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Review

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Abstract

Ips typographus (L.) and *Pityogenes chalcographus* (L.) (Coleoptera: Curculionidae) are two common bark beetle species on Norway spruce in Eurasia. Multiple biotic and abiotic factors affect the life cycles of these two beetles, shaping their ecology and evolution. In this article, we provide a comprehensive and comparative summary of selected life-history traits. We highlight similarities and differences in biotic factors, like host range, interspecific competition, host colonization, reproductive behaviour and fungal symbioses. Moreover, we focus on the species' responses to abiotic factors and compare their temperature-dependent development and flight behaviour, cold adaptations and diapause strategies. Differences in biotic and abiotic traits might be the result of recent, species-specific evolutionary histories, particularly during the Pleistocene, with differences in glacial survival and postglacial recolonization. Finally, we discuss future research directions to understand ecological and evolutionary pathways of the two bark beetle species, for both basic research and applied forest management.

Introduction

Bark beetles (Coleoptera: Curculionidae: Scolytinae) are among the most destructive forest pests worldwide (Raffa *et al.*, 2015). This group of weevils harbours highly diverse species that spend the majority of their life cycles in various tissues of woody and herbal plants (Kirkendall *et al.*, 2015). Bark beetles are of high ecological importance, as the majority of species lives in dead or dying plants, thus being early decomposers in forest ecosystems (Raffa *et al.*, 2015). Only a small number of species can successfully breed in living hosts (Kirkendall *et al.*, 2015). These species, however, make bark beetles major forest or agricultural pests (Grégoire *et al.*, 2015; Raffa *et al.*, 2015). In addition, bark beetles are interesting study systems in evolutionary research, as several traits, e.g. feeding modes, reproductive systems, sex determination systems and levels of sociality, often originated multiple times independently (Kirkendall *et al.*, 2015).

Bark beetles are commonly found in conifer forests of the northern hemisphere. *Ips*, *Dendroctonus* and *Pityogenes* are the most ecologically and socio-economically important genera in Europe and North America (Schelhaas *et al.*, 2003; Grégoire and Evans, 2004; Raffa *et al.*, 2008; Cognato, 2015; Six and Bracewell, 2015). Norway spruce, *Picea abies* (L.) Karst., is a major tree species in Europe and gets infested by several bark beetles (Pfeffer, 1995). In some regions, Norway spruce-dominated forests have been affected mainly by two scolytine species: *Ips typographus* (L.) and *Pityogenes chalcographus* (L.). Mass outbreaks usually follow abiotic disturbances, like wind-throw, snow-break or drought, providing high amounts of suitable material for brood production, subsequently resulting in rapid population growth and colonization of moderately stressed trees (Schroeder and Eidmann, 1993; Schroeder and Lindelöw, 2002; Hedgren *et al.*, 2003; Hedgren, 2004; Wermelinger, 2004). However, these outbreaks are facilitated by other biotic and abiotic factors as well (Grégoire *et al.*, 2015; Netherer *et al.*, 2015; Raffa *et al.*, 2015; Seidl *et al.*, 2015; Biedermann *et al.*, 2019; Netherer *et al.*, 2021). Here we compare life-history traits of *I. typographus* and *P. chalcographus*, discuss them in the light of their evolutionary past and propose future research directions for a better understanding of the biology and ecology of these bark beetles.

Ips typographus and *P. chalcographus* – an overview

Both *I. typographus* and *P. chalcographus* have a similar geographic range and are distributed from the Mediterranean region to Northern Scandinavia and from Western Europe to East Asia (Knizek, 2011). The life cycles of *I. typographus* and *P. chalcographus* correspond to that of 'standard' polygynous phloem breeders (Sauvard, 2004). In brief, after hibernation adults leave their overwintering habitat and start to swarm in spring. In both species the

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male initiates a breeding system on a host that was selected on the basis of visual, olfactory and gustatory cues. After overcoming initial tree defence mechanisms, e.g. resin flow, the male bores through the bark and establishes a mating chamber in the phloem (Postner, 1974; Wermelinger, 2004). By releasing aggregation pheromones, other male and female conspecifics are subsequently attracted (Francke *et al.*, 1977; Schlyter *et al.*, 1987a, 1987b; Byers *et al.*, 1988, 1989; Birgersson *et al.*, 1990). In both species usually multiple females enter the mating chamber, copulate with a single male and start to excavate individual mother tunnels. On either side of these tunnels eggs are deposited in small niches. Male and female parents express subsocial behaviour, as they perform brood care, e.g. by grooming eggs, providing a well-protected environment and a highly disposable food source for their offspring. Larvae establish individual tunnels in the phloem layer and finally pupate in pupal chambers. Afterwards young adults perform a maturation feeding in the surrounding phloem for gonad and flight muscle development, bore through the outer bark and disperse to establish the next generation (Postner, 1974). Additionally, parental beetles of both species can re-emerge after a first brood establishment and initiate another offspring generation, i.e. a sister brood (Annala, 1969; Postner, 1974; Anderbrant and Lofqvist, 1988; Anderbrant, 1989). Under favourable environmental conditions *I. typographus* and *P. chalcographus* can establish up to three generations (plus sister broods) per year (Postner, 1974; Wermelinger, 2004; Wermelinger *et al.*, 2012), even though the discrimination of different generations and sister broods in the field is difficult.

Comparison of selected life-history traits

Biotic factors

Host range

Both *I. typographus* and *P. chalcographus* can utilize different conifer species of the family Pinaceae. However, they differ in their potential host range, their preference for and their performance on different tree species (table 1, fig. 1) (Postner, 1974; Pfeffer, 1995; Bertheau *et al.*, 2009b).

Ips typographus is generally classified as a monophagous bark beetle, whereas *P. chalcographus* is regarded to be oligophagous (Eidmann, 1987; Mayer *et al.*, 2015). The primary host of both beetles is Norway spruce, as it was proven by presence-abundance data under natural conditions or by preference-performance studies in the laboratory (Postner, 1974; Pfeffer, 1995; Bertheau *et al.*, 2009a, 2009b; Cognato, 2015; Schroeder and Cocos, 2018). Secondary, less commonly used hosts of both species are from the genera *Pinus*, *Larix*, *Abies* or *Pseudotsuga*, both native and non-native species (Postner, 1974; Bertheau *et al.*, 2009b; Schroeder and Cocos, 2018). Although the two beetles can colonize and breed in similar host species, *P. chalcographus* is more abundant on all secondary hosts (Bertheau *et al.*, 2009b; Schroeder and Cocos, 2018). The oligophagous behaviour can confer an ecological and evolutionary advantage to *P. chalcographus*, as it can shift to other plants when primary hosts are scarce or absent, e.g. when new habitats are invaded.

Interspecific competition

Resource partitioning and competition have been described from various bark beetles (Paine *et al.*, 1981; Light *et al.*, 1983; Bouhot *et al.*, 1988; Rankin and Borden, 1991). Smaller-sized species colonize upper, thin-barked parts of trees, whereas larger-sized beetles

are found in lower, thick-barked sections. This separation in ecological niches reduces interspecific competition and is driven by the diameter of the body (Grünwald, 1986; Schlyter and Anderbrant, 1993; Amezaga and Rodriguez, 1998). Hence, given the larger body size of *I. typographus*, it prevails in thicker host material/stem sections than *P. chalcographus*, although overlaps occur (table 1, fig. 1) (Grünwald, 1986; Göthlin *et al.*, 2000). The latter one can utilize a broader range of bark sections, including those preferred by *I. typographus*. In these thicker parts, however, *P. chalcographus* is apparently outcompeted (Grünwald, 1986).

Mating system, reproductive performance and gallery morphology

Ips typographus and *P. chalcographus* are polygynous bark beetles, however, they differ markedly in the number of females attracted per male (table 1, fig. 1). After building a mating chamber in the phloem, *P. chalcographus* males can mate with up to nine females (Schwerdtfeger, 1929), whereas *I. typographus* has harem sizes of generally two or three, sometimes four, females (Wermelinger, 2004).

The two beetles also differ in their fecundity. One female of *I. typographus* can deposit up to 80, or even 100, eggs per gallery (Anderbrant and Lofqvist, 1988; Anderbrant, 1990; Wermelinger, 2004), whereas one *P. chalcographus* female can lay up to 40 eggs (Schwerdtfeger, 1929; Führer and Mühlenbrock, 1983). The average reproductive output per female, however, is much lower and highly variable under natural conditions (Thalenhorst, 1958), depending on various factors, like the quality of the breeding material and inter- and intraspecific competition (Anderbrant and Lofqvist, 1988; Anderbrant, 1990; Faccoli and Bernardinelli, 2011). About 30 eggs per female likely reflect the average reproductive potential per gallery of *P. chalcographus* (Schwerdtfeger, 1929) and 25 to 60 eggs for *I. typographus* (Thalenhorst, 1958; Anderbrant and Lofqvist, 1988; Anderbrant, 1990).

Both species differ in the architecture of their galleries (table 1, fig. 1). After mating *I. typographus* females build their mother tunnels in a vertical direction, following the fibre direction of the host. In contrast, females of *P. chalcographus* construct their mother tunnels in different directions starting from a central mating chamber, resulting in a stellar breeding system (Postner, 1974). Obviously, these galleries are shaped by the number of females per male but underlying evolutionary drivers for these differences in the reproductive biology are unknown. It is also unclear if there is an optimal direction for maternal or larval tunnels, which might be influenced by factors, like the spatial structure of nutrients and tree defences as well as growth properties of associated fungi.

Pityogenes chalcographus usually shows higher attack densities and higher egg gallery densities on hosts and tends to be more ubiquitous than *I. typographus* (Hedgren *et al.*, 2003; Hedgren, 2004). The latter one, however, has a much higher tree-killing ability on living hosts (Hedgren, 2004). Moreover, *P. chalcographus* is often found on trees that have already been attacked by *I. typographus* (Hedgren, 2004). In habitats with plenty of suitable breeding material, e.g. storm-felled trees, *P. chalcographus* is more abundant in later phases of a post-storm period (Hedgren, 2004; Schroeder and Cocos, 2018), underlining different preferences for host quality.

Fungal symbionts

Bark beetles are generally associated with a wide variety of filamentous fungi and yeasts (Six, 2013; Biedermann and Vega, 2020) and more than 30 different fungus species have been

Table 1. Selected life-history traits of *Ips typographus* and *Pityogenes chalcographus*

Life-history traits	<i>Ips typographus</i>	<i>Pityogenes chalcographus</i>
Relative host range	Largely monophagous (primary host Norway spruce)	Oligophagous (primary host Norway spruce)
Host niche	Thick-barked tree sections (bark thickness >2.5 mm; mean body diameter ~1.8 mm)	Preferably thin-barked tree sections (broad range of bark thickness, also <2.5 mm; mean body diameter ~0.8 mm)
Tree-killing ability	High	Low
Mating system	Polygynous, male-initiated, <4 ♀/ 1 ♂	Polygynous, male-initiated, <9 ♀/ 1 ♂
Gallery morphology	Vertical maternal tunnels	Stellar maternal tunnels
Fecundity per female	<100 eggs/♀	<40 eggs/♀
Sister broods	Yes	Yes
Attack density (under outbreak conditions)	~150 entrance holes m ⁻²	~480–650 entrance holes m ⁻²
Key filamentous fungal symbionts, with role in host tree exhaustion or detoxification of tree defences	<i>Endoconidiophora polonica</i> , <i>Grosmannia penicillata</i> , <i>Grosmannia europhioides</i>	None
Key yeast symbionts, with role in host tree exhaustion or detoxification of tree defences	<i>Pichia holstii</i> , <i>Candida diddensii</i>	Present but undescribed
Cold tolerance strategy	Freeze avoidant	Freeze avoidant
Overwintering developmental stages (low sub-zero temperatures)	Adult	Larva, pupa, adult
Diapause	Adult reproductive diapause	Adult reproductive diapause (likely)
Induction of facultative diapause	Photoperiod (modified by temperature)	Photoperiod (modified by temperature)

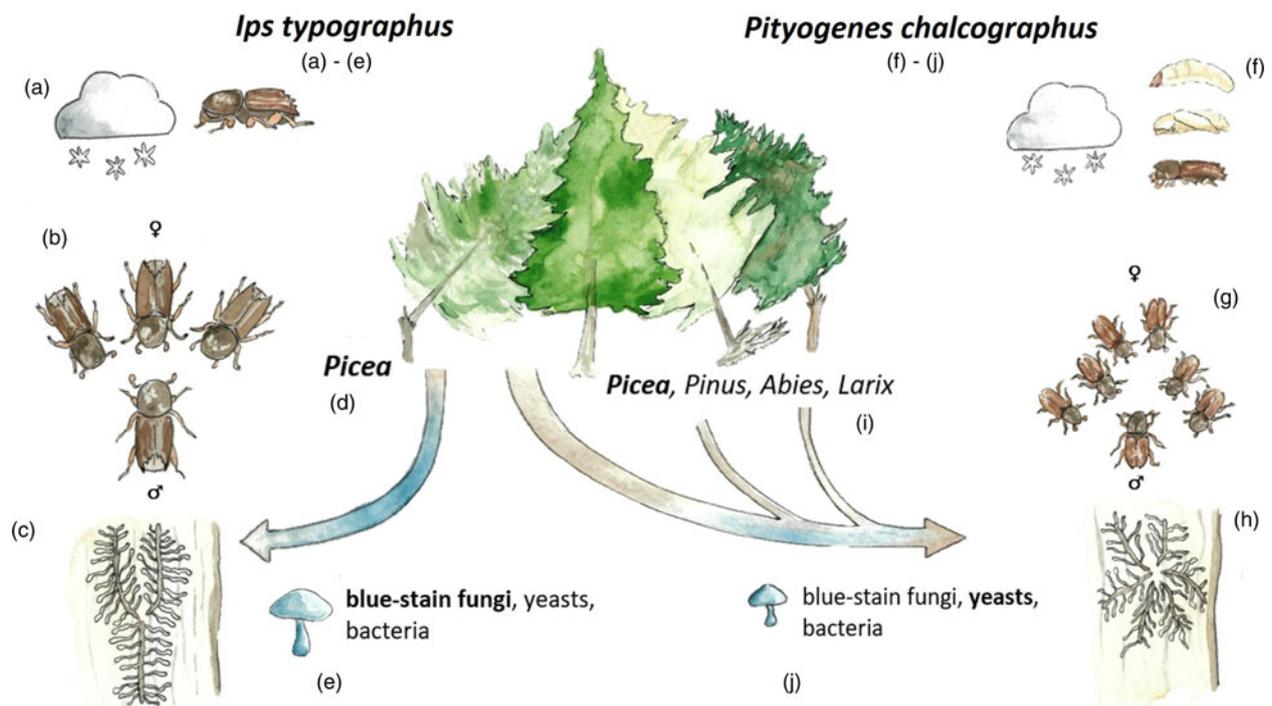


Figure 1. Overview on life-histories of *Ips typographus* (left) and *Pityogenes chalcographus* (right). *Ips typographus*: (a) Overwintering usually as an adult. (b) Polygynous reproduction, with a common harem size of three females. (c) Typical breeding system with vertical maternal galleries. (d) Monophagous feeding behaviour with Norway spruce (*Picea abies*) as the main host. (e) Associated microbes with blue-stain fungi as most relevant symbionts. *Pityogenes chalcographus*: (f) Overwintering as larva, pupa, and adult. (g) Polygynous reproduction, with a harem size of up to nine females. (h) Typical stellar breeding system. (i) Oligophagous feeding behaviour on various conifer genera with Norway spruce as the main host. (j) Associated microbes with yeasts as most relevant symbionts.

isolated from the galleries of *I. typographus* and *P. chalcographus* (table 1, fig. 1) (Kirschner, 1998; Kirisits, 2004; Giordano *et al.*, 2013; Jankowiak *et al.*, 2014). Most of these species are likely commensals or antagonists, however, bark beetles usually also have a few beneficial fungal associates. These mutualistic species provide nutritional benefits, aid in detoxification of tree defensive compounds and pheromone production and/or protect their hosts against antagonistic microbes (Francke-Grosmann, 1967; Birkmoe *et al.*, 2018; Davis *et al.*, 2019; Biedermann and Vega, 2020). Likely candidates for mutualistic roles in *I. typographus* and *P. chalcographus* are fungal species in the ascomycete Ophiostomatales, i.e. the genera *Ophiostoma*, *Grosmannia* and *Ceratocystiopsis*, and Microascales, i.e. the genus *Endoconidiophora* (Harrington, 2005; Six, 2013). Both species, however, lack mycetangia/mycangia, i.e. external spore-carrying pockets (Francke-Grosmann, 1956, 1959, 1963; Vega and Biedermann, 2020), and many of the fungi are found only irregularly. Therefore, for *P. chalcographus* fungal symbionts have been regarded unimportant (Grosmann, 1930; Mathiesen-Käärik, 1960; Kirisits, 2004). For *I. typographus* debates on the importance and phytopathogenic properties of fungal symbionts to overcome healthy trees are still ongoing (Kirisits, 2004; Salle *et al.*, 2005; Lieutier *et al.*, 2009; Six and Wingfield, 2011). Fungi are exchanged between the two bark beetles, in particular Ophiostomatales from *I. typographus* to *P. chalcographus*, when they co-occur on the same tree (Grosmann, 1930; Mathiesen-Käärik, 1953). This co-occurrence usually results in the isolation of the same fungal species from galleries of the two bark beetles, even though several studies suggest that filamentous fungi are more common in *I. typographus* relative to *P. chalcographus* galleries (Grosmann, 1930; Mathiesen-Käärik, 1960; Krokene and Solheim, 1996; Kirisits, 2004). The simple reason might be that thinner phloem dries out more quickly, providing worse conditions for fungal growth (Grosmann, 1930; Mathiesen-Käärik, 1953). This is supported by the fact that relatively dry- and heat-resistant fungi, e.g. Hypocreales in the genus *Geosmithia*, are more common in galleries of *P. chalcographus* (Kolarik and Jankowiak, 2013; Jankowiak *et al.*, 2014).

Frequency differences of fungal associates, however, might result in different tree-killing abilities of the two bark beetle species (Krokene and Solheim, 1996). *Ips typographus* is commonly associated with the highly virulent fungus *Endoconidiophora polonica* that may help beetles to overcome trees (Horntvedt *et al.*, 1983; but see Six and Wingfield, 2011) by over-stimulation of host defence (Lieutier *et al.*, 2009). Frequencies of *E. polonica* are locally highly variable and appear to differ between epidemic and non-epidemic populations (Harding, 1989; Solheim, 1993; Krokene and Solheim, 1996). Likely this fungus is a good colonizer of well-defended phloem of trees during epidemics (Solheim, 1992; Gibbs, 1993). Like other symbionts, it can cope with tree defensive compounds, e.g. terpenes or phenolics, and can even use those substances as a carbon source for growth (Krokene and Solheim, 1998; Hammerbacher *et al.*, 2013; Krokene, 2015; Wadke *et al.*, 2016).

The second important fungal associate of *I. typographus* is *Grosmannia penicillata*. Like *E. polonica*, it is transmitted by dispersing beetles on the body surface via sticky spores (Furniss *et al.*, 1990) and is virulent to Norway spruce (Horntvedt *et al.*, 1983). Recently, it has also been shown that it can synthesize components of the aggregation pheromone of *I. typographus* (Zhao *et al.*, 2015) and together with another associate *Grosmannia europhioides* it is even more efficient in degrading beetle-toxic

phenolics than *E. polonica* (Zhao *et al.*, 2019). Furthermore, adult beetles prefer to feed on artificial spruce substrate colonized and thus detoxified by these fungi (Zhao *et al.*, 2019). These three fungi (*E. polonica*, *G. penicillata*, *G. europhioides*) were also the only ones emitting volatiles that attracted adult *I. typographus* in behavioural assays on an artificial spruce substrate and may thus be regarded as mutualists (Kandasamy *et al.*, 2019). Other common associates, like *Ophiostoma piceae* and *Ophiostoma bicolor*, are neither attractive nor repellent to *I. typographus* and may thus be regarded as commensals (Kandasamy *et al.*, 2019). Interestingly, bark beetle-infesting parasitoids can use volatiles emitted by certain microorganisms to detect their hosts, adding another part to these multi-trophic systems (Wegensteiner *et al.*, 2015).

Assays like those for *I. typographus* are lacking for *P. chalcographus* but given the lower abundance of fungi within their galleries beneficial effects might be smaller. Several studies, however, indicate that *Geosmithia* and yeasts that are transmitted by *P. chalcographus* are less dry-sensitive than Ophiostomatales and Microascales associated with *I. typographus* (Grosmann, 1930; Kolarik and Jankowiak, 2013; Jankowiak *et al.*, 2014). Grosmann (1930), for example, showed that yeasts are abundant in young breeding systems, especially surrounding eggs, from where they are picked up by larvae and can later be found as gut symbionts. If these early observations are true, *P. chalcographus* may profit from internal fungi in detoxification of defensive tree compounds but typically lacks external fungal symbionts that can help *I. typographus* to overwhelm living trees.

Yeasts are generally understudied in bark beetles (Davis, 2015) and their role has only been partly elucidated for *I. typographus* (Leufven, 1991). Main *I. typographus* pheromone components are synthesized by beetles *de novo* (Blomquist *et al.*, 2010). However, several gut yeasts of *I. typographus*, the most common ones are *Pichia holstii* and *Candida diddensii*, oxygenate tree-defensive monoterpenes like α -pinene that beetles themselves oxidize to cis-verbenol, to either trans-verbenol or verbenone (Leufven *et al.*, 1984, 1988; Leufven and Nehls, 1986). Interestingly, cis-verbenol acts as an aggregation pheromone for *I. typographus* but not for *P. chalcographus*, whereas yeast-produced trans-verbenol or verbenone have anti-aggregation effects for both species (Leufven, 1991; Davis, 2015). The yeasts of *P. chalcographus* have not been studied for their semiochemical role and it needs to be determined if both species harbour different yeasts and how frequently they get exchanged.

Overwintering and diapause

Adverse conditions during cold winters can cause high mortality in bark beetle populations and thus drive population dynamics (Faccoli, 2002; Kostal *et al.*, 2011, 2014; Wang *et al.*, 2017). Numerous insects enter diapause to overcome unfavourable periods, like harsh winters in temperate regions. During diapause, development and reproduction are arrested, the metabolic rate is reduced and resistance against environmental stressors is increased (Kostal, 2006). Other adaptations of insects to cold are directly related to mitigating the lethal effects of low temperatures (Lee, 2010). The diapause and overwintering behaviour of *I. typographus* has recently been reviewed in a comprehensive manner (Schebeck *et al.*, 2017). Therefore, we will cover this species just briefly, rather focus on *P. chalcographus* and especially highlight similarities and differences between the two bark beetles (table 1, fig. 1).

Cold tolerance

Major adaptations of insects to survive cold winters are strategies to cope with the freezing of body fluids. *Ips typographus* and *P. chalcographus* are both freeze-avoidant species (Kostal *et al.*, 2011, 2014), as they die when ice formation in body fluids occurs – the temperature when ice is built is defined as the supercooling point (SCP) (Bale, 1993; Lee, 2010; Sinclair *et al.*, 2015). Both species evolved a high supercooling capacity to survive cold conditions, by using a set of sugars and polyols to decrease the freezing point of the haemolymph (Kostal *et al.*, 2007, 2011, 2014). Adults of *P. chalcographus* from Central European populations survived cold conditions below average temperatures of -26°C in mid-winter, with some individuals surviving even -36°C (Kostal *et al.*, 2011, 2014). Adult beetles of Central European *I. typographus* had average SCPs in mid-winter of about $-20/-22^{\circ}\text{C}$, with single individuals reaching SCPs of almost -27°C (Kostal *et al.*, 2011). In addition, both beetles have also a high chilling potential to survive sub-zero temperatures above the SCP, even over long periods (Kostal *et al.*, 2011, 2014). Cold tolerance and survival is a plastic response, as insects can acclimatize to ambient conditions. In Northern Europe where winter conditions can be harsher than in more southern latitudes *I. typographus* can cope with temperatures as low as -32°C , with an average of about -29°C in mid-winter (Annala, 1969). Moreover, *I. typographus* and *P. chalcographus* show similar patterns in their seasonal supercooling capacity, with the lowest SCP values in December/January (Kostal *et al.*, 2011, 2014), reflecting modifications depending on prevailing temperature conditions.

As the two bark beetles often overwinter under the bark of host trees, they might get in contact with ice in the moist, frozen phloem layer. This can result in inoculative freezing, a process when environmental ice enters the body via orifices or through the cuticle and results in freezing of body fluids (Lee, 2010). Both species evolved adaptations to avoid inoculative freezing (Kostal *et al.*, 2011, 2014). Experiments with adult *P. chalcographus*, however, suggest that it can survive harsher conditions in the presence of external ice (Kostal *et al.*, 2014) than adult *I. typographus* (Kostal *et al.*, 2011). The overwintering performance of the two beetle species was also tested under natural field conditions. In a Czech study, adult *P. chalcographus* survival rates over a winter ranged in most cases between ~ 30 and $\sim 75\%$ (Kostal *et al.*, 2014). Considering also the survival rates under laboratory conditions and the SCP data obtained by Kostal *et al.* (2014), high proportions of *P. chalcographus* populations might survive cold temperatures during Central European winters. Low temperatures, however, are not the only limiting factors for overwintering survival. Biotic and abiotic parameters that can vary on a very small, local scale contribute to a complex picture that determine mortality during cold.

Ips typographus overwinters either under the bark of hosts or in the forest litter (Biermann, 1977). In Central Europe, overwintering survival rates of *I. typographus* (across all developmental stages) hibernating under the bark of Norway spruce of about 50% were reported (Faccoli, 2002). In Northern Europe, however, mortality of adult *I. typographus* overwintering under the bark ranges from ~ 60 to 100%, whereas adult survival in the litter or moss layer – with an additional insulating snow cover – is over 90% (Annala, 1969). Unfortunately, studies on the overwintering behaviour and survival of *P. chalcographus* outside of host trees, e.g. in the forest litter, are currently lacking. Such data would be important to get a comprehensive picture of the beetle's life history.

One major difference in the overwintering biology of the two bark beetles concerns the developmental stages surviving low sub-zero conditions. In *I. typographus* only the adult stage can survive low sub-zero temperatures (Annala, 1969; Faccoli, 2002; Dworschak *et al.*, 2014), whereas pre-imaginal stages survive only mild but still sub-zero conditions (Stefkova *et al.*, 2017). In *P. chalcographus* larvae, pupae and adults are able to survive low winter temperatures (Kostal *et al.*, 2014). *Ips typographus* might face a decrease of population levels when beetles do not reach the adult stage before winter – which can happen when cold autumn temperatures slow down development or when warm conditions hamper the induction of diapause (details see below). In *P. chalcographus*, however, beetles that started their individual development late in the season or whose development was slowed down due to thermal conditions might still be able to survive winter although not completing their entire life cycle. This could relax selection on the timing of oviposition and thus increase the length of the egg-laying period, although the effects of a photoperiodically regulated reproductive diapause are not entirely clear (see below). Moreover, *I. typographus* overwintering only as adults could result in a synchronization of populations which might be advantageous during host colonization in the following season.

Diapause

Diapause expression is a major strategy for *I. typographus* to increase stress resistance during winter and additionally regulates development, reproduction and voltinism (Schopf, 1985, 1989; Dolezal and Sehnal, 2007; Schebeck *et al.*, 2017; Schroeder and Dalin, 2017; Schebeck *et al.*, 2022). The induction of the facultative reproductive diapause of the adult in the larval/pupal instars is driven by short-day photoperiods and the critical day length for Central European beetles is about 15 h (Schopf, 1989; Dolezal and Sehnal, 2007). Diapause induction is not regulated by photoperiod alone, as the effect of day length is overridden by high temperatures (Dolezal and Sehnal, 2007). Moreover, the critical day length increases with latitude, to respond to local environmental conditions (Schroeder and Dalin, 2017). Diapause termination occurs in mid-winter after experiencing a chilling period. Afterwards *I. typographus* remains in a post-diapause quiescence and resumes development and reproduction when conditions are favourable again (Dolezal and Sehnal, 2007). In addition, several lines of evidence suggested that this species expresses a second diapause phenotype. Observations on suppressed development, reproduction and dispersal – despite permissive environmental conditions – indicated the presence of an obligate diapause, with both diapause phenotypes in one population (Schopf, 1985, 1989; Dolezal and Sehnal, 2007; Schroeder and Dalin, 2017). Schebeck *et al.* (2022) proved the existence of facultative (photoperiod-dependent) and obligate (independent of photoperiod) diapause phenotypes in *I. typographus*, showing varying portions in Central and Northern European populations with implications for seasonality and voltinism.

Pityogenes chalcographus seems to enter a photoperiodically regulated diapause in the adult stage as well (Führer and Chen, 1979). Developmental studies under long-day and short-day conditions at different temperatures showed that all individuals of a generation emerge from their breeding systems at warmer conditions with only a minor influence of photoperiod. At lower temperatures, however, a distinct influence of day length on development was described, suggesting a photoperiodically mediated diapause which is modified by warm temperatures (Führer and Chen, 1979). This would be a similar mechanism

as described in *I. typographus* (Schopf, 1985, 1989; Dolezal and Sehnal, 2007), however, additional studies are necessary to get a comprehensive picture.

Although bark beetles spend the majority of their live cycles in subcortical environments, they can process photoperiodic signals in various developmental stages. Even pre-imaginal stages, like larvae that lack eyes (stemmata) were reported to respond to photoperiodic cues, as it was shown in the mountain pine beetle, *Dendroctonus ponderosae*, by opsin gene expression and negative phototactic behaviour (Wertman et al., 2018).

Thermal effects on life history

The temperature-dependent development of *I. typographus* has been studied extensively under laboratory and field conditions (Annala, 1969; Lobinger, 1994; Coeln et al., 1996; Wermelinger and Seifert, 1998, 1999; Baier et al., 2007). Data on developmental times, developmental thresholds or optimum temperature differ considerably among studies (Annala, 1969; Coeln et al., 1996; Wermelinger and Seifert, 1998). These differences are likely related to the experimental design or population-related factors. Values for the lower developmental threshold for the whole life cycle range from 5 °C (Annala, 1969), to 8.3 °C (Wermelinger and Seifert, 1998) and even to 12.3 °C (Coeln et al., 1996). Data from the most recent study by Wermelinger and Seifert (1998), however, are commonly used to model the phenology and voltinism of *I. typographus* and they reliably predict its development under natural conditions (Baier et al., 2007; Jönsson et al., 2009). The optimum temperatures for development and reproduction are about 30 °C (Wermelinger and Seifert, 1998) and around 29 °C (Wermelinger and Seifert, 1999), respectively. The upper developmental threshold is about 39 °C (Wermelinger and Seifert, 1998) and Annala (1969) reported a strong increase of *I. typographus* mortality of all developmental stages at temperatures above 45 °C.

Data on the thermal performance of *P. chalcographus* are scarce. The temperature-dependent development was studied by Coeln et al. (1996). These data on developmental thresholds are probably higher than under natural field conditions. Additional comprehensive and comparative studies on all temperature-related parameters have to be conducted to get a better understanding of its thermal performance.

In addition, temperature affects the flight activity of *I. typographus* and *P. chalcographus*. For both species, the lower limit for swarming initiation is relatively similar, about 16.5 °C/17 °C. The upper limit, however, is 30 °C in *I. typographus*, while *P. chalcographus* was still observed swarming at 35 °C (Lobinger, 1994).

Although developmental parameters, like lower thermal thresholds or developmental times, of *I. typographus* and *P. chalcographus* seem to differ from each other, some similar patterns have been observed. For example, the developmental time of the larval stage is about threefold longer than the embryonic or pupal development, respectively. Furthermore, the maturation period of young adults comprises roughly 40% of the whole development in both beetles (Coeln et al., 1996; Wermelinger and Seifert, 1998; Baier et al., 2007).

Comparison of recent evolutionary histories

Biogeography

Differences in certain life-history traits of *I. typographus* and *P. chalcographus* could be related to differences in their evolutionary

histories. Previous studies focused on processes during the last ice ages and assessed the effects of climate-driven range changes during glacial-interglacial periods (Stauffer et al., 1999; Salle et al., 2007; Avtzis et al., 2008; Bertheau et al., 2013; Mayer et al., 2015; Schebeck et al., 2018, 2019).

Studies on various European and North American bark beetles revealed that Pleistocene climatic oscillations shaped the genetic structure of several species. Moreover, these events are related to certain life-history traits, like the evolution of pheromone races, developmental variations, reproductive incompatibilities and the formation of novel sex chromosomes (Cognato et al., 1999, 2003; Mock et al., 2007; Bracewell et al., 2011, 2017; Dowe et al., 2017). Both *I. typographus* and *P. chalcographus* survived Pleistocene glaciation events in multiple, geographically isolated European refugia, shared with their main host plant Norway spruce (Stauffer et al., 1999; Salle et al., 2007; Avtzis et al., 2008; Bertheau et al., 2013; Mayer et al., 2015; Schebeck et al., 2018). Apart from this general pattern, the two species exhibit important differences in their Pleistocene histories. *Pityogenes chalcographus* survived glacial periods in three major refugia: in the Russian plain, in the Carpathian Mountains and in the Italian-Dinaric region, followed by postglacial secondary contact (Avtzis et al., 2008; Bertheau et al., 2013; Schebeck et al., 2018). In addition to these main refugia, *P. chalcographus* might also have survived cold events in smaller areas, like in the Apennine Mountains (Schebeck et al., 2019) and other regions of Norway spruce Pleistocene survival (Tollefsrud et al., 2008).

In contrast, the Pleistocene history of *I. typographus* is less clearly resolved; specifically, the number and locality of refugia is still under debate. Recent studies propose that European populations are generally structured in two major genetic groups with an overall pattern of north-south clustering (Bertheau et al., 2013; Mayer et al., 2015) with slight signals of sub-structure (Krascsenitsova et al., 2013; Mayer et al., 2014, 2015). Irrespective of the exact number of refugial areas, the locality of one or several regions is also unknown but was very likely shared with one refugium of Norway spruce (Schmidt-Vogt, 1977; Tollefsrud et al., 2008) and additional minor areas were Norway spruce was present (Tollefsrud et al., 2008). A genome-wide survey as well as a thorough population sampling across the species' range might elucidate this open question in bark beetle biogeography.

Evolutionary history

Differences in certain life-history traits of *I. typographus* and *P. chalcographus* could additionally be the result of the species' different evolutionary age. Present mitochondrial *P. chalcographus* lineages diverged about 100,000 years ago, whereas the evolutionary history of *I. typographus* is about five times younger (Bertheau et al., 2013). The genetic structure of both beetles is characterized by high levels of gene flow, however, *P. chalcographus* has a deeper structure than *I. typographus* (Stauffer et al., 1999; Avtzis et al., 2008; Bertheau et al., 2012, 2013). Differences in age, genetic structure and glacial refugia could be related to varying patterns in host range, overwintering biology or thermal performance, however, detailed future studies have to test these hypotheses on the evolution of these two bark beetles.

Summary and outlook

Ips typographus and *P. chalcographus* are two common and widespread bark beetle species with diverse life histories. *Ips*

typographus is clearly a stronger tree killer than *P. chalcographus*. Given in particular its narrower host range and higher host-quality demands, we hypothesize that selection for tree-killing is stronger in *I. typographus*. This could explain the evolution of *I. typographus* as a facultative tree-killer. If this hypothesis is correct and the lower adaptability could indeed be linked to the lower genetic diversity as a result of the last ice ages, tree-killing might be a relatively recent trait in *I. typographus*.

Although these two species are most likely the best-studied bark beetles in Europe, many facets of their evolutionary ecology remain unknown. Based on our comparative review, we propose the following future research directions that should be approached ideally using not only *I. typographus* and *P. chalcographus*, but several representatives of the species-rich group of Scolytinae:

1. Host usage: Studying physiological mechanisms, e.g. detoxification of defence-related tree metabolites, and the influence of different phloem properties, like moisture or nutrients, on performance in trees would help to understand host colonization by bark beetles (Krokene, 2015).
2. Reproduction: Bark beetle mating systems are highly diverse, from monogamy to inbreeding and harem polygyny (Kirkendall, 1983). Also within harem-polygynous species there is variation in the number of females per gallery, as seen for the two species reviewed here. Whether this is the consequence of higher mortality of males during dispersal flights, host search and gallery establishment and whether this is affected by host species, host quality or quality of male beetles are only some research directions to shed light on the evolution of bark beetle mating behaviour (Kirkendall, 1983).
3. Symbioses: The roles of fungi, yeasts and bacteria in the life histories of most bark beetles are largely unknown (for example, Six, 2013; Davis, 2015; Zhao *et al.*, 2019). Elucidating their nutritional values, detoxification potential, influence on feeding habits or effects on pheromone production are only some examples for future research directions. Moreover, unravelling the evolutionary history of these associations will be crucial for understanding these bark beetle symbioses.
4. Life-cycle regulation: Effects of abiotic factors on the life histories of bark beetles are mainly known for economically important species. Data on the influence of temperature and photoperiod on ontogenetic development, diapause expression, survival or phenology from a wide range of species are essential to understand their ecology and evolution.

The rapid increase in modern 'omic' tools and the increasing availability of whole-genome data for bark beetles (Keeling *et al.*, 2013; Bracewell *et al.*, 2018; Powell *et al.*, 2021) gives us the opportunity to tackle these questions with more sophisticated approaches than in the past. Such research on these and other bark beetle species (i) can help to understand basic evolutionary processes, e.g. population dynamics, niche construction, tree-killing ability, mating system evolution and the evolution of symbioses, and (ii) are the basis for developing novel control measures against these major forest pests.

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References

- Amezaga I and Rodriguez MA (1998) Resource partitioning of four sympatric bark beetles depending on swarming dates and tree species. *Forest Ecology and Management* **109**, 127–135.
- Anderbrant O (1989) Reemergence and second brood in the bark beetle *Ips typographus*. *Holarctic Ecology* **12**, 494–500.
- Anderbrant O (1990) Gallery construction and oviposition of the bark beetle *Ips typographus* (Coleoptera: Scolytidae) at different breeding densities. *Ecological Entomology* **15**, 1–8.
- Anderbrant O and Lofqvist J (1988) Relation between first and second brood production in the bark beetle *Ips typographus* (Scolytidae). *Oikos* **53**, 357–365.
- Annala E (1969) Influence of temperature upon the development and voltinism of *Ips typographus* L. (Coleoptera, Scolytidae). *Annales Zoologici Fennici* **6**, 161–208.
- Avtzis DN, Arthofer W and Stauffer C (2008) Sympatric occurrence of diverged mtDNA lineages of *Pityogenes chalcographus* (Coleoptera, Scolytinae) in Europe. *Biological Journal of the Linnean Society* **94**, 331–340.
- Baier P, Pennerstorfer J and Schopf A (2007) PHENIPS – a comprehensive phenology model of *Ips typographus* (L.) (Col., Scolytinae) as a tool for hazard rating of bark beetle infestation. *Forest Ecology and Management* **249**, 171–186.
- Bale JS (1993) Classes of insect cold hardiness. *Functional Ecology* **7**, 751–753.
- Bertheau C, Salle A, Roux-Morabito G, Garcia J, Certain G and Lieutier F (2009a) Preference-performance relationship and influence of plant relatedness on host use by *Pityogenes chalcographus* L. *Agricultural and Forest Entomology* **11**, 389–396.
- Bertheau C, Salle A, Rossi JP, Bankhead-Dronnet S, Pineau X, Roux-Morabito G and Lieutier F (2009b) Colonisation of native and exotic conifers by indigenous bark beetles (Coleoptera: Scolytinae) in France. *Forest Ecology and Management* **258**, 1619–1628.
- Bertheau C, Bankhead-Dronnet S, Martin C, Lieutier F and Roux-Morabito G (2012) Lack of genetic differentiation after host range extension argues for the generalist nature of *Pityogenes chalcographus* (Curculionidae: Scolytinae). *Annals of Forest Science* **69**, 313–323.
- Bertheau C, Schuler H, Arthofer W, Avtzis DN, Mayer F, Krumbock S, Moodley Y and Stauffer C (2013) Divergent evolutionary histories of two sympatric spruce bark beetle species. *Molecular Ecology* **22**, 3318–3332.
- Biedermann PHW and Vega FE (2020) Ecology and evolution of insect-fungus mutualisms. *Annual Review of Entomology* **65**, 431–455.
- Biedermann PHW, Müller J, Gregoire JC, Gruppe A, Hage J, Hammerbacher A, Hofstetter RW, Kandasamy D, Kolarik M, Kostovcik M, Krokene P, Salle A, Six DL, Turrini T, Vanderpool D, Wingfield MJ and Bässler C (2019) Bark beetle population dynamics in the Anthropocene: challenges and solutions. *Trends in Ecology and Evolution* **34**, 914–924.
- Biermann G (1977) Zur Überwinterung des Buchdruckers, *Ips typographus* (L.), in der Bodenstreu (Col. Scolytidae). *Journal of Applied Entomology* **84**, 59–74.
- Birgersson G, Byers JA, Bergstrom G and Lofqvist J (1990) Production of pheromone components, chalcogran and methyl (E,Z)-2,4-decadienoate, in the spruce engraver *Pityogenes chalcographus*. *Journal of Insect Physiology* **36**, 391–395.
- Birkmoe T, Jacobsen RM, Sverdrup-Thygeson A and Biedermann PHW (2018) Insect-fungus interactions in dead wood systems. In Ulyshen MD (ed), *Saproxylous Insects: Diversity, Ecology and Conservation*. Heidelberg, Germany: Springer, pp. 377–427.

- Blomquist GJ, Figueroa-Teran R, Aw M, Song MM, Gorzalski A, Abbott NL, Chang E and Tittiger C (2010) Pheromone production in bark beetles. *Insect Biochemistry and Molecular Biology* **40**, 699–712.
- Bouhot L, Lieutier F and Debouzie D (1988) Spatial and temporal distribution of attacks by *Tomicus piniperda* L. and *Ips sexdentatus* Boern. (Col., Scolytidae) on *Pinus sylvestris*. *Journal of Applied Entomology* **106**, 356–371.
- Bracewell RR, Pfrender ME, Mock KE and Bentz BJ (2011) Cryptic postzygotic isolation in an eruptive species of bark beetle (*Dendroctonus ponderosae*). *Evolution* **65**, 961–975.
- Bracewell RR, Bentz BJ, Sullivan BT and Good JM (2017) Rapid neo-sex chromosome evolution and incipient speciation in a major forest pest. *Nature Communications* **8**, 1593.
- Bracewell RR, Vanderpool D, Good JM and Six DL (2018) Cascading speciation among mutualists and antagonists in a tree – beetle – fungi interaction. *Proceedings of the Royal Society B-Biological Sciences* **285**, 20180694.
- Byers JA, Birgersson G, Lofqvist J and Bergstrom G (1988) Synergistic pheromones and monoterpenes enable aggregation and host recognition by a bark beetle. *The Science of Nature* **75**, 153–155.
- Byers JA, Hogberg HE, Unelius CR, Birgersson G and Lofqvist J (1989) Structure-activity studies on aggregation pheromone components of *Pityogenes chalcographus* (Coleoptera: Scolytidae) – all stereoisomers of chalcogran and methyl 2,4-decadienoate. *Journal of Chemical Ecology* **15**, 685–695.
- Coeln M, Niu YZ and Führer E (1996) Entwicklung von Fichtenborkenkäfern in Abhängigkeit von thermischen Bedingungen verschiedener montaner Waldstufen (Coleoptera: Scolytidae). *Entomologia Generalis* **21**, 37–54.
- Cognato AI (2015) Biology, systematics, and evolution of *Ips*. In Vega FE and Hofstetter RW (eds), *Bark Beetles: Biology and Ecology of Native and Invasive species*. New York, USA: Academic Press, pp. 351–370.
- Cognato AI, Seybold SJ and Sperling FAH (1999) Incomplete barriers to mitochondrial gene flow between pheromone races of the North American pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae). *Proceedings of the Royal Society B-Biological Sciences* **266**, 1843–1850.
- Cognato AI, Harlin AD and Fisher ML (2003) Genetic structure among pin-yon pine beetle populations (Scolytinae: *Ips confusus*). *Environmental Entomology* **32**, 1262–1270.
- Davis TS (2015) The ecology of yeasts in the bark beetle holobiont: a century of research revisited. *Microbial Ecology* **69**, 723–732.
- Davis TS, Stewart JE, Mann A, Bradley C and Hofstetter RW (2019) Evidence for multiple ecological roles of *Leptographium abietinum*, a symbiotic fungus associated with the North American spruce beetle. *Fungal Ecology* **38**, 62–70.
- Dolezal P and Sehna F (2007) Effects of photoperiod and temperature on the development and diapause of the bark beetle *Ips typographus*. *Journal of Applied Entomology* **131**, 165–173.
- Dowle EJ, Bracewell RR, Pfrender ME, Mock KE, Bentz BJ and Ragland GJ (2017) Reproductive isolation and environmental adaptation shape the phylogeography of mountain pine beetle (*Dendroctonus ponderosae*). *Molecular Ecology* **26**, 6071–6084.
- Dworschak K, Gruppe A and Schopf R (2014) Survivability and post-diapause fitness in a scolytid beetle as a function of overwintering developmental stage and the implications for population dynamics. *Ecological Entomology* **39**, 519–526.
- Eidmann HH (1987) Der Befall von Scolytiden und Cerambyciden an Stammabschnitten fremdländischer Koniferen in Schweden. *Journal of Applied Entomology* **103**, 278–283.
- Faccoli M (2002) Winter mortality in sub-corticolous populations of *Ips typographus* (Coleoptera, Scolytidae) and its parasitoids in the south-eastern Alps. *Journal of Pest Science* **75**, 62–68.
- Faccoli M and Bernardinelli I (2011) Breeding performance of the second generation in some bivoltine populations of *Ips typographus* (Coleoptera Curculionidae) in the south-eastern Alps. *Journal of Pest Science* **84**, 15–23.
- Francke-Grosman H (1956) Hautdrüsen als Träger der Pilzsymbiose bei Ambrosiakäfern. *Zeitschrift für Morphologie und Ökologie der Tiere* **45**, 275–308.
- Francke-Grosman H (1959) Beiträge zur Kenntnis der Übertragungsweise von Pflanzenkrankheiten durch Käfer. In *Proceedings of the International Congress of Plant Protection*, Hamburg, 1959, pp. 805–809.
- Francke-Grosman H (1963) Some new aspects in forest entomology. *Annual Review of Entomology* **8**, 415–438.
- Francke-Grosman H (1967) Ectosymbiosis in wood-inhabiting beetles. In Henry SM (ed), *Symbiosis*. New York, USA: Academic Press, pp. 141–205.
- Francke W, Heemann V, Gerken B, Renwick JAA and Vite JP (1977) 2-Ethyl-1,6-dioxaspiro[4.4]nonane, principal aggregation pheromone of *Pityogenes chalcographus* (L.). *The Science of Nature* **64**, 590–591.
- Führer E and Chen ZY (1979) Zum Einfluß von Photoperiode und Temperatur auf die Entwicklung des Kupferstechers, *Pityogenes chalcographus* L. (Col., Scolytidae). *Forstwissenschaftliches Centralblatt* **98**, 87–91.
- Führer E and Mühlenbrock B (1983) Brutexperimente mit *Pityogenes chalcographus* L. an verschiedenen Nadelbaumarten. *Journal of Applied Entomology* **96**, 228–232.
- Furniss MM, Solheim H and Christiansen E (1990) Transmission of blue-stain fungi by *Ips typographus* (Coleoptera, Scolytidae) in Norway spruce. *Annals of the Entomological Society of America* **83**, 712–716.
- Gibbs JN (1993) The biology of ophiostomatoid fungi causing sapstain in trees and freshly cut logs. In Wingfield MJ, Seifert KA and Webber JF (eds), *Ceratocystis and Ophiostoma: Taxonomy, Ecology, and Pathogenicity*. St. Paul, USA: APS Press, pp. 141–152.
- Giordano L, Garbelotto M, Nicolotti G and Gonthier P (2013) Characterization of fungal communities associated with the bark beetle *Ips typographus* varies depending on detection method, location, and beetle population levels. *Mycological Progress* **12**, 127–140.
- Göthlin E, Schroeder LM and Lindelöw A (2000) Attacks by *Ips typographus* and *Pityogenes chalcographus* on windthrown spruces (*Picea abies*) during the two years following a storm felling. *Scandinavian Journal of Forest Research* **15**, 542–549.
- Gregoire JC and Evans HF (2004) Damage and control of BAWBILT organisms. An overview. In Lieutier F, Day KR, Gregoire JC and Evans HF (eds), *Bark and Wood Boring Insects in Living Trees in Europe, A Synthesis*. Dordrecht, The Netherlands: Kluwer Academic Publishers, pp. 19–37.
- Grégoire J-C, Raffa KF and Lindgren BS (2015) Economics and politics of bark beetles. In Vega FE and Hofstetter RW (eds), *Bark Beetles: Biology and Ecology of Native and Invasive species*. New York, USA: Academic Press, pp. 585–613.
- Grosman H (1930) Beiträge zur Kenntnis der Lebensgemeinschaft zwischen Borkenkäfern und Pilzen. *Parasitology Research* **3**, 56–102.
- Grünwald M (1986) Ecological segregation of bark beetles (Coleoptera, Scolytidae) of spruce. *Journal of Applied Entomology* **101**, 176–187.
- Hammerbacher A, Schmidt A, Wadke N, Wright LP, Schneider B, Bohlmann J, Brand WA, Fenning TM, Gershenson J and Paetz C (2013) A common fungal associate of the spruce bark beetle metabolizes the stilbene defenses of Norway spruce. *Plant Physiology* **162**, 1324–1336.
- Harding S (1989) *The Influence of Mutualistic Blue-Stain Fungi on Bark Beetle Population Dynamics*. Copenhagen, Denmark: Royal Veterinary and Agricultural University Copenhagen.
- Harrington TC (2005) Ecology and evolution of mycophagous bark beetles and their fungal partners. In Vega FE and Blackwell M (eds), *Ecological and Evolutionary Advances in Insect-Fungal Associations*. New York, USA: Oxford University Press, pp. 257–291.
- Hedgren PO (2004) The bark beetle *Pityogenes chalcographus* (L.) (Scolytidae) in living trees: reproductive success, tree mortality and interaction with *Ips typographus*. *Journal of Applied Entomology* **128**, 161–166.
- Hedgren PO, Weslien J and Schroeder LM (2003) Risk of attack by the bark beetle *Pityogenes chalcographus* (L.) on living trees close to colonized felled spruce trees. *Scandinavian Journal of Forest Research* **18**, 39–44.
- Hornftvedt R, Christiansen C, Solheim H and Wang S (1983) Artificial inoculation with *Ips typographus*-associated blue-stain fungi can kill healthy Norway spruce trees. *Meddelelser fra Norsk Institutt for Skogforskning* **38**, 1–20.
- Jankowiak R, Kolarik M and Bilanski P (2014) Association of *Geosmithia* fungi (Ascomycota: Hypocreales) with pine- and spruce-infesting bark beetles in Poland. *Fungal Ecology* **11**, 71–79.
- Jönsson AM, Appelberg G, Harding S and Barring L (2009) Spatio-temporal impact of climate change on the activity and voltinism of the spruce bark beetle, *Ips typographus*. *Global Change Biology* **15**, 486–499.
- Kandasamy D, Gershenson J, Andersson MN and 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.
- Keeling CI, Yuen MMS, Liao NY, Docking TR, Chan SK, Taylor GA, Palmquist DL, Jackman SD, Nguyen A, Li M, Henderson H, Janes JK, Zhao YJ, Pandoh P, Moore R, Sperling FAH, Huber DPW, Birol I, Jones SJM and Bohlmann J** (2013) Draft genome of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, a major forest pest. *Genome Biology* **14**, R27.
- Kirisits T** (2004) Fungal associates of European bark beetles with special emphasis on the ophiostomatoid fungi. In Lieutier F, Day KR, Gregoire JC and Evans HF (eds), *Bark and Wood Boring Insects in Living Trees in Europe, A Synthesis*. Dordrecht, The Netherlands: Kluwer Academic Publishers, pp. 181–235.
- Kirkendall LR** (1983) The evolution of mating systems in bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae). *Zoological Journal of the Linnean Society* **77**, 293–352.
- Kirkendall LR, Biedermann PHW and Jordal BH** (2015) Evolution and diversity of bark and ambrosia beetles. In Vega FE and Hofstetter RW (eds) *Bark Beetles: Biology and Ecology of Native and Invasive species*. New York, USA: Academic Press, pp. 85–156.
- Kirschner R** (1998) *Diversität mit Borkenkäfern assoziierter filamentöser Mikropilze*. Tübingen, Germany: Eberhard-Karls-University Tübingen.
- Knizek M** (2011) Scolytinae. In Löbl I and Smetana A (eds), *Catalogue of Palaearctic Coleoptera, Curculionidae I. Stenstrup*. Denmark: Apollo Books, pp. 204–250.
- Kolarik M and Jankowiak R** (2013) Vector affinity and diversity of *Geosmithia* fungi living on subcortical insects inhabiting Pinaceae species in Central and Northeastern Europe. *Microbial Ecology* **66**, 682–700.
- Kostal V** (2006) Eco-physiological phases of insect diapause. *Journal of Insect Physiology* **52**, 113–127.
- Kostal V, Zahradnickova H, Simek P and Zeleny J** (2007) Multiple component system of sugars and polyols in the overwintering spruce bark beetle, *Ips typographus*. *Journal of Insect Physiology* **53**, 580–586.
- Kostal V, Dolezal P, Rozsypal J, Moravcova M, Zahradnickova H and Simek P** (2011) Physiological and biochemical analysis of overwintering and cold tolerance in two Central European populations of the spruce bark beetle, *Ips typographus*. *Journal of Insect Physiology* **57**, 1136–1146.
- Kostal V, Miklas B, Dolezal P, Rozsypal J and Zahradnickova H** (2014) Physiology of cold tolerance in the bark beetle, *Pityogenes chalcographus* and its overwintering in spruce stands. *Journal of Insect Physiology* **63**, 62–70.
- Krascenitsova E, Kozanek M, Ferencik J, Roller L, Stauffer C and Bertheau C** (2013) Impact of the Carpathians on the genetic structure of the spruce bark beetle *Ips typographus*. *Journal of Pest Science* **86**, 669–676.
- Krokene P** (2015) Conifer defense and resistance of bark beetles. In Vega FE and Hofstetter RW (eds), *Bark Beetles: Biology and Ecology of Native and Invasive species*. New York, USA: Academic Press, pp. 177–207.
- Krokene P and Solheim H** (1996) Fungal associates of five bark beetle species colonizing Norway spruce. *Canadian Journal of Forest Research* **26**, 2115–2122.
- Krokene P and Solheim H** (1998) Pathogenicity of four blue-stain fungi associated with aggressive and nonaggressive bark beetles. *Phytopathology* **88**, 39–44.
- Lee RE** (2010) A primer on insect cold-tolerance. In Denlinger DL and Lee RE (eds), *Low-Temperature Biology of Insects*. Cambridge, UK: Cambridge University Press, pp. 3–34.
- Leufven A** (1991) Role of microorganisms in spruce bark beetle-conifer interactions. In Barbosa P, Krischik VA and Jones CG (eds), *Microbial Mediation of Plant-Herbivore Interactions*. New York, USA: John Wiley and Sons, pp. 467–481.
- Leufven A and Nehls L** (1986) Quantification of different yeasts associated with the bark beetle, *Ips typographus*, during its attack on a spruce tree. *Microbial Ecology* **12**, 237–243.
- Leufven A, Bergstrom G and Falsen E** (1984) Interconversion of verbenols and verbenone by identified yeasts isolated from the spruce bark beetle *Ips typographus*. *Journal of Chemical Ecology* **10**, 1349–1361.
- Leufven A, Bergstrom G and Falsen E** (1988) Oxygenated monoterpenes produced by yeasts, isolated from *Ips typographus* (Coleoptera, Scolytidae) and grown in phloem medium. *Journal of Chemical Ecology* **14**, 353–362.
- Lieutier F, Yart A and Salle A** (2009) Stimulation of tree defenses by Ophiostomatoid fungi can explain attack success of bark beetles on conifers. *Annals of Forest Science* **66**, 801.
- Light DM, Birch MC and Paine TD** (1983) Laboratory study of intraspecific and interspecific competition within and between two sympatric bark beetle species, *Ips pini* and *Ips paraconfusus*. *Journal of Applied Entomology* **96**, 233–241.
- Lobinger G** (1994) Die Lufttemperatur als limitierender Faktor für die Schwärmaktivität zweier rindenbrütender Fichtenborkenkäferarten, *Ips typographus* L. und *Pityogenes chalcographus* L. (Col., Scolytidae). *Journal of Pest Science* **67**, 14–17.
- Mathiesen-Käärik A** (1953) Eine Übersicht über die gewöhnlichsten mit Borkenkäfer assoziierten Bläuepilze in Schweden. *Meddelanden fran Statens Skogsforsinginstiut* **43**, 1–74.
- Mathiesen-Käärik A** (1960) Studies on the ecology, taxonomy and physiology of Swedish insect-associated blue stain fungi, especially the genus *Ceratocystis*. *Oikos* **11**, 1–25.
- Mayer F, Bjorklund N, Wallen J, Langstrom B and Cassel-Lundhagen A** (2014) Mitochondrial DNA haplotypes indicate two postglacial re-colonization routes of the spruce bark beetle *Ips typographus* through northern Europe to Scandinavia. *Journal of Zoological Systematics and Evolutionary Research* **52**, 285–292.
- Mayer F, Piel FB, Cassel-Lundhagen A, Kirichenko N, Grumiau L, Okland B, Bertheau C, Gregoire JC and Mardulyn P** (2015) Comparative multi-locus phylogeography of two Palaearctic spruce bark beetles: influence of contrasting ecological strategies on genetic variation. *Molecular Ecology* **24**, 1292–1310.
- Mock KE, Bentz BJ, O'Neill EM, Chong JP, Orwin J and Pfrender ME** (2007) Landscape-scale genetic variation in a forest outbreak species, the mountain pine beetle (*Dendroctonus ponderosae*). *Molecular Ecology* **16**, 553–568.
- Netherer S, Matthews B, Katzensteiner K, Blackwell E, Henschke P, Hietz P, Pennerstorfer J, Rosner S, Kikuta S, Schume H and Schopf A** (2015) Do water-limiting conditions predispose Norway spruce to bark beetle attack? *New Phytologist* **205**, 1128–1141.
- Netherer S, Kandasamy D, Jirosova A, Kalinova B, Schebeck M and 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.
- Paine TD, Birch MC and Svihra P** (1981) Niche breadth and resource partitioning by four sympatric species of bark beetles (Coleoptera: Scolytidae). *Oecologia* **48**, 1–6.
- Pfeffer A** (1995) *Zentral- und westpaläarktische Borken- und Kernkäfer (Coleoptera: Scolytidae, Platypodidae)*. Basel, Switzerland: Pro Entomologia, Naturhistorisches Museum Basel.
- Postner M** (1974) Scolytidae (= Ipsidae), Borkenkäfer. In Schwenke W (ed), *Die Forstschädlinge Europas*. Hamburg, Berlin, Germany: Verlag Paul Parey, pp. 334–482.
- Powell D, Große-Wilde E, Krokene P, Roy A, Chakraborty A, Löfstedt C, Vogel H, Andersson MN and Schlyter F** (2021) A highly-contiguous genome assembly of the Eurasian spruce bark beetle, *Ips typographus*, provides insight into a major forest pest. *Communications Biology* **4**, 1059.
- Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG and Romme WH** (2008) Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *Bioscience* **58**, 501–517.
- Raffa KF, Grégoire J-C and Lindgren BS** (2015) Natural history and ecology of bark beetles. In Vega FE and Hofstetter RW (eds), *Bark Beetles: Biology and Ecology of Native and Invasive species*. New York, USA: Academic Press, pp. 1–40.
- Rankin LJ and Borden JH** (1991) Competitive interactions between the mountain pine beetle and the pine engraver in lodgepole pine. *Canadian Journal of Forest Research* **21**, 1029–1036.
- Salle A, Monclus R, Yart A, Garcia J, Romary P and Lieutier F** (2005) Fungal flora associated with *Ips typographus*: frequency, virulence, and ability to stimulate the host defence reaction in relation to insect population levels. *Canadian Journal of Forest Research* **35**, 365–373.
- Salle A, Arthofer W, Lieutier F, Stauffer C and Kerdelhue C** (2007) Phylogeography of a host-specific insect: genetic structure of *Ips*

- typographus* in Europe does not reflect past fragmentation of its host. *Biological Journal of the Linnean Society* **90**, 239–246.
- Sauvard D (2004) General biology of bark beetles. In Lieutier F, Day KR, Gregoire JC and Evans HF (eds), *Bark and Wood Boring Insects in Living Trees in Europe, A Synthesis*. Dordrecht, The Netherlands: Kluwer Academic Publishers, pp. 63–88.
- Schebeck M, Hansen EM, Schopf A, Ragland GJ, Stauffer C and Bentz BJ (2017) Diapause and overwintering of two spruce bark beetle species. *Physiological Entomology* **42**, 200–210.
- Schebeck M, Dowle EJ, Schuler H, Avtzis DN, Bertheau C, Feder JL, Ragland GJ and Stauffer C (2018) Pleistocene climate cycling and host plant association shaped the demographic history of the bark beetle *Pityogenes chalcographus*. *Scientific Reports* **8**, 14207.
- Schebeck M, Schuler H, Einramhof B, Avtzis DN, Dowle EJ, Faccoli M, Battisti A, Ragland GJ, Stauffer C and Bertheau C (2019) The Apennines as a cryptic Pleistocene refugium of the bark beetle *Pityogenes chalcographus* (Coleoptera: Curculionidae). *Biological Journal of the Linnean Society* **127**, 24–33.
- Schebeck M, Dobart N, Ragland GJ, Schopf A and 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.
- Schelhaas MJ, Nabuurs GJ and Schuck A (2003) Natural disturbances in the European forests in the 19th and 20th centuries. *Global Change Biology* **9**, 1620–1633.
- Schlyter F and Anderbrant O (1993) Competition and niche separation between two bark beetles: existence and mechanisms. *Oikos* **68**, 437–447.
- Schlyter F, Byers JA and Löfqvist J (1987a) Attraction to pheromone sources of different quantity, quality, and spacing: density-regulation mechanisms in bark beetle *Ips typographus*. *Journal of Chemical Ecology* **13**, 1503–1523.
- Schlyter F, Birgersson G, Byers JA, Löfqvist J and Bergström G (1987b) Field response of spruce bark beetle, *Ips typographus*, to aggregation pheromone candidates. *Journal of Chemical Ecology* **13**, 701–716.
- Schmidt-Vogt H (1977) *Die Fichte*. Hamburg, Berlin, Germany: Verlag Paul Parey.
- Schopf A (1985) Zum Einfluß der Photoperiode auf die Entwicklung und Kälteresistenz des Buchdruckers, *Ips typographus* L. (Col., Scolytidae). *Journal of Pest Science* **58**, 73–75.
- Schopf A (1989) Die Wirkung der Photoperiode auf die Induktion der Imaginaldiapause von *Ips typographus* (L.) (Col., Scolytidae). *Journal of Applied Entomology* **107**, 275–288.
- Schroeder M and Cocos D (2018) Performance of the tree-killing bark beetles *Ips typographus* and *Pityogenes chalcographus* in non-indigenous lodgepole pine and their historical host Norway spruce. *Agricultural and Forest Entomology* **20**, 347–357.
- Schroeder M and Dalin P (2017) Differences in photoperiod-induced diapause plasticity among different populations of the bark beetle *Ips typographus* and its predator *Thanosimus formicarius*. *Agricultural and Forest Entomology* **19**, 146–153.
- Schroeder LM and Eidmann HH (1993) Attacks of bark- and wood-boring Coleoptera on snow-broken conifers over a two-year period. *Scandinavian Journal of Forest Research* **8**, 257–265.
- Schroeder LM and Lindelöw A (2002) Attacks on living spruce trees by the bark beetle *Ips typographus* (Col. Scolytidae) following a storm-felling: a comparison between stands with and without removal of wind-felled trees. *Agricultural and Forest Entomology* **4**, 47–56.
- Schwerdtfeger F (1929) Ein Beitrag zur Fortpflanzungsbiologie des Borkenkäfers *Pityogenes chalcographus* L. *Journal of Applied Entomology* **15**, 335–427.
- Seidl R, Müller J, Hothorn T, Bassler C, Heurich M and Kautz M (2015) Small beetle, large-scale drivers: how regional and landscape factors affect outbreaks of the European spruce bark beetle. *Journal of Applied Ecology* **53**, 530–540.
- Sinclair BJ, Alvarado LEC and Ferguson LV (2015) An invitation to measure insect cold tolerance: methods, approaches, and workflow. *Journal of Thermal Biology* **53**, 180–197.
- Six DL (2013) The bark beetle holobiont: why microbes matter. *Journal of Chemical Ecology* **39**, 989–1002.
- Six DL and Bracewell R (2015) *Dendroctonus*. In Vega FE and Hofstetter RW (eds), *Bark Beetles: Biology and Ecology of Native and Invasive species*. New York, USA: Academic Press, pp. 305–350.
- Six DL and Wingfield MJ (2011) The role of phytopathogenicity in bark beetle-fungus symbioses: a challenge to the classic paradigm. *Annual Review of Entomology* **56**, 255–272.
- Solheim H (1992) Fungal succession in sapwood of Norway spruce infested by the bark beetle *Ips typographus*. *European Journal of Forest Pathology* **22**, 136–148.
- Solheim H (1993) Fungi associated with the spruce bark beetle *Ips typographus* in an endemic area in Norway. *Scandinavian Journal of Forest Research* **8**, 118–122.
- Stauffer C, Lakatos F and Hewitt GM (1999) Phylogeography and postglacial colonization routes of *Ips typographus* L. (Coleoptera, Scolytidae). *Molecular Ecology* **8**, 763–773.
- Stefkova K, Okrouhlik J and Dolezal P (2017) Development and survival of the spruce bark beetle, *Ips typographus* (Coleoptera: Curculionidae: Scolytinae) at low temperatures in the laboratory and the field. *European Journal of Entomology* **114**, 1–6.
- Thalenhorst W (1958) Grundzüge der Populationsdynamik des großen Fichtenborkenkäfers *Ips typographus* L. *Schriftenreihe der Forstlichen Fakultät der Universität Göttingen und Mitteilungen der Niedersächsischen Forstlichen Versuchsanstalt* **21**, 1–126.
- Tollefsrud MM, Kissling R, Gugerli F, Johnsen O, Skroppa T, Cheddadi R, van Der Knaap WO, Latalowa M, Terhurne-Berson R, Litt T, Geburek T, Brochmann C and Sperisen C (2008) Genetic consequences of glacial survival and postglacial colonization in Norway spruce: combined analysis of mitochondrial DNA and fossil pollen. *Molecular Ecology* **17**, 4134–4150.
- Vega FE and Biedermann PHW (2020) On interactions, associations, mycetangia, mutualists and symbiotes in insect-fungus symbioses. *Fungal Ecology* **44**, 100909.
- Wadke N, Kandasamy D, Vogel H, Lah L, Wingfield BD, Paetz C, Wright LP, Gershenson J and Hammerbacher A (2016) The bark-beetle-associated fungus, *Endoconidiophora polonica*, utilizes the phenolic defense compounds of its host as a carbon source. *Plant Physiology* **171**, 914–931.
- Wang J, Gao GQ, Zhang RR, Dai LL and Chen H (2017) Metabolism and cold tolerance of Chinese white pine beetle *Dendroctonus armandi* (Coleoptera: Curculionidae: Scolytinae) during the overwintering period. *Agricultural and Forest Entomology* **19**, 10–22.
- Wegensteiner R, Wermelinger B and Herrmann M (2015) Natural enemies of bark beetles: predators, parasitoids, pathogens, and nematodes. In Vega FE and Hofstetter RW (eds), *Bark Beetles: Biology and Ecology of Native and Invasive species*. New York, USA: Academic Press, pp. 247–304.
- 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.
- Wermelinger B and Seifert M (1998) Analysis of the temperature-dependent development of the spruce bark beetle *Ips typographus* (L.) (Col., Scolytidae). *Journal of Applied Entomology* **122**, 185–191.
- Wermelinger B and Seifert M (1999) Temperature-dependent reproduction of the spruce bark beetle *Ips typographus*, and analysis of the potential population growth. *Ecological Entomology* **24**, 103–110.
- Wermelinger B, Epper C, Kenis M, Ghosh S and Holdenrieder O (2012) Emergence patterns of univoltine and bivoltine *Ips typographus* (L.) populations and associated natural enemies. *Journal of Applied Entomology* **136**, 212–224.
- Wertman DL, Bleiker KP and Perlman SJ (2018) The light at the end of the tunnel: photosensitivity in larvae of the mountain pine beetle (Coleoptera: Curculionidae: Scolytinae). *The Canadian Entomologist* **150**, 622–631.
- Zhao T, Axelsson K, Krokene P and Borg-Karlson AK (2015) Fungal symbionts of the spruce bark beetle synthesize the beetle aggregation pheromone 2-methyl-3-buten-2-ol. *Journal of Chemical Ecology* **41**, 848–852.
- Zhao T, Kandasamy D, Krokene P, Chen JY, Gershenson J and 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.