthermore, activation of flavanone synthases by jasmonic acid, salicylic acid and ABA (Fig. 1) has been linked to increased tolerance to biotic and abiotic stress, including drought (Felicijan et al. 2016; Hammerbacher et al. 2019; Nagy et al. 2004). So far, no clear relationships between drought and phenolics have been found (Holopainen et al. 2018). Much more research on the complex biochemical processes in conifers coupling anti-oxidative and insect/pathogen defence (Witzell and Martín 2008) is therefore needed.

The ophiostomatoid fungus perspective

Fungal symbionts of *I. typographus*

Microorganisms play important roles in the successful colonisation and reproduction of most conifer bark beetles. Many bark beetles have complex and dynamic multipartite interactions with bacteria, yeasts and fungi (Davis 2015; Popa et al. 2012; Six 2013) modulated by various factors such as temperature, humidity, moisture content of plant tissues, host phytochemistry and the presence of other interacting organisms in their galleries such as mites and nematodes (Biedermann et al. 2019). Among microbes, associations between bark beetles and fungi are relatively well studied (Franceschi et al. 2005; Kirisits 2004; Six 2012). The majority of fungal associates of bark beetles are ascomycetes, commonly known as ophiostomatoid or blue-stain fungi. *Ips typographus* has numerous fungal partners where compositions of fungal communities change with space and time (Chang et al. 2019; Linnakoski et al. 2012). Based on analyses of *I. typographus* fungal communities, the following species are considered to be the most frequent and most dominant symbionts: *E. polonica*, *Grosmannia penicillata*, *Ophiostoma bicolor*, *Grosmannia euophioides* (synonym *Grosmannia piceiperda*) and *Ophiostoma ainoae* (Kirisits 2004; Linnakoski et al. 2012). According to the ‘classical

paradigm’, fungi are considered to support bark beetle attack by overcoming and exhausting the host tree defence system and aid beetles to promote tree death (Christiansen et al. 1987; Krokene 2015; Krokene et al. 2001; Lieutier et al. 2009). Fungi are not able to penetrate the outer rigid bark of trees but are inoculated into the phloem tissue after successful host colonisation by bark beetles (Franceschi et al. 2000). Once inside the phloem, fungi trigger extensive hypersensitive reactions around the infection site with very high accumulation of specialised metabolites resulting in necrosis of phloem tissues (Berryman 1972; Erbilgin et al. 2006; Franceschi et al. 2005; Lieutier et al. 2009; Zhao et al. 2011a, b). Furthermore, fungi can deplete or consume tree reserves such as NSC and lipids that are necessary to synthesise new inducible defence chemicals against invaders (Lahr and Krokene 2013). In this way, fungi might benefit from the stored tree resources to establish itself in the tree and consequently, reduce the ability of the tree (exhaust tree defences) to mount new resistance against pathogens. After successfully colonising phloem and sapwood, fungi appear to remobilise the nutrients back to the phloem for the benefit of larvae and callow adults. Nutritional hypothesis put forth by Six and Elser (2020) and Six and Wingfield (2011) suggests that fungi provide nutrition for both primary and secondary bark beetles. Symbiotic fungi concentrate nitrogen and phosphorous close to beetle’s feeding galleries and can fulfil the nutritional requirement of larvae and callow adults (Six 2019; Six and Elser 2020). Moreover, they supply essential dietary nutrients such as vitamins, amino acids and also ergosterol, a fungal sterol essential for oogenesis and larval development that are absent or only present at low concentrations in the phloem (Bentz and Six 2006; Davis et al. 2019). However, provision of nutrients by fungi for their beetle vectors first requires exhaustion of tree defences.

Role of fungi in modulating beetle colonisation

Increasing evidence suggests that fungal symbionts of bark beetles, in addition to overwhelming tree defence and improving beetle nutrition, have multiple roles in the life cycles of these insects. For example, ophiostomatoid fungi could serve as a source of bark beetle semiochemicals (Fig. 1 and Table 2) and may influence the behaviour of both conspecifics and heterospecifics (Kandasamy et al. 2016). The anti-aggregation or spacing pheromone verbenone produced by symbiotic microbes plays a major role in minimising intraspecific competition among offspring for the resource that directly affects their performance (Bakke 1981; Byers 1989). By inhibiting newly arriving beetles, fungi also benefit from avoiding direct competition for resources from new microbes introduced by conspecifics or heterospecifics (Cale et al. 2019). Interestingly, recent studies have shown that fungal symbionts

of *I. typographus* such as *G. europioides* and *G. penicillata* produce aggregation pheromone components of bark beetles (Table 2). Beetle pheromonal compounds such as 2-methyl-3-buten-2-ol, *exo*- and *endo*-brevicomin, and *trans*-conophthorin are synthesised by fungi *de novo*. This leads to an intriguing hypothesis that both beetles and their symbiotic fungi could have convergently evolved chemical communication signals that mutually benefit each other (Zhao et al. 2015, 2019a). However, ecological relevance for fungi that synthesise and release these bark beetle pheromones in nature is yet to be investigated. Fungal symbionts of *I. typographus* also produce a mixture of simple aliphatic, aromatic alcohols and their acetate esters. These compounds may help callow adult beetles during their maturation phase to feed on symbionts with high nutritional quality and actively select and disperse with beneficial fungi to a new host tree (Kandasamy et al. 2019, 2016).

Responses of associated fungi to specialised metabolites

In addition to provision of nutrients, fungi alter host tissues by metabolising host tree defence compounds such as terpenoids and phenolics, which are toxic to both bark beetles and fungi (Krokene 2015; Raffa et al. 2015). As discussed in Sect. 3.4, phenolics have shown both anti-feedant and anti-nutritional effects on *I. typographus* in bioassays (Faccoli and Schlyter 2007; Hammerbacher et al. 2019); yet seem to have little effect on ophiostomatoid fungi. Interestingly, some fungi are able to degrade phenolics and utilise them as a carbon source (Wadke et al. 2016). Fungal species appear to differ in their ability to metabolise phenolics and their efficiency is positively correlated with fungal virulence (Zhao et al. 2019b). Different fungi within the symbiotic community of *I. typographus* can fulfil the role of metabolising host tree defences, thus supporting bark beetles in successful colonisation and brood production (Zhao et al. 2019b). In multi-choice (cafeteria) bioassays, beetles did not discriminate strictly among fungi based on their degradation efficiency; yet, different virulent fungi that effectively degrade phenolics such as *E. polonica*, *G. penicillata* and *G. europioides* were equally preferred by tunnelling adult beetles over other less virulent fungi (Kandasamy et al. 2019; Zhao et al. 2019b). Moreover, the beetle's preference towards virulent fungi is mediated by olfactory cues. The volatile profile of *E. polonica*, *G. penicillata* and *G. europioides* was highly attractive to the young adults of *I. typographus*, whereas volatiles from avirulent *Ophiostoma* species were unattractive (Kandasamy et al. 2019). These results collectively show that the fungal community of *I. typographus* forms a redundant and interchangeable group,

and the loss of one fungus could be compensated by another fungal species performing similar functions such as detoxification of phenolics.

Effect of temperature and drought on fungus-tree interactions

The growth of ophiostomatoid fungi is influenced by various factors such as phloem temperature, moisture and chemistry (Six 2012). Based on their temperature optima, the fungal community of *I. typographus* can be classified into two groups: cold-tolerant fungi including *E. polonica*, *G. penicillata* and *G. europioides* with a temperature optimum of around 20–23 °C, and warm tolerant fungi such as *O. bicolor* with optimum temperatures of around 30 °C (Solheim 1991). These variations in temperature optima explain regional differences in the composition of fungal communities with *O. bicolor* dominating in warmer regions over *E. polonica* and *Grosmannia* species being prevalent in colder regions (Marin et al. 2005; Solheim 1991).

Increasing temperatures are often accompanied by drought, predisposing trees to bark beetle and fungal attack. Drought, via the altered provision of host defence chemicals, presumably influences the formation of the hypersensitive wound reaction zones in response to pathogens (Netherer et al. 2016). Longer lesions indicate that trees are susceptible to pathogen attack or that the pathogen is highly virulent, whereas shorter lesions indicate that trees are resistant to pathogen attack or that the pathogen is less virulent (Christiansen et al. 1987). Drought alone does not drastically change the constitutive chemical defences of trees in the short term but reduces the hydrolytic conductivity of the vascular tissues (Croisé et al. 2001). However, drought shows clear effects on a tree's chemical response when challenged with pathogens or herbivores (Klutsch et al. 2017). Experiments conducted with conifer seedlings and field grown trees with modified water availability showed that tree age plays an important role in resistance or susceptibility to a particular pathogen. Norway spruce trees, subject to mild drought for several months, increased resistance (short lesion) to the pathogen *E. polonica* when inoculated experimentally (Christiansen and Glosli 1996). Similarly, mild drought stress on hybrid pine (*P. contorta* x *P. banksiana*) trees resulted in shorter lesion lengths after inoculation with *G. clavigera* compared to well-watered trees (Arango-Velez et al. 2014). In contrast, Norway spruce seedlings exposed to mild drought conditions were susceptible to pathogens (long lesions and high mortality of seedlings) compared to healthy seedlings (Linnakoski et al. 2017). Similarly, mild water stress on *Pinus taeda* seedlings resulted in higher pathogenicity of *Leptographium terebrantis* compared to normal water conditions (Devkota et al. 2018). Additionally, susceptibility of conifers to pathogens under different levels

of drought stress is determined by the type of fungal species and is also strain specific (Devkota et al. 2018; Linnakoski et al. 2017). These findings suggest that conifer seedlings are susceptible to pathogen attack under mild drought stress. On the other hand, mild drought could enhance the resistance of mature trees to pathogen attack with potential negative implications for beetle colonisation and reproduction.

Concluding remarks and outlook on future research directions

Effects of drought on bark beetle-induced Norway spruce mortality are still poorly understood

Despite intense research on Norway spruce defence mechanisms, *I. typographus* population dynamics and the role of fungal symbionts in beetle life history, knowledge on the particular effects of drought on these multitrophic relationships is still surprisingly scarce. While severe precipitation deficits have been recognised to increase the risk of bark beetle outbreaks decades ago (Merker 1956; Worrell 1983; Zinecker 1957), we still do not fully understand the physiological and biochemical processes explaining drought-mediated *I. typographus* attack. In a changing climate, various abiotic stress factors such as increasing temperatures and rising levels of atmospheric CO₂ potentially interact in synergistic or antagonistic ways and affect tree resistance to biotic stressors (Holopainen et al. 2018; Niinemets 2010). Thus, field observations gained after natural drought events may strongly differ from experimental data obtained from (semi-) controlled conditions (Allen et al. 2010; Berini et al. 2018). Controlled greenhouse studies with clone seedlings, saplings, or even cell cultures (Messner and Schröder 1999) can reduce the interference of external factors, whereas field experiments using bioassays on mature forest trees (Gaylord et al. 2013; Netherer et al. 2015; Turcani and Nakladal 2007) simulate more natural but highly fluctuating conditions. Moreover, relationships among tree substrate, beetle and fungi are complex and only tree-beetle or beetle-fungus interactions have been studied under laboratory or in field conditions (Hammerbacher et al. 2019; Kandasamy et al. 2019; Linnakoski et al. 2017; Solheim 1991; Wadke et al. 2016; Zhao et al. 2019b). While moderate drought seems to overall strengthen tree defences, multiple stressors can increase tree susceptibility to pathogens and bark beetles. To fully unravel the effects of drought on interactions among trees, fungi, and bark beetles, multifaceted experimental approaches in field and laboratory conditions including molecular biology (Chakraborty et al. 2020a, b; Powell et al. 2020) should focus on multiple interacting partners in the bark beetle system.

Future research directions

Future work should focus on all the players in the multi-partite relationship between Norway spruce, *I. typographus*, and associated microbes and combine chemo-ecological, molecular and behavioural approaches.

- (1) Comprehensively evaluate **Norway spruce** stress and defence status, involving stress history and molecular mechanisms underlying stress-related biochemical processes by:
 - Tracing the allocation, storage and mobilisation of NSC within the tree using CO₂ isotope labelling and measuring multiple tree parameters to better understand carbon source and sink dynamics and to unravel trade-offs between primary and secondary metabolism of Norway spruce, as recently proposed by Huang et al. (2019) but with specific focus on drought effects.
 - Linking molecular, biochemical and physiological markers of tree drought stress such as capacity of specialised metabolite biosynthesis and indicators of tree water potential to bark beetle attack and colonisation success in order to improve assessment of stress-related Norway spruce susceptibility to *I. typographus* infestation.
- (2) Provide an updated, comprehensive view on ***I. typographus*-Norway spruce** interactions considering behavioural sequence from dispersal to acceptance of host tissue by:
 - Studying attraction, host selection and acceptance from landscape level to bark sections of individual trees in (semi-) field and laboratory bioassays, to clearly identify the decisive environmental and tree parameters for host choice.
 - Relating visual, olfactory, gustatory and haptic cues from the forest environment to the basic sensory mechanisms of host identification and selection to allow deeper insights in the molecular biology and ecology of *I. typographus*, using the recently available genome (Powell et al. 2020).
 - Taking advantage of dropping costs of modern DNA sequencing methods, transcriptomic, proteomic and even whole-genome data for *I. typographus* should be generated under various biotic and abiotic interactions. Such analyses support a deeper understanding of underlying mechanisms of *I. typographus* life history and interactions with its environment and provide an opportunity for large-scale comparative studies to understand the evolution of bark beetles and other herbivorous insects.
- (3) Improve our understanding of the role of **fungal symbionts** on *I. typographus* performance by:
 - Elucidating nutritional and detoxification roles of fungal symbionts by assessing the performance or fitness of bark beetles in the presence and absence of fungal

symbionts in terpenes or phenolics-enriched diet. Tree chemicals should be tested as single compounds and as mixtures to better understand synergistic properties of diverse spruce defence chemicals on bark beetles and fungi.

- Focusing on how drought affects the growth rates of ophiostomatoid fungi in phloem and consequent effects on their production of volatile cues that mediate interactions between fungi and beetles to better understand multitrophic interactions under changing climatic conditions.
- Field trapping of *I. typographus* using live cultures of fungi or synthetic olfactory-active fungal volatiles to improve our knowledge on the role of fungi in host choice, aggregation and anti-aggregation of *I. typographus*.
- Quantifying the relationship between fungal establishment in the phloem and insect semiochemical production to elucidate the role of fungal volatiles in successful tree attack and brood establishment.

Conclusions

Tree resistance, insect and pathogen performance are strongly modified by the intensity, timing and duration of drought events. A clear definition of ‘moderate’ versus ‘severe’ and ‘acute’ as opposed to ‘chronic’ water deficit is necessary for a meaningful interpretation of multiple studies on drought-mediated effects (Caldeira 2019; Gely et al. 2020). A known fact is that trees’ resilience to adapt to constant, persistent unfavourable site conditions can enhance their potential to endure drought periods and also to defend biotic invaders (Berini et al. 2018; Ferrenberg et al. 2017). These chronically stressed trees seem to be less susceptible to *I. typographus* infestations than trees suddenly exposed to drought as well as fast growing trees of high tissue quality but moderately impaired defence (Baier et al. 2002; Blomqvist et al. 2018; Netherer et al. 2019).

A focus on surviving trees, i.e. trees without attacks or those which succeeded to fight-off invasions even at high attack pressure (Balogh et al. 2018; Schiebe et al. 2012; Six et al. 2018), can help to reveal the causalities of *I. typographus* infestations. In natural forests, bark beetle outbreaks likely act as natural selection events in favour of tree genotypes better adapted to warm and dry conditions and escaping *I. typographus* attacks (Jakuš et al. 2011). The future mitigation of drought-related forest mortality also relies on the promotion of particular tree species and genotypes with enhanced individual defence capacity (Telford et al. 2014). High species diversity and natural species communities are expected to stimulate selective processes that enhance the

resistance of European forests to specialised herbivores and pathogens (Grossiord 2019) such as *I. typographus* and its associated organisms.

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Author contributions SN, AJ and FS composed the outline and assembled all co-authors. All authors performed the literature research and contributed to writing. SN, AJ, FS and DK conceptualised the figures and the table. SN, DK, MS and FS critically revised the work.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Consent to publish All authors read and approved the manuscript.

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