REVIEW

The pine bark beetle *Ips acuminatus*: an ecological perspective on life-history traits promoting outbreaks

Eva Papek[1] · Elisabeth Ritzer[1] · Peter H. W. Biedermann[2] · Anthony I. Cognato[3] · Peter Baier[1] · Gernot Hoch[4] · Thomas Kirisits[1] · Martin Schebeck[1]

Abstract

The bark beetle *Ips acuminatus* is an important pest in pine-dominated forests of Eurasia. Recently, the frequency of *I. acuminatus* outbreaks and mortality of host trees have increased, most likely as a result of climate change-related alterations in environmental conditions. Therefore, detailed information on the species' natural history is essential to understand its potential to damage forests and to apply sustainable management measures. We provide a comprehensive overview on the life history of *I. acuminatus*, focusing on traits that might explain outbreaks and the ability to cause tree mortality. We review its importance for European forestry, outbreak behavior, host plant usage, reproductive biology, temperature-dependent development, diapause and overwintering behavior, and interactions with fungi, bacteria, nematodes and other arthropods. Interestingly, *I. acuminatus* has a strong nutritional dependency on the fungus *Ophiostoma macrosporum*, underlined by the presence of a prominent oral mycetangium, a spore-carrying organ, in females, which is not known for other *Ips* species. Moreover, *I. acuminatus* can reproduce sexually and asexually (pseudogamy). Additionally, information on the species' evolutionary past provides valuable insights into the origin of certain traits. We present a phylogeny of the genus *Ips* and examine selected life-history traits in an evolutionary context. Together with its sister species *Ips chinensis*, *I. acuminatus* forms a separate clade within *Ips*. The ancestor of *Ips* bark beetles originated about 20 million years ago and was a pine-colonizing species inhabiting the Holarctic. Finally, open fields of research are identified to guide future work on this ecologically and economically important pine bark beetle.

✉ Martin Schebeck
  martin.schebeck@boku.ac.at

1   Institute of Forest Entomology, Forest Pathology and Forest Protection, Department of Forest and Soil Sciences, University of Natural Resources and Life Sciences Vienna, BOKU, Vienna, Austria

2   Chair of Forest Entomology and Protection, Institute of Forestry, University of Freiburg, Freiburg/Breisgau, Germany

3   Holistic Insect Systematics Laboratory, Department of Entomology, Michigan State University, East Lansing, MI, USA

4   Department of Forest Protection, Austrian Research Centre for Forests (BFW), Vienna, Austria

Key message

- *Ips acuminatus* has a phloeomycetophagous lifestyle with a mutalistic ambrosia fungus
- It has a prominent oral mycetangium, i.e., a spore-carrying organ, for fungal transmission
- It has both sexual and asexual, i.e., pseudogamous, reproduction
- Female harems of *I. acuminatus* males are much larger than in other *Ips* species
- *I. acuminatus* has a very specific phylogenetic position explaining some life-history traits

Introduction

European pine forests: relevance and forest protection issues

Pine-dominated forests are widespread ecosystems in Europe fulfilling numerous ecological and economic functions. The two pine species *Pinus sylvestris* (Scots pine) and *Pinus nigra* (European black pine) are among the most important conifers in Europe, occurring in major parts of the continent across a wide latitudinal and altitudinal range (www.euforgen.org). *Pinus sylvestris* is the most abundant pine species worldwide, being native to Eurasia and introduced to North America, and is of great ecological and economical importance (Hytteborn et al. 2005; Eckenwalder 2009; Matías and Jump 2012; Houston Durrant et al. 2016). The wide geographic range of Scots pine can be explained by its broad ecological amplitude, as it is able to cope with a wide range of abiotic environmental conditions, including drought and frost (Matías and Jump 2012).

Pinus sylvestris-dominated ecosystems are affected by various abiotic disturbances (including high temperatures and drought) and biotic stressors, like fungi, nematodes and insects (Bigler et al. 2006; Dobbertin et al. 2007; Blumenstein et al. 2021). The most important fungal pathogens are *Dothistroma septosporum* and *Dothistroma pini* (Barnes et al. 2022) causing red band needle blight, *Lecanosticta acicula* leading to brown spot needle blight (Tubby et al. 2023), *Diplodia sapinea* responsible for Diplodia tip and shoot blight (Bußkamp et al. 2021), *Gremmeniella abietina* inciting Scleroderris canker (Romeralo et al. 2023), and root and butt-rot diseases caused by *Heterobasidion annosum* (Kovalchuk et al. 2022) and *Armillaria* spp. (Kim et al. 2022). The most relevant pathogenic pine-associated nematode, also for *P. sylvestris*, is *Bursaphelenchus xylophilus,* which is native to North America and was introduced from Asia (where it is also invasive) into Europe in the late 1990s, causing pine wilt (Mota et al. 1999). So far, *B. xylophilus* has been recorded from south-western Europe, i.e., Spain and Portugal (including the island of Madeira) (EPPO 2023).

In addition, insects from various functional groups are important pests of Scots pine, mainly defoliators as well as phloem- and xylem-feeding/breeding species. Among the most relevant needle-feeding species are the nun moth *Lymantria monacha*, the pine lappet moth *Dendrolimus pini*, and pine sawflies, e.g., *Diprion pini* (Hentschel et al. 2018). Insects spending at least parts of their life cycles in the woody tissue of *P. sylvestris* are wood wasps of the genus *Sirex* and *Monochamus* longhorn beetles (Akbulut and Stamps 2012; Ryan and Hurley 2012). Finally, *P. sylvestris* is host for various phloem breeders, mainly scolytine bark beetles (Coleoptera: Curculionidae), and to a lesser extent weevils of the genus *Pissodes* and buprestid beetles, such as *Phaenops cyanea* (Wermelinger et al. 2008; Foit and Čermák 2014; Hlávková and Doležal 2022).

Ecologically and economically relevant bark beetle genera on Scots pine are *Ips* (e.g., *Ips acuminatus*, *Ips sexdentatus*), *Tomicus* (*Tomicus piniperda*, *Tomicus minor*, *Tomicus destruens*), *Orthotomicus* (e.g., *Orthotomicus erosus*) and *Pityogenes* (e.g., *Pityogenes bidentatus*, *Pityogenes chalcographus*) (Pfeffer 1995; Knížek 2011; Hlávková and Doležal 2022). These bark beetles are regarded as secondary pests, selecting hosts with impaired defenses for colonization and brood establishment (Foit and Čermák 2014; Hlávková and Doležal 2022). Abiotic events like storms, heavy snowfall, wildfires, high temperatures or drought can damage trees and thereby provide suitable hosts for attack (remaining treetops and branches after logging operations are frequently colonized as well). High temperatures provide favorable conditions for insect performance, fostering rapid bark beetle population growth (Lieutier 2004; Dobbertin et al. 2007; Colombari et al. 2012; Chinellato et al. 2014). As extreme weather events, particularly long periods with high temperatures and drought, are currently becoming more frequent (and are going to occur even more likely in near future) (Legg 2021), the importance of the above-mentioned secondary bark beetles will very likely increase as well.

In this review article, we focused on the pine bark beetle *I. acuminatus*, one of the most relevant forest pests of Scots pine and other conifer species (Grégoire and Evans 2004; Hlávková and Doležal 2022). We compiled and summarized the available scientific literature on the natural history of this insect, to get a better understanding of life-history traits as well as biotic and abiotic factors that contribute to the beetle's potential to damage trees and subsequently cause major disturbances in pine-dominated forest ecosystems. We focused on the species' host usage behavior, its reproductive biology, its interactions with other organisms from different trophic levels and the effects of major abiotic drivers on life-cycle regulation. Moreover, we re-analyzed the phylogenetic relationships of representatives of the genus *Ips* (36 out of 37 species) to put certain ecological traits into an evolutionary framework. This updated and comprehensive phylogeny allowed us to infer evolutionary pathways of key traits of a bark beetle group with outstanding natural histories, which can have severe ecological and economic impacts on forest ecosystems of the Northern Hemisphere. Finally, *I. acuminatus* is a fascinating insect, as it expresses an exceptional life cycle, for example, regarding its feeding behavior, morphological adaptations and its reproduction. Therefore, this review paper will not only be of high interest for ecologists and evolutionary biologists interested in scolytine bark beetles, but it will also be relevant for colleagues working

in applied fields to infer sustainable and biologically based forest management strategies.

Summary of the *Ips acuminatus* life cycle

Ips acuminatus is a widespread bark beetle species in Europe and parts of Asia, with a geographic range from the Mediterranean region to Scandinavia and from western Europe to Asia (Pfeffer 1995; Knížek 2011; Cognato 2015). In Asia, its range overlaps with its sister species *Ips chinensis* (Knížek and Cognato 2017). Primary host trees are found in the genus *Pinus*, but other conifer species can be utilized as well (Table 1) (Pfeffer 1995; Cognato 2015). With an average body length between 2.2 and 3.9 mm (Postner 1974; Pfeffer 1995; Cognato 2015), it preferably colonizes smooth-barked sections with thin phloem, such as the upper parts of the trunk or branches (Bakke 1968a). It is a polygynous species, where male individuals are the gallery-initiating sex, which subsequently mate with multiple females in a nuptial chamber; however, deviations from this 'standard' reproductive biology of a polygynous bark beetle occur (for details, see section 'Reproductive biology'). During initial colonization by male beetles, conspecifics of both sexes are attracted by releasing aggregation pheromones, resulting in further establishment of galleries (Bakke 1978; Kohnle et al. 1988). After copulation, females construct individual maternal tunnels where eggs are deposited (Fig. 1). Larvae develop individually in the phloem (etching the xylem), feeding on both plant tissue and a specific mutualistic fungus (Francke-Grosmann 1952). Therefore, *I. acuminatus* is regarded a phloeomycetophagous bark beetle (details see below) (Francke-Grosmann 1952). After pupation in the phloem and outer sapwood, young adults feed on fungal and phloem tissue to attain sexual maturity. Depending on environmental conditions and the time of the season, young adults either disperse to establish a new generation (potentially multivoltine) or prepare for hibernation (Bakke 1968a; Faccoli et al. 2012).

Ips acuminatus—a forest pest of increasing importance

Ips acuminatus as a secondary bark beetle species, i.e., colonizing trees with impaired defenses (Foit and Čermák 2014; Hlávková and Doležal 2022), was historically considered a minor threat to pine trees; the major economic damages were related to the transmission of ophiostomatoid fungi and the resulting blue-staining of the sapwood (Bakke 1968a; details see below). However, according to Francke-Grosmann (1952), population densities of *I. acuminatus* can increase quickly when environmental conditions are favorable, resulting in an increased potential to damage young pines. In recent years, increased *I. acuminatus*-related damages on pines have been reported from various European countries (Fig. 2), including France (Lieutier et al. 1991), Switzerland (Dobbertin et al. 2007; Wermelinger et al. 2008), Austria (Krehan 2011; Steyrer et al. 2020), Italy (Colombari et al. 2012, 2013; Faccoli et al. 2012; Chinellato et al. 2014), Poland (Plewa and Mokrzycki 2017), Finland (Siitonen 2014), Ukraine (Davydenko et al. 2017; Davydenko 2019; Baturkin and Davydenko 2020) and Czechia (Knížek and Liška 2023).

These recent increases of outbreaks are proposed to be related to altered abiotic conditions, most likely driven by climate change (Colombari et al. 2012, 2013; Chinellato et al. 2014). For example, severe drought events at the end of the 1990s and the beginning of the 2000s resulted in significant damage to pines by *I. acuminatus*, mostly in southern and central European countries (Dobbertin et al. 2007; Wermelinger et al. 2008; Colombari et al. 2012, 2013). The combined effects of weakened host trees and suitable warm conditions for beetle development were most likely triggering high *I. acuminatus* population densities and Scots pine mortality (Dobbertin et al. 2007; Wermelinger et al. 2008). Such events are of particularly high relevance in southern regions and dry inner alpine valleys, which are prone to heat and drought. In addition, an increase in Scots pine mortality and *I. acuminatus* occurrence was reported from northern and eastern Europe, which was related to favorable climatic conditions (Siitonen 2014; Davydenko et al. 2017). Moreover, insufficient forest protection measures, e.g., neglecting the timely removal of potential breeding material and infested trees, can contribute to *I. acuminatus* outbreaks in pine forests (Liška et al. 2021).

Suitable host plants and colonization behavior

Besides the preferred genus *Pinus*, *I. acuminatus* can also colonize and breed in species of *Picea*, *Larix* or *Abies* (Bakke 1968a; Postner 1974; Pfeffer 1995). In addition, it can also utilize the non-native Douglas fir, *Pseudotsuga menziesii* (Blaschke et al. 2008; Steyrer et al. 2020; Schüler and Chakraborty 2021), which has been commonly planted in European forests in recent decades (Thomas et al. 2022).

As briefly mentioned above, *I. acuminatus* is regarded a secondary species colonizing stressed host trees (Wermelinger et al. 2008; Foit and Čermák 2014). During recent years, for example, Scots pines were heavily attacked by various phloem-breeding insects, including *I. acuminatus*, particularly during periods with high temperatures and extensive drought, leading to severe tree mortality of *P. sylvestris* (Dobbertin et al. 2007; Wermelinger et al. 2008; Colombari et al. 2013; Siitonen 2014; Jaime et al. 2019; Hunziker et al.

Table 1 Selected life-history traits of *Ips acuminatus*

| Life-history traits	*Ips acuminatus*	Sources
Geographic range	Eurasia: the Asian range of *I. acuminatus* overlaps with that of its sister species, *I. chinensis*	Pfeffer 1995; Cognato 2015; Knížek 2011
Relative host range	Oligophagous: mostly species of *Pinus*, but also of *Picea*, *Larix*, *Abies*, and *Pseudotsuga menziesii*	Bakke 1968a; Postner 1974; Pfeffer 1995; Blaschke et al. 2008; Steyrer et al. 2020; Schüler and Chakraborty 2021
Host niche	Thin-barked tree sections with smooth bark (2–3 mm phloem thickness), upper part of tree trunk, treetops and branches	Bakke 1968a; Postner 1974
Nutrition	Phloeomycetophagous	Francke-Grosmann 1952
Aggressiveness	Secondary pest species; among the first colonizers of physiologically stressed pines	Guérard et al 2000; Wermelinger et al. 2008; Colombari et al. 2012; Foit and Čermák 2014; Plewa and Mokrzycki 2017; Hlávková and Doležal 2022
Mating system	Male-initiated, polygynous, sexual and parthenogenetic (pseudogamy), up to twelve females per male	Bakke 1968a; Bakke 1968b; Stenseth et al. 1985; Lanier and Kirkendall 1986; Kirkendall and Stenseth 1990; Løyning and Kirkendall 1996
Aggregation pheromones	Blend of ipsenol, ipsdienol and cis-verbenol	Bakke 1978; Kohnle et al. 1988
Anti-aggregation	Not tested, but possibly (−)-ipsdienol	Kohnle et al. 1986; Frühbrodt et al. 2023
Gallery morphology	Long maternal tunnels (up to 45 cm), depends on quantity of females, relatively short larval tunnels (< 15 mm)	Bakke 1968a; Bakke 1968b; Kirkendall 1989
Fecundity per female in the field (eggs per maternal tunnel)	Asexual: 42.5–50.1 [1], sexual: 24.6–47.2 [1]; 4.2–16.7 [2] (underlying reasons for the high variability are unknown)	Løyning 2000 [1], Colombari et al. 2012 [2]
Breeding performance (calculated as percentage of eggs resulting in emerging adults)	Overall mean of 16.5%, higher in the second generation	Colombari et al. 2012
Pre-imaginal mortality (during development)	47.7%, increasing with colonization density	Colombari et al. 2012
Sister broods	Yes	Bakke 1968a; Vallet 1981; Herard and Mercadier 1996
Lethal attack density (number of boring holes per m²)	725–850 per m² (compared to 150 per m² for *I. typographus* [1])	Guérard et al. 2000; Colombari et al. 2012; Schebeck et al. 2023 [1]
Cold tolerance	Freeze-avoidant; ethylene glycol, mannitol, sorbitol and dulcitol as cryoprotectant substances; super cooling point in winter between − 20 °C and − 34 °C	Gehrken 1984; Gehrken 1985; Gehrken 1989; Gehrken 1992; Gehrken 1995
Overwintering habitat	Under the bark, in the litter	Bakke 1968a; Colombari et al. 2012
Overwintering developmental stage	Adult (pre-imaginal stages only withstand mild sub-zero temperatures)	Bakke 1968a; Gehrken 1984; Colombari et al. 2012; Knížek et al. 2021
Diapause	Facultative reproductive diapause as adults	Gehrken 1985
Induction of facultative diapause	Photoperiod and temperature (likely)	Gehrken 1985
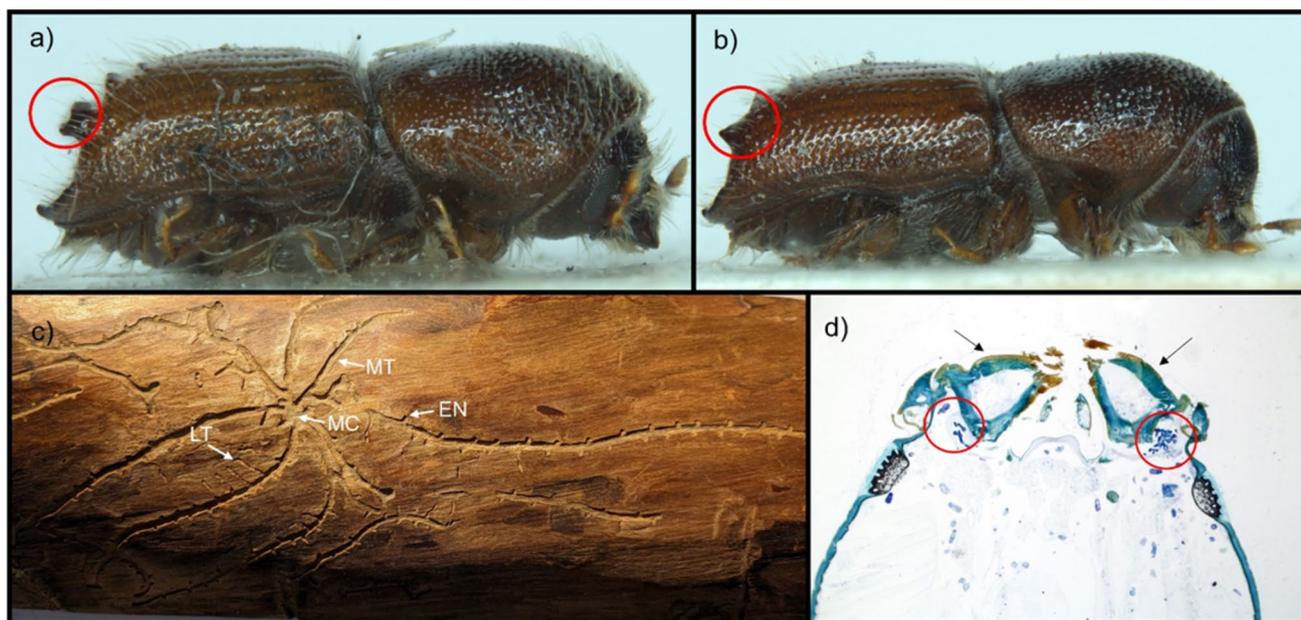
Fig. 1 **a** *Ips acuminatus* male and **b** female. Circled in red in **a** and **b** is the third spine of the elytral declivity, which is the distinctive feature of the sexes: Males have a double spine, whereas female individuals have a single spine. **c** Breeding system of *I. acuminatus* scratching the xylem with a mating chamber (marked with MC) and multiple maternal tunnels (one is marked with MT), egg niches (one is marked with EN) and larval tunnels (one is marked with LT). **d** Histologic section through head and mouth parts of a female. The mandibles are marked with black arrows and the internal oral mycetangia, containing fungal structures (likely spore masses showing thick-walled, septate, arthrospore-like propagules (blue)), are circled in red.

Fig. 2 Amount of damaged pine wood by *Ips acuminatus* in Austria and the German states of Baden-Wurttemberg, Brandenburg, Rhineland-Palatinate, Saarland and Saxony (data from Baden-Wurttemberg, Rhineland-Palatinate, Saarland account for bark breeding insects on pines in general, including *I. acuminatus*) from 2012 to 2022. Source: AFZ 2013-AFZ 2023
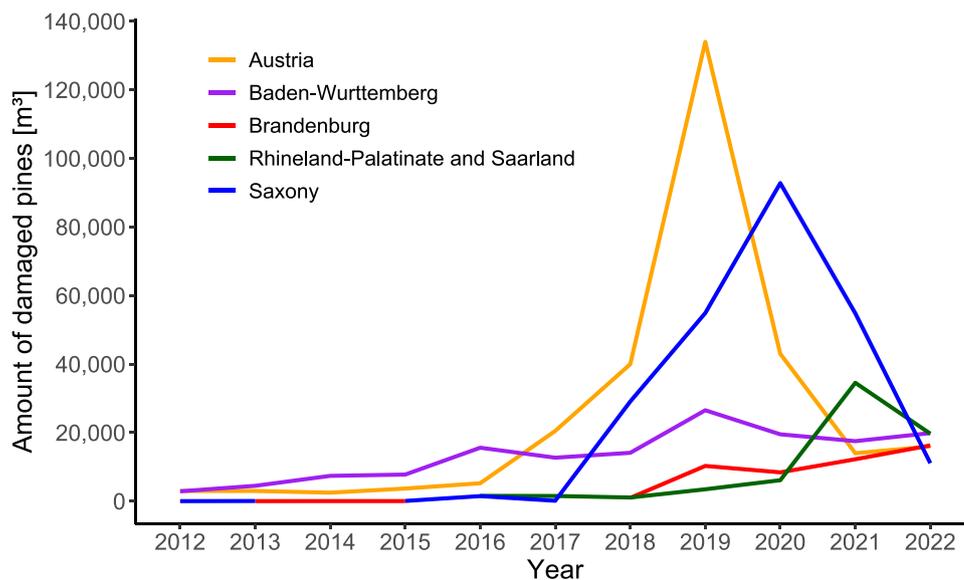
2022). Pines (and other conifer tree species) react to heat and drought by closing their stomata and by shedding needles, which ultimately affects photosynthetic activity leading to a shortage in carbohydrate resources (Croisé and Lieutier 1993; Bigler et al. 2006; Dobbertin et al. 2007; Adams et al. 2017; Hammond and Adams 2019). Subsequently, this lack of carbohydrates influences the secondary metabolism of plants, which is crucial for the activation of defense mechanisms against various stressors, including bark beetles (McDowell et al. 2008; Ferrenberg et al. 2014).

The preference of *I. acuminatus* for physiologically stressed hosts is underlined by a field experiment where *P. sylvestris* trees were girdled to lower tree defenses and to induce attacks by bark- and wood-boring insects. In this

multi-year study, *I. acuminatus* was part of a group of species involved in the early phases of host colonization (Foit and Čermák 2014). A similar colonization behavior was observed in Switzerland, where *I. acuminatus* and *P. cyanea* colonized Scots pines with 30 to 90% needle loss at high beetle densities. Those two species were considered relatively aggressive compared to other species, e.g., *T. minor* (Wermelinger et al. 2008). While aggregation pheromones have been described for *I. acuminatus* (Bakke 1978) and synthetic pheromone lures are commercially available, there is a lack of understanding the primary attraction of this species by host trees. Brattli et al. (1998) found no attraction to the host trees. However, research on this aspect of the species' life history is scarce. Future studies should focus on the chemical ecology and interactions with hosts of this bark beetle to better understand this critical part of its life cycle.

In contrast to other bark beetle species that show eruptive population dynamics, e.g., the spruce bark beetle *Ips typographus,* which often kills large, continuous forest stands, *I. acuminatus* usually shows a spot-like outbreak behavior where it only colonizes small groups of trees. In a five-year study performed in the Italian Alps, spot sizes strongly depended on the outbreak phase. Large infestation spots (26 to more than 50 trees) were dominant during the years with the highest tree mortality and high population densities of *I. acuminatus* (peak of outbreak), whereas lower beetle abundance correlated with smaller spot sizes (up to 10 infested trees per spot) (Colombari et al. 2013). In Finland, the average spot size ranged from one to twelve trees per spot (Siitonen 2014). Interestingly, spot proliferation, i.e., long-range dispersal and subsequent establishment of new spots (distance to new spots between ~ 165 and 280 m), was observed only in spring by overwintering adults (Colombari et al. 2013). In contrast, the second generation in summer showed short-range dispersal, resulting in spot growth by colonizing adjacent trees (Colombari et al. 2013). This behavior might be a strategy to avoid the establishment of natural enemies in a given area to mitigate the harmful effects of high population densities and to increase fitness (Coulson 1979).

Reproductive biology

To a certain extent, the reproductive behavior of *I. acuminatus* is similar to that of other polygynous bark beetle species, e.g., that of the widespread genera *Ips* or *Pityogenes*. Males bore through the outer bark and initiate a new gallery in the phloem–sapwood interface by building a mating chamber (Trägårdh 1939; Bakke 1968a). During this early phase of host tree colonization and gallery construction, males release a blend of aggregation pheromones consisting of ipsenol, ipsdienol and cis-verbenol to further attract male and female conspecifics (Vité et al. 1972; Bakke 1978; Kohnle et al. 1988). Interestingly, the efficacy of the *I. acuminatus* aggregation pheromone was reduced when males of another pine bark beetle, *I. sexdentatus*, were present (Kohnle et al. 1986). The common anti-aggregation pheromone verbenone was not tested in *I. acuminatus* (Frühbrodt et al. 2024).

After courtship behavior between males and females, e.g., pushing against each other, copulation occurs in the mating chamber (Løyning and Kirkendall 1996). Harem size in *I. acuminatus* varies, but can be exceptionally large, ranging from two to twelve females per male (Bakke 1968a, 1968b; Kirkendall 1989). Subsequently, each female constructs an independent maternal tunnel (Trägårdh 1939; Francke-Grosmann 1963; Bakke 1968a). Post-copulation behavior of males includes blocking the entrance hole or helping with frass removal (Kirkendall 1983, 1989, 1990; Sauvard 2004). Each female deposits multiple eggs on either side of its tunnel and covers them with phloem tissue/boring dust (Kirkendall 1989, 1990). After development through three larval instars, pupation and maturation feeding within the natal gallery, young adults complete their life cycle (Kirkendall 1990). Larval tunnels of *I. acuminatus* are relatively short for an *Ips* species, i.e., < 15 mm compared to 30–50 mm for *I. typographus* (Kirkendall 1989), possibly due to its mutualism with a nutritional fungus (see below). Short larval tunnels decrease competition among females in one harem and may thus enable the large harem sizes of *I. acuminatus* (Kirkendall 1989).

In addition to this 'standard' polygynous sexual reproduction, *I. acuminatus* can also produce offspring asexually (Bakke 1968a, 1968b; Lanier and Kirkendall 1986; Kirkendall 1989). In sexual reproduction, both males and females pass on their genetic material to the offspring generation (Bakke 1968b; Lanier and Kirkendall 1986; Kirkendall 1990). The other mode of reproduction in *I. acuminatus* is pseudogamy, a special form of parthenogenesis (Bakke 1968b; Lanier and Kirkendall 1986). Although sperm are required to trigger embryogenesis, offspring are produced asexually, and the genetic material of males is not transmitted to female-only progeny (Bakke 1968b; Lanier and Kirkendall 1986; Kirkendall 1990). Unmated females cannot produce viable offspring, i.e., no larvae emerge from such eggs (Kirkendall 1990). Thus, pseudogamous females are regarded 'sperm parasites' of males (Lanier and Kirkendall 1986) and their frequency might be limited by the availability of males.

First observations indicating parthenogenesis in *I. acuminatus* date back to the late nineteenth century (see Bakke 1968b), when studies found strongly female-biased sex ratios in certain populations. This is in contrast to other bark beetle species (including certain *I. acuminatus* populations), where equal ratios of male and female offspring were described (see Bakke 1968b). Studying the sex ratios of newly emerged

offspring from various northern European populations, Bakke (1968b) found a high variation among locations, ranging from 1:1.4 to 1:416 (male/female), whereas the sex ratios in sexual broods were equal (Bakke 1968b). Moreover, Bakke (1968b) described the morphology of female-biased galleries and found more than twenty maternal tunnels in a gallery with a strong female bias; additionally, single maternal tunnels were present directly next to these galleries. Even though the distribution of female-biased populations differed among geographic regions in northern Europe, no consistent pattern was found (Bakke 1968b). Pseudogamous reproduction seems to be present where *I. acuminatus* occurs in low abundances or where the main host tree, *P. sylvestris*, is scarce (Bakke 1968b). Moreover, pseudogamy appears to be affected by climatic conditions in a region (Bakke 1968b), as the fecundity of females was higher in cold/dry habitats than in warm/moist habitats (Løyning 2000). However, more studies are needed to understand the relationship between the abiotic environment and the reproductive performance of asexual females (Bakke 1968b; Løyning 2000).

The different reproductive modes of *I. acuminatus* are linked to chromosomal variation, as sexual females are diploid ($2n = 32$) and pseudogamous females are triploid ($3n = 48$) (Lanier and Kirkendall 1986; Kirkendall and Stenseth 1990); the two types of females in *I. acuminatus* are morphologically indistinct (Bakke 1968b). An endosymbiont-mediated or endosymbiont-enhancing influence on parthenogenesis by maternally transmitted bacterial endosymbionts (e.g., *Wolbachia*), common in other arthropods (Werren et al. 2008), was not found in *I. acuminatus* (Schebeck et al. 2019). Interestingly, the reproductive mode seems to be somewhat related to heritable traits, as the offspring of sexual broods also produced sexual progeny. In contrast, the progeny of all-female broods also had pure female offspring (Bakke 1968b). Moreover, small numbers of females were reported to mate before emergence (but most likely with unrelated conspecifics), resulting in female-only broods (Bakke 1968b; Kirkendall 1990). Pseudogamy is also present in other North American *Ips* species, i.e., *Ips tridens*, *Ips borealis*, *Ips pilifrons* and *Ips perturbatus,* and also mediated by chromosomal variation (Fig. 3) (Lanier and Oliver 1966; Lanier and Kirkendall 1986).

From an evolutionary perspective, the presence of both sexual and asexual reproduction in *I. acuminatus* is a compelling topic. Parthenogenetic females can transmit the entire genetic information to their offspring, as the genetic material of males is not passed over, thus having a reproductive advantage over sexual females (Kirkendall 1990). However, both sexual and pseudogamous populations occur and coexist in the same spatiotemporal context (Kirkendall and Stenseth 1990; Løyning and Kirkendall 1996). Although asexual females can invade populations of sexual individuals, sexual populations cannot get replaced over time because clonal female reproduction is dependent on males (Kirkendall and Stenseth 1990). This should lead to a frequency-dependent coexistence of sexual and asexual females, as female-only populations would become extinct (Kirkendall 1990; Kirkendall and Stenseth 1990). Even though pseudogamous females seem to have higher reproductive success than their sexual conspecifics (Løyning 2000), male *I. acuminatus* chose sexual females over the asexual parasites of their sperm to increase their own fitness (Løyning and Kirkendall 1996). When frequencies of asexual to sexual females are high, it is likely that competition for males is high (Kirkendall 1990; Kirkendall and Stenseth 1990). Even if there is competition for sperm in female-biased populations, the frequency of pre-emergence mating was low, mainly because freshly emerged males are not sexually mature yet (Kirkendall 1990).

Generally, despite male-parasitism by asexual females, a stable coexistence of sexual and asexual forms of reproduction in *I. acuminatus* might confer an evolutionary advantage. As pure-asexually reproducing individuals could accumulate deleterious mutations over time due to their triploidy, resulting in fitness costs, recombination during sexual reproduction results in the potential to respond to selection pressures (Kirkendall 1990; Kirkendall and Stenseth 1990). Asexual reproduction seems advantageous under harsh temperature conditions, as offspring might be better adapted to cold and/or higher female-biased sex-ratios under these conditions are possible (Bakke 1968b; Løyning 2000; Meirmans et al. 2006). So far it remains unclear if asexuals are pure parasites of sexuals or a mix of both forms is advantageous for the long-term ecological and evolutionary success of the species.

Effects of temperature and photoperiod on flight, development, reproduction and survival

Temperature-dependent development

Temperature is a major driver of insect performance (Angilletta 2009; Rebaudo and Rabhi 2018) and affects numerous aspects of bark beetle life cycles, including swarming behavior, habitat selection, host tree colonization, feeding behavior, ontogenetic development and reproductive output (Annila 1969; Bentz et al. 1991; Wermelinger and Seifert 1998, 1999; Sauvard 2004; Wermelinger et al. 2012; Gent et al. 2017; Pineau et al. 2017; Schebeck and Schopf 2017; Davídková and Doležal 2019). Some field and laboratory studies have aimed to evaluate the effects of temperature on key life-history traits of *I. acuminatus*, e.g., upper and lower developmental thresholds, optimum developmental
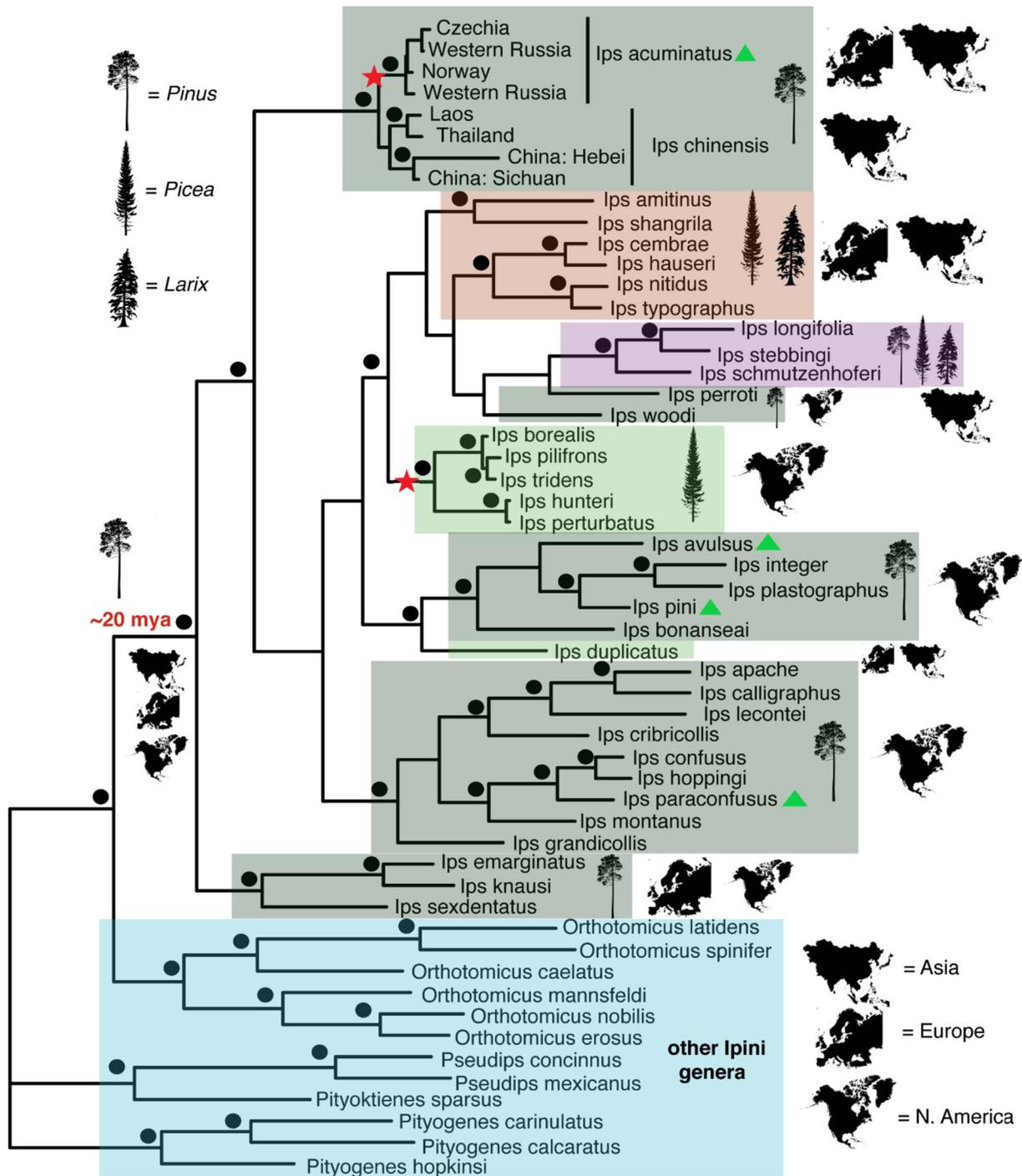
Fig. 3 Phylogenetic tree of 36 of 37 *Ips* species. Primary host tree genera (*Pinus, Picea* and *Larix*), as well as the current geographic distribution, are displayed for major clades. Nodes with species showing parthenogenesis are highlighted with red stars and species with strong fungal dependency for nutrition are marked with green triangles. Closed circles equal > 95% posterior probabilities. The ancestor of *Ips* originated ~ 20 million years ago, fed on *Pinus* species and likely occurred in the Holarctic. Multiple individuals represent *I. acuminatus* and *I. chinensis,* which are reciprocally monophyletic and morphologically distinct (Knížek and Cognato 2017)

temperature or onset of flight. These data are not only essential to understand the influence of abiotic environmental conditions on a species' fitness, survival or geographic range, they are also of high relevance for applied purposes, as they help to assess the developmental time, phenology, reproductive potential or voltinism of insect pests, parameters that

are essential to estimate their damage potential as well as to plan and time preventive and control measures (Bentz and Jönsson 2015).

An important part of the life cycle of *I. acuminatus* is the swarming phase, in order to colonize new host trees and subsequently establish a new offspring generation. In Europe, spring swarming usually occurs in April or May. Temperature thresholds for the onset of flight were described between 14 °C and 16 °C, and intense swarming of beetles from northern and southern European populations was observed at temperatures higher than 18 °C (Bakke 1968a; Lekander et al. 1977; Hernández et al. 2004, 2007; Pérez and Sierra 2006; Colombari et al. 2012). Subsequent gallery initiation is temperature dependent as well. Under laboratory conditions, male individuals establish entrance holes and nuptial chambers at temperatures between 20 °C and 38 °C, but prefer temperatures between 26 °C and 34 °C, with a mean preference temperature of about 30 °C (Bakke 1968a). Information on the effects of temperature on the developmental times of various ontogenetic stages is scarce. Bakke (1968a) performed developmental experiments under laboratory conditions at constant temperatures of 12 °C, 22 °C and 27 °C. Based on observations of gallery construction by adult females and the development of the offspring, a lower limit for development at 12 °C was inferred, as gallery initiation success of females at this temperature was low and life cycles of offspring were not completed even after nearly four months. The total development from gallery construction to brood development until the first emerging adults took 24 days at 27 °C and 30 days at 22 °C (Bakke 1968a). To date, these are the only available data from laboratory studies on the temperature-dependent development of *I. acuminatus,* and information regarding the upper and lower developmental thresholds and the optimum temperature for reproduction and brood establishment is lacking.

Although information on *I. acuminatus* temperature-dependent life-history traits is scarce, existing data on this and other pine-breeding scolytines, e.g., *T. piniperda*, *T. minor* or *I. sexdentatus*, can be used to understand phenological patterns of these beetles in the same habitat. While *I. acuminatus* and *I. sexdentatus* swarm in late spring, *T. minor* and *T. piniperda* swarm early in spring when temperatures exceed 10–12 °C (Bakke 1968a; Långström 1983). In addition, the above-mentioned species preferred lower temperatures for gallery initiation and construction than *I. acuminatus* (Bakke 1968a). Moreover, the lower developmental threshold of *T. minor* and *T. piniperda* was estimated at approximately 7 °C (Yvon and Wegensteiner 2015), which is lower than that of *I. acuminatus*.

Other common European conifer bark beetles, e.g., *I. typographus* and *P. chalcographus*, show similar phenological flight patterns, as the temperatures for the onset of flight are in the same range as *I. acuminatus* (Lobinger 1994; Wermelinger 2004; Schebeck et al. 2023). The lower developmental thresholds of *I. typographus* (~ 8 °C) (Wermelinger and Seifert 1998), *P. chalcographus* (~ 10.5 °C) (Coeln et al. 1996) and *I. sexdentatus* (~ 11 °C) (Pineau et al. 2017) are lower than the estimated developmental threshold of *I. acuminatus*. The upper developmental threshold of *I. typographus* is about 39 °C and of *I. sexdentatus* 36 °C, and the optimum temperature for brood development for *I. typographus* is about 30 °C and for *I. sexdentatus* 29 °C (Wermelinger and Seifert 1998; Pineau et al. 2017); it would be interesting if *I. acuminatus* also has a higher optimum developmental temperature and upper developmental threshold. These differences in response to temperature conditions suggest that *I. acuminatus* is somewhat adapted to warm environments, but more studies are needed to confirm this assumption. This is also underlined by field observations, where *I. acuminatus* prefers to colonize sun-exposed parts of a tree (Siitonen 2014). Moreover, this beetle has the potential to respond to specific habitat conditions (Colombari et al. 2012) and adjusts its life cycle to local environments.

Cold tolerance and dormancy strategies

During winter, insects in temperate regions employ various physiological and behavioral strategies to cope with harsh environmental conditions to increase survival and mitigate harmful effects of cold temperatures. As insects are ectothermic, they must deal with ice formation in body fluids, cells and tissues when they face sub-zero temperature conditions (Lee 2010). As a physiological response, numerous species evolved a strategy called supercooling and lower the freezing point of body water by accumulating cryoprotectant substances like sugars or polyols (Sinclair et al. 2015). The temperature when initial ice formation inside the body occurs is the supercooling point (SCP) (Lee 2010). Depending on whether insects can persist this initial ice formation, two basic types of cold tolerance strategies are distinguished (as for most insects in temperate and polar habitats) (Bale 1993; Sinclair et al. 2015). First, freeze-avoidant (or freeze-intolerant) species die when reaching the SCP; second, freeze-tolerant insects survive the ice formation at the SCP and subsequently can cope with even lower temperatures, as ice is initially built in the extra-cellular space or they tolerate freezing of certain body parts (further details and additional cold tolerance strategies not relevant here, see, e.g., Bale 1993, Lee 2010 or Sinclair et al. 2015).

Studies on the effects of low temperatures on the mortality of overwintering adults of *I. acuminatus* showed that it is freeze-avoidant, similar to other scolytine species of the Northern Hemisphere, e.g., *Ips* spp. and *Dendroctonus* spp. (Schebeck et al. 2017). SCP values are not steady over an entire year, as they follow a seasonal trend in response to changing environmental conditions. In a Norwegian study,

I. acuminatus mean SCPs were found to vary with ambient temperature from November until the end of April, with the lowest SCP value of about −34 °C measured in February (Gehrken 1984). With conditions becoming more favorable again with the onset of spring, an increase in mean SCPs was also observed. By the accumulation of cryoprotectants (e.g., ethylene glycol, mannitol, sorbitol and dulcitol) and a reduction of water content in the body during winter, *I. acuminatus* reaches a high supercooling capacity and mean SCPs can be as low as −20 °C to −34 °C; in particular, ethylene glycol seems to be of high importance (Gehrken 1984, 1989, 1995). Temperature is not the only factor triggering the formation of cryoprotective substances. Probably, photic clues, i.e., shortening of day length, also affect the cold tolerance of the species. In addition, the loss of cryoprotective proteins is induced by photoperiod (Gehrken 1984, 1989, 1995).

In contrast to adults, pre-imaginal stages of *I. acuminatus* die at moderate sub-zero temperatures (Bakke 1968a; Colombari et al. 2012; Knížek et al. 2021). Adult *I. acuminatus* either overwinter under the bark of host trees or in the forest litter (Bakke 1968a; Colombari et al. 2012), as described for other scolytine species, and the choice of the overwintering habitat depends on the geographic location (Schebeck et al. 2017). Adults from alpine populations rarely overwinter under the bark of host trees, but possibly in the forest litter (Colombari et al. 2012). In contrast, other populations in northern and southern Europe mainly hibernate under the bark (Bakke 1968a; Lekander et al. 1977; Hernández et al 2004; Wermelinger et al. 2008). Overwintering in the forest litter provides more buffered temperature conditions, but could also be an adaption to escape antagonists under the bark (Bakke 1968a; Colombari et al. 2012). The forest litter and the phloem can be moist. Thus, water can freeze at moderate sub-zero temperatures, which might expose overwintering beetles to the risk of inoculative freezing, i.e., ice from surrounding tissues enters the insect body and triggers freezing of the hemolymph, ultimately leading to death (Salt 1963). In *I. acuminatus*, inoculative freezing has only been observed in individuals lacking antifreeze proteins and ethylene glycol (at around –14 °C). This process did not occur in cold-adapted individuals, and wet-treated individuals under laboratory conditions could avoid freezing even at temperatures of about –31 °C (Gehrken 1992).

To time the seasonal occurrence, to exploit favorable resources as efficiently as possible and to increase survival during periods of adversity, many insects enter a dormant state (Denlinger 2022). In seasonally changing environments, like in the Northern Hemisphere, many insects express dormancy during winter (Wilsterman et al. 2021). Dormancy is characterized by reduced metabolic rates, suppressed development, suspended reproduction, increased stress tolerance and extended lifespan (Koštál 2006; Denlinger 2022). Dormancy is either expressed as quiescence,

i.e., an immediate response to harsh environmental conditions like low temperatures, or as diapause, i.e., an alternative developmental pathway that is genetically and hormonally regulated and already entered before the onset of adversity (Denlinger 2022). Diapause is not a steady state. Instead, it is a dynamic developmental process divided into three phases: initiation, maintenance and termination (Koštál 2006; Ragland et al. 2019).

Ips acuminatus enters facultative reproductive diapause in the adult stage. The induction of facultative diapause depends on an external signal that is strongly correlated with future adverse events (Tauber et al. 1986; Danks 1987; Denlinger 2022). As in many other insects of the Northern Hemisphere, *I. acuminatus* diapause is most likely induced by photoperiod. Gehrken (1985) proposed that pre-imaginal stages of *I. acuminatus* experience short day length in late summer or early fall and diapause is induced in immature adults shortly after pupation. However, detailed studies confirming this assumption are currently lacking. Diapause in *I. acuminatus* is accompanied by reproductive and developmental arrest (e.g., inhibition of ovarian development), reduced respiration rates and increased cold hardiness. This goes along with water loss in the body fluids and the accumulation of ethylene glycol and other cryoprotectants (for details, see above) (Gehrken 1985, 1995). Diapause in *I. acuminatus* is terminated in mid-winter (Gehrken 1985). A study from northern Europe showed that diapause termination is characterized by a rise in oxygen consumption, increased weight loss and a resumption of pre-vitellogenesis from January onwards (Gehrken 1985). However, it is unclear which cues lead to diapause termination. Subsequently, *I. acuminatus* enters a post-diapause quiescence, which lasts until environmental conditions become permissive again to resume ovarian maturation (for vitellogenesis, warm temperatures and photic cues are necessary). The early termination of diapause allows *I. acuminatus* to exploit occasional favorable conditions in early spring for development, which might confer fitness benefits (Gehrken 1985).

In comparison, other scolytine species, such as *I. typographus* or *P. chalcographus,* which are also widely distributed in the Northern Hemisphere, are likewise freeze-avoidant insects (Koštál et al. 2011, 2014; Schebeck et al. 2017, 2023). These species have similar adaptations to survive the harsh conditions during winter in their natural range. *Ips typographus* also hibernates in the adult stage under the bark or the forest litter (pre-imaginal stages only survive mild sub-zero temperatures) (Schebeck et al. 2017). In contrast, *P. chalcographus* has only been observed overwintering in the phloem, and it can sustain cold winter temperatures as an adult and in the larval and pupal stages (Schebeck et al. 2023). Their cold hardiness (i.e., lowest SCPs), achieved by the accumulation of cryoprotective substances, is greatest in mid-winter (December/January) (Koštál et al. 2011,

2014), similar to that of *I. acuminatus*. *Ips acuminatus*, *I. typographus* and *P. chalcographus* differ in the main accumulated cryoprotectants but share some other solutes, e.g., sorbitol and mannitol (Gehrken 1984; Koštál 2006; Koštál et al. 2011, 2014). *Ips typographus* and *P. chalcographus* both enter reproductive diapause in the adult stage, which is induced by photoperiod (i.e., short day length), but diapause induction can be postponed by high autumn temperatures in both species (Führer and Chen 1979; Doležal and Sehnal 2007; Schebeck et al. 2017, 2023). Similar to *I. acuminatus,* the diapause of *I. typographus* is terminated in mid-winter, which requires exposure to cold temperatures (Doležal and Sehnal 2007; Schebeck et al. 2017, 2022, 2023). Diapause not only increases the chance of winter survival, but also synchronizes individuals of a certain population, e.g., for the timing of spring emergence, to enable reproduction and the overcoming of host tree defenses.

Effects of temperature and photoperiod on voltinism

The number of generations per year (voltinism) is strongly affected by two main abiotic environmental parameters: temperature and photoperiod. High temperatures decrease developmental time, allowing earlier spring emergence and host colonization, potentially affecting voltinism. Differences in environmental conditions, e.g., between northern and southern Europe, can result in different numbers of generations per year. Usually, *I. acuminatus* populations in northern Europe are univoltine, whereas populations in more southern regions are often bivoltine. The population dynamics of *I. acuminatus* are also affected by sister broods (i.e., an additional establishment of a brood by re-emerging parental beetles) (Bakke 1968a; Lekander et al. 1977; Vallet 1981; Herard and Mercadier 1996; Hernández et al. 2004, 2007; Pérez and Sierra 2006).

Moreover, diapause can affect voltinism, as this dormancy strategy is characterized by suppressed development and reproduction. Under suitable environmental conditions, *I. acuminatus* has the potential for a multivoltine lifestyle until photoperiod induces diapause in late summer/early fall. However, temperature affects photoperiodically regulated diapause induction in other bark beetles, e.g., in *I. typographus* (Doležal and Sehnal 2007; Schebeck et al. 2017), which might also be the case for *I. acuminatus*. Therefore, a temperature-driven delay in diapause induction can affect voltinism, as an additional generation could be established. This additional generation would need to reach the adult stage before the onset of winter (as only adults can survive low sub-zero temperatures), similar to *I. typographus* (Schebeck et al. 2017). Data on the effects of warm fall conditions on diapause induction in *I. acuminatus* would add important

knowledge to the reproductive potential of this bark beetle but are currently lacking.

Associations with heterospecifics from different trophic levels

Bark beetles form complex and dynamic associations with various organisms sharing the same habitat, including microorganisms like fungi and bacteria. Interactions range from mutualism and commensalism to antagonism, but most interactions are poorly understood (Hofstetter et al. 2015; Wegensteiner et al. 2015). These relationships are context-dependent, particularly for fungi. Thus, the same association can be beneficial in one phase of the insect life cycle and detrimental in another and/or relationships may change in response to varying environmental conditions (Kirisits 2004; Six 2012; Six and Klepzig 2021).

Fungi

The most frequent fungi associated with bark beetles are ophiostomatoid species, so-called blue-stain fungi, due to the discoloration of colonized sapwood (Kirisits 2004, 2013; Harrington 2005). These ascomycetes have previously been assigned to the genera *Ophiostoma* and/or *Ceratocystis* but have recently been divided into different phylogenetic lineages in the orders Microascales and Ophiostomatales (De Beer et al. 2013, 2022). They show strong morphological adaptions to the association with bark beetles, such as perithecia with long beaks, sticky ascospores and conidia (Hofstetter et al. 2015). Apart from ophiostomatoid fungi, many bark beetles are associated with *Geosmithia* species, which have been neglected as bark beetle associates for long time (Kolařík and Hulcr 2023). *Ips acuminatus* belongs to the group of scolytines that is intimately associated with ophiostomatoid fungi (Table 2) (Kirisits 2004; Kolařík and Hulcr 2023), whereas *Geosmithia* species have only been reported once (Davydenko 2019).

Fungal community

Fungal associates of *I. acuminatus* on Scots pine have been studied in several European countries, with a focus on ophiostomatoid species (Table 2). Some studies also recorded fungi of other systematic groups (all investigations so far addressed *I. acuminatus* attacking Scots pine) (Davydenko et al. 2017; Baturkin and Davydenko 2020; Davydenko 2019; 2021). Many ophiostomatoid fungi have been found as associates of *I. acuminatus,* but only a few species occur at relatively high frequencies (Table 2). In addition to frequency, fungal associates of bark beetles vary in their specificity, i.e., whether they have been exclusively recorded with

Table 2 Ophiostomatoid fungi in the order Ophiostomatales and Microascales associated with *Ips acuminatus* on *Pinus sylvestris* in Europe, on *Pinus kesiya* in China[2] and on *Pinus densiflora* in Japan[20], as well as pathogenicity/virulence of ophiostomatoid fungi toward *P. sylvestris* in Europe[1,3,5,6,11,12,26]

Fungal species	Country	Pathogenicity/Virulence*	Commentary
Europe			
Order Ophiostomatales			
***Ceratocystiopsis* species**			
C. norroenii	Norway[14]	not tested	mainly associated with *I. acuminatus* (isolated from 54% of the investigated beetles), but also with *Pityogenes quadridens* on *Pinus sylvestris*[14]
C. minima	France[17]	not tested	isolated at low frequencies[17]
C. minuta	Sweden[22]	not tested	rare associate[21], as *C. minuta* represents a species complex, this record likely represents one of the recently described taxa, possibly *C. norrenii*[14]
C. rollhanseniana	Norway[14]	not tested	associated with various bark beetles on *Picea abies* and *Pinus sylvestris*, isolated at low frequencies (11%) from *I. acuminatus* beetles[14]
***Graphilbum* species**			
G. acuminatum	Austria[25], Norway[13], Poland[13,15]	not tested	frequent associate of *I. acuminatus* in recent studies[13,15,25], occurs most commonly with *I. acuminatus*, but also with other bark beetles on *P. sylvestris* and *P. abies*[13], *Graphilbum* sp. 1 from Norway[28] represents *G. acuminatum*[13]
G. fragrans	Poland[15]	not tested	was isolated at low frequency (0.5%) from sapwood around *I. acuminatus* galleries in Poland[15], occurs at low frequencies with several conifer-infesting bark beetles[16,18]
G. cf. *rectangulosporium /G. rectangulosporium*	Ukraine[3–5]	moderate[3,5,6]	was among the most frequent ophiostomatoid fungi associated with *I. acuminatus* in Ukraine[3,4] (e.g., isolated from 8.3–22.9% of the beetles at 6 sites[4]), this taxon does not represent *G. acuminatum* but is a different species closely related to *G. crescericum*, *G. niveum* and *G. sexdentatum*[15]
Graphilbum sp. 1	Norway[28]	not tested	species most frequently isolated from *I. acuminatus* beetles (87%) in the study in Norway[28], this taxon represents the recently described *G. acuminatum*[13]
***Grosmannia* species**			
G. olivacea	Ukraine[3–6]	not pathogenic[3], low[5]	was isolated at low (0.8%)[3] to moderate (9.0%)[4] frequencies from *I. acuminatus* beetles in Ukraine, this species is also associated with several other pine- and spruce infesting bark beetles[16,18]
Grosmannia sp. 1	Ukraine[1,4,6]	moderate[1,6]	this undetermined species was detected at low frequencies from *I. acuminatus* beetles[4] and isolated at moderate frequencies from sapwood[1] in Ukraine
***Leptographium* species**			
L. lundbergii	Sweden[21,23]	not tested	rare associate of *I. acuminatus* in Swedish studies[21,23], it is also associated with several other pine-infesting bark beetles[16,18]

Table 2 (continued)

Fungal species	Country	Pathogenicity/Virulence*	Commentary
L. cf. piceiperdum	Austria[25]	not tested	Leptographium piceiperdum is a species complex containing several taxa[8,18], one species in this complex was isolated from I. acuminatus beetles and sapwood in Austria[25]
L. procerum	Poland[15]	not tested	was isolated at low frequency (1.5%) from sapwood around I. acuminatus galleries in Poland[15], it is also associated with several other conifer-infesting bark beetles[16,18]
L. sosnaicola	Poland[15]	moderate[5]	was isolated at low frequency (0.5%) from sapwood around I. acuminatus galleries in Poland[15], it is also associated with several other conifer-infesting bark beetles
Ophiostoma species			
O. bicolor	Ukraine[1,4,6]	low[1,5,6]	was detected at moderate (16.0%) frequencies from I. acuminatus beetles[4] and at high frequencies from sapwood[1] in Ukraine[4], it is also associated with several other pine- and spruce-infesting bark beetles[16,18]
O. canum	Austria[25], Sweden[21,23], Ukraine[1,4,6]	low[1,5,6]	this species is mainly associated with pine-infesting bark beetles, particularly Tomicus minor, but also with I. acuminatus[9,16,18,21,22,23], in studies in Ukraine, it was among the ophiostomatoid fungi most frequently associated with I. acuminatus[1,4,6] (e.g., detected on 19.1% of the investigated beetles[4])
O. clavatum	Austria[19,25], Finland[12], France[11,17,19], Germany[10,19], Italy[19,27], Norway[28], Sweden[9,10,19,21–24], former Yugoslavia[10]	low[11,12,26]	was in some studies recorded as a frequent associate of I. acuminatus (but not at all in recent investigations in Ukraine[3–7] and Poland[15]), records of this species from other bark beetles are questionable[19], in French studies[11,17] O. brunneo-ciliatum was recorded, but it is most likely that these authors in fact dealt with O. clavatum[19,27]
O. ips	France[17], Norway[28], Sweden[23], Ukraine[1,3–7]	low[1,3,5,6]	is known as associate of many pine-infesting bark beetles including I. acuminatus[16,18], in studies in France[17] and Ukraine[1,3–7] it was among the most frequent ophiostomatoid fungi associated with I. acuminatus
O. macrosporum	Austria[25], Germany[10], Norway[28], Sweden[9,10,21,23], former Yugoslavia[10]	low[26]	this species is regarded as the nutritionally important ambrosia fungus of I. acuminatus[9,10], it was not recorded in recent studies in Poland[15] and Ukraine[3–7], there are no records of this fungus from other bark beetle species
O. minus	Austria[25], France[17], Norway[28], Poland[15], Sweden[21,23,24], Ukraine[1,3–7]	moderate to high[1,3,5,6]	is one of the most common species associated with conifer-infesting bark beetles in Europe[16,18], in studies in Sweden[21,23,24] and Ukraine[1,3–7] it was among the most frequent ophiostomatoid fungi associated with I. acuminatus, while it was rare[15,17,25,28] in other studies, O. minus is the most virulent ophiostomatoid fungus associated with I. acuminatus[1,3,5,6]

Table 2 (continued)

Fungal species	Country	Pathogenicity/Virulence*	Commentary
O. piceae	Austria[25], Sweden[9,21,23], Ukraine[1,3–7]	low[1,3,5,6]	is an unspecific fungal associate that can occur with a wide range of conifer-infesting bark beetles but also on trees and logs without insect infestations[16,18], it was recorded at relatively high frequencies with I. acuminatus in studies in Ukraine[1,3–7]
O. pallidulum	Ukraine[3–5]	low[3,5]	is associated at low frequencies with various bark beetles[18], including I. acuminatus in Ukraine[3–5]
O. piliferum	Sweden[9,21,23], former Yougoslavia[10]	not tested	is an unspecific fungal associate that can occur with several conifer-infesting bark beetles but also on trees and logs without insect infestations[16,18], it was occasionally recorded also with I. acuminatus[9,10,21,23]
O. tingens	Austria[25]	not tested	this nutritionally important fungus of Tomicus minor[9] has also been recorded with other pine bark beetles[16,18], and it was occasionally isolated from I. acuminatus beetles in Austria[25]
Ophiostoma spp.	France[17], Sweden[21,23,24], Ukraine[1,4,7]	low (Ophiostoma sp. 1 from Ukraine[1,6])	includes one unidentified species from France[17] and several ones from Sweden[21,23,24] and Ukraine[1,4,7]
Sporothrix species			
S. pseudoabietina	Poland[15]	not tested	is a widely distributed associate of various bark beetles, in a Polish study it was after G. acuminatum the second most frequent ophiostomatoid fungus isolated from I. acuminatus beetles and sapwood around the beetles' galleries[15]
Order Microascales			
Endoconidiophora species			
Endoconidiophora coerulescens	Sweden[9,21,23]	not tested	is not closely associated with insects, was recorded at low frequencies with I. acuminatus, T. minor and other pine bark beetles in Sweden[9,21,23]
Graphium species			
G. pseudormiticum	Austria[25], Poland[15]	not tested	occurs at low frequencies with various conifer-infesting bark beetles[16,18], in Poland it was isolated from 10% of the investigated I. acuminatus beetles[15]
G. pycnocephalum	Sweden[21,23]	not tested	this species with unclear taxonomic status was recorded at low frequency from I. acuminatus in Sweden[21,23]
Graphium sp.	Norway[28]	not tested	was isolated only from one beetle in the Norwegian study[28]
Graphium sp.	Ukraine[1,4]	moderate[1,5,6]	was detected at low frequencies on I. acuminatus beetles[4] and isolated at moderate frequencies from sapwood[1] in Ukraine; this species may not belong to the genus Graphium, as it was isolated onto media with cycloheximide[1] to which Graphium ssp. are sensitive
Asia			
Order Ophiostomatales			
Graphilbum species			

Table 2 (continued)

Fungal species	Country	Pathogenicity/Virulence*	Commentary
G. puerense	China (Yunnan)[2]	not tested	relatively frequent associate of *I. acuminatus* and its phoretic mites on *Pinus kesiya*, also (but less frequently) associated with *Polygraphus szemaoensis* and its phoretic mites[2]
***Leptographium* species**			
L. yunnanense	China (Yunnan)[2], Japan (Honshū)[20]	not tested	was isolated at low frequency from *I. acuminatus* galleries on *P. kesiya* in China, occurs also with other bark beetles and their phoretic mites[2]; is associated with several bark beetle species on *Pinus densiflora* in Japan and was isolated from one single *I. acuminatus* beetle[20]
L. koreanum	Japan (Honshū)[20]	not tested	is associated with numerous bark beetle species on *P. densiflora*, was isolated at high frequencies (52.6%) from beetles at one out of three sample sites[20]
***Ophiostoma* species**			
O. acororum	China (Yunnan)[2]	not tested	was isolated at low frequency from *I. acuminatus* galleries and a phoretic mite on *P. kesiya*, was mainly obtained from phoretic mites of various bark beetles[2]
O. clavatum	Japan[19]	not tested	only known record of *O. clavatum* from Asia, it has not been confirmed by DNA sequencing[19]
O. ips	China (Yunnan)[2], Japan (Honshū)[20]	not tested	most frequent ophiostomatoid fungus associated with *I. acuminatus* and its phoretic mites on *P. kesiya* in China, where it also occurs with other conifer bark beetles and their phoretic mites[2]; on *Pinus densiflora* in Japan, it was frequently isolated from *I. acuminatus* beetles (71%) and from sapwood around galleries (79%), it is also associated with other bark beetles[20]
O. quercus	China (Yunnan)[2]	not tested	was isolated only once from an *I. acuminatus* gallery on *Pinus kesiya*[2]
O. cf. *stenoceras*	Japan (Honshū)[20]	not tested	occurs at low frequencies with several bark beetle species on *P. densiflora*, was isolated from one single *I. acuminatus* beetle[20]
***Sporothrix* species**			
S. nebularis	China (Yunnan)[2]	not tested	was isolated only once from an *I. acuminatus* gallery on *P. kesiya*, was mainly obtained from phoretic mites of bark beetles[2]
Order Microascales			
***Graphium* species**			
G. pseudormiticum	China (Yunnan)[2]	not tested	was isolated only once from a phoretic mite of *I. acuminatus* on *P. kesiya*[2]

*The pathogenicity/virulence of ophiostomatoid fungi was classified as low, moderate or high based on the severity of stem symptoms (necrotic phloem lesions, desiccation or blue-stain in the wood, resin flow) and external symptoms (decline, mortality) following artificial wound inoculation of seedlings[1,3,5,6] or young trees[11,12,26] of Scots pine. Only inoculation experiments carried out with fungal isolates obtained from *I. acuminatus* were considered

References: [1]Baturkin and Davydenko (2020); [2]Chang et al. (2017); [3]Davydenko et al. (2017); [4]Davydenko (2019); [5]Davydenko (2021); [6]Davydenko and Baturkin (2020a); [7]Davydenko and Baturkin (2020b); [8]De Beer et al. (2022); [9]Francke-Grosmann (1952); [10]Francke-Grosmann (1963); [11]Guérard et al. (2000); [12]Isberg et al. (2022); [13]Jankowiak et al. (2020); [14]Jankowiak et al. (2022); [15]Jankowiak et al. (2023); [16]Kirisits (2004); [17]Lieutier et al. (1991); [18]Linnakoski et al. (2012); [19]Linnakoski et al. (2016); [20]Masuya et al. (2009); [21]Mathiesen (1950); [22]Mathiesen (1951); [23]Mathiesen-Käärik (1953); [24]Rennerfelt (1950); [25]Ritzer, Schebeck and Kirisits unpublished data; [26]Villari et al. (2012); [27]Villari et al. (2013); [28]Waalberg (2015).

I. acuminatus or other bark beetle species, as well as on pine or other host trees (Table 2).

In early studies in Sweden, two fungal species, *Ophiostoma macrosporum* and *Ophiostoma clavatum*, were most frequently detected (Mathiesen 1950, 1951; Rennerfelt 1950; Francke-Grosmann 1952; Mathiesen-Käärik 1953). These two fungi, which have recently also been recorded in Central Europe (Table 2), are specific associates of *I. acuminatus*, as they have not been found with any other bark beetle species. *Ophiostoma macrosporum* is considered a nutritionally important ambrosia fungus of *I. acuminatus* (Francke-Grosmann 1952, 1963). Remarkably, *O. macrosporum* and *O. clavatum* were not detected in recent studies in Ukraine and Poland (Davydenko et al. 2017; Davydenko 2019, 2021; Jankowiak et al. 2023). *Ophiostoma clavatum* is morphologically very similar to *Ophiostoma brunneo-ciliatum* and these two species are part of a complex of seven species that can only be distinguished using molecular markers (Linnakoski et al. 2016). Therefore, the two species might have been confused in other studies (Lieutier et al. 1991; Guérard et al. 2000).

A frequent associate of *I. acuminatus* is *Graphilbum acuminatum,* which is often found with this beetle and rarely with other pine and spruce bark beetles (Waalberg 2015; Jankowiak et al. 2020, 2023; Elisabeth Ritzer, Martin Schebeck and Thomas Kirisits, unpublished data), and another *Graphilbum* species, referred to as *Graphilbum* cf. *rectangulosporium* (Davydenko et al. 2017; Davydenko 2019). Frequent ophiostomatoid fungi of *I. acuminatus* also include *Ophiostoma canum, Ophiostoma ips, Ophiostoma minus* and *Sporothrix pseudoabietina* (Table 2), which are rather unspecific associates that are transmitted by other conifer bark beetles as well (Kirisits 2004; Linnakoski et al. 2012).

As described above for *O. macrosporum* and *O. clavatum,* there are substantial differences in the presence and frequencies of fungi associated with *I. acuminatus* in different countries and sampling sites (Table 2) (Davydenko et al. 2017; Davydenko 2019; Jankowiak et al. 2023). The variation in the assemblages of fungi in various studies can have several reasons. These include methods of sampling (e.g., collecting beetles from pheromone traps or galleries in living or dead trees) and isolation (e.g., medium with or without cycloheximide; source of isolation from beetle, phloem, sapwood; use of surface sterilization; maceration and plating out of beetles or placing intact beetles onto the medium; temperature of incubation of isolation plates; time of isolation) or detection (DNA isolation and amplification), as well as identification procedures and the researchers' experience (Kirisits 2004; Linnakoski et al. 2016). Moreover, phoretic mites of bark beetles carry ophiostomatoid fungi (Hofstetter et al. 2015; Chang et al. 2017) and can influence the fungal composition associated with bark beetles, including *I. acuminatus.* Nevertheless, it is likely that differences among various studies also reflect the influence of climatic conditions such as temperature and precipitation at the sampling sites and/or some geographic variation of the fungal assemblages (Davydenko et al. 2017; Jankowiak et al. 2023). The relevance of the variation of the fungal community for the life history of *I. acuminatus* (and other bark beetles) is poorly understood (Kirisits 2004; 2010). To compare the results of different investigations, we suggest developing and following standard protocols for the study of fungal communities of *I. acuminatus.*

There are two comprehensive studies on the community of ophiostomatoid fungi of *I. acuminatus* in Asia, i.e., from China (Chang et al. 2017) and from Japan (Masuya et al. 2009). Only two fungi, *O. ips* and *Graphium pseudormiticum*, were associated with *I. acuminatus* both in Asia and Europe (Table 2; Chang et al. 2017; Masuya et al. 2009). Additionally, there is one record of *O. clavatum* in Japan (Aoshima 1965) which was not confirmed by DNA sequencing (Linnakoski et al. 2016). *Ophiostoma ips*, which occurs with many bark beetle species in the Northern Hemisphere, was the most frequent associate of *I. acuminatus* in China and Japan, while other fungal species occurred at lower frequencies (Table 2; Chang et al. 2017; Masuya et al. 2009). Besides *O. ips*, the only fungus found both in China and Japan (at low frequencies) was *Leptographium yunnanense*. In China, *I. chinensis*, which is morphologically similar to *I. acuminatus*, occurs (Knížek and Cognato 2017), and at least some of the records of ophiostomatoid fungi from *I. acuminatus* in Asia may actually refer to *I. chinensis*. Hence, differences in fungal communities between Europe and Asia might reflect the evolutionary history of the two scolytine species.

Noteworthy, Davydenko et al. (2017) reported a high number of fungi (not only ophiostomatoid species) from *I. acuminatus* beetles in Ukraine. The fungal community comprised 80% ascomycetes, 11.7% basidiomycetes and 8.3% zygomycetes. Most of the non-ophiostomatoid species might be casual encounters with *I. acuminatus* with unknown roles. However, two frequently recorded species, *Entomocorticium* sp. and *Diplodia sapinea*, are remarkable findings (Davydenko et al. 2017). *Entomocorticium* spp. are known as nutritionally important fungi of North American bark beetles (Harrington 2005; Six 2012; Hofstetter et al. 2015; Harrington et al. 2021) and *D. sapinea* is the causal agent of Diplodia shoot blight of pines and other conifers (Zlatković et al. 2017; Blumenstein et al. 2022; Ritzer et al. 2023), which was also frequently isolated from *I. acuminatus* in Austria (Elisabeth Ritzer, Martin Schebeck and Thomas Kirisits, unpublished data).

Blue-stain in the sapwood of *Pinus sylvestris* following *Ips acuminatus* attacks

As observed with other bark beetles on Scots pine, attacks by *I. acuminatus* rapidly lead to intense blue-staining of sapwood (Rennerfelt 1950; Francke-Grosmann 1952; Mathiesen-Käärik 1953). Blue-stain seems to become significant during early larval development, and the sapwood is completely stained when late larval stages or pupae are present (Francke-Grosmann 1952; Mathiesen-Käärik 1953; Elisabeth Ritzer, Martin Schebeck and Thomas Kirisits, unpublished data). It is unclear which ophiostomatoid fungi are primarily responsible for the blue-staining of Scots pine sapwood following attacks by *I. acuminatus*. Due to its high frequency, *O. clavatum* was initially considered the primary blue-stain fungus (Rennerfelt 1950; Mathiesen 1950, 1951; Mathiesen-Käärik 1953). Francke-Grosmann (1952) suggested *O. macrosporum* to be the primary agent of blue-stain, but this is questionable, as some studies failed to isolate this species from sapwood adjacent to galleries (Jankowiak et al. 2023) or recorded it only at low frequencies (Elisabeth Ritzer, Martin Schebeck and Thomas Kirisits, unpublished data). Instead, *G. acuminatum* and *S. pseudoabietina* were consistently isolated at high frequencies from the sapwood near galleries (Jankowiak et al. 2023). Thus, these two species may be mainly involved in blue-staining the sapwood (although they form white mycelium in culture). In an Austrian study, *G. acuminatum* was consistently isolated at the front of the fungal invasion into the sapwood of Scots pine, followed by *O. clavatum* and, less frequently, other ophiostomatoid fungi (Elisabeth Ritzer, Martin Schebeck and Thomas Kirisits, unpublished data). More studies with isolations at different stages of brood development of *I. acuminatus* and different sapwood depths would be desirable to characterize the primary agents of blue-stain and the fungal succession into the sapwood of Scots pine.

Nutritional importance of fungi

Ips acuminatus is unique among European bark beetles because females possess a prominent mycetangium; in this species, paired membranous pouches at the base of their mandibles (Fig. 1d). Mycetangia are specialized invaginations on the insect body to transport only their mutualistic fungal partners selectively and are an indication for strong insect–fungus relationships (Francke-Grosmann 1956; 1967; Mayers et al. 2022). Francke-Grossmann (1963) described that *I. acuminatus* selectively transports conidia of *O. macrosporum* in its mycetangium, indicating a strong dependency between insect and fungus, supporting the role of *O. macrosporum* as a nutritionally essential species.

Ips acuminatus (together with *T. minor*) has an exceptional life history because its biology and feeding behavior are intermediate between a bark beetle (primarily feeding on phloem) and an ambrosia beetle (primarily feeding on fungi cultivated in galleries) (Francke-Grosmann 1952; 1963). *Ips acuminatus* is a phloeomycetophagous species feeding on phloem and fungal structures. It mainly colonizes thin-barked areas, where its larvae excavate short tunnels, which often scratch the outer sapwood, and particularly later larval stages and teneral adults predominantly or exclusively feed on fungi (Francke-Grosmann 1952).

Among the various fungi associated with *I. acuminatus*, Francke-Grosmann (1952, 1963) considered only *O. macrosporum* as its nutritionally important ambrosia fungus. This species forms thick ambrosia layers—nutrient-rich cell aggregates with round conidia—in the beetles' galleries, which are essential for the nutrition of both larvae and teneral adults (Francke-Grosmann 1952). The ambrosia layers decline after beetles leave the galleries, and then, *O. clavatum* and other fungi quickly overgrow *O. macrosporum*. The maternal tunnels of *I. acuminatus* contain many ventilation holes in the bark, which likely supports the supply of oxygen to *O. macrosporum* and is necessary to regulate the humidity in the galleries. In addition, adult *I. acuminatus* beetles regularly clog maternal tunnels with frass. This unusual behavior may contribute to maintaining sufficient oxygen and moisture levels in the galleries, facilitating the growth of *O. macrosporum*. This behavior is critical in thin-barked areas because otherwise, the phloem/xylem would dry out too quickly, and fungal development would stop. The creation of airholes and clogging of galleries with frass could be interpreted as a form of fungal farming that resembles the behavior of wood-inhabiting ambrosia beetles to regulate abiotic conditions and ambrosial fungal growth in their galleries (Francke-Grosmann 1952; Biedermann and Vega 2020).

Given the biological significance of *O. macrosporum* described by Francke-Grosmann (1952, 1963), it is surprising that this fungus was not detected in several other studies (Lieutier et al. 1991; Davydenko et al. 2017; Davydenko 2019; Jankowiak et al. 2023). These findings can likely be explained by the low competitiveness of *O. macrosporum*, leading to overgrowth by other fungi when standard isolation methods (placing beetles or infected host material onto agar media) are used. Difficulties in isolating *O. macrosporum* have already been mentioned by Francke-Grosmann (1952, 1963); however, she described that it can be readily isolated in pure culture using the shake flask method with repeated dilutions. Alternatively, there may be other overlooked fungi that are nutritionally important for *I. acuminatus*. For example, an *Entomocorticium* species was obtained from *I. acuminatus* in Ukraine (Davydenko et al. 2017; Davydenko 2019). *Entomocorticium* spp. are known as nutritionally essential fungi of North American bark beetles, particularly

Dendroctonus spp. and *Ips avulsus* (Harrington 2005; Six 2012; Hofstetter et al. 2015; Harrington et al. 2021). Perhaps some of Francke-Grosmann's (1952, 1963) findings regarding phloeomycetophagy and the role of *O. macrosporum* should be critically re-examined.

Besides *I. acuminatus*, the only other European bark beetle species where phloeomycetophagy has been described is the pine bark beetle *T. minor*, which is associated with the nutritionally important fungus *Ophiostoma tingens*, a species closely related to *O. macrosporum* (Francke-Grossmann 1952). *Tomicus minor* also colonizes thin-barked pine tree areas and forms short larval tunnels. However, in contrast to *I. acuminatus*, no mycetangium has been detected in *T. minor* (Francke-Grosmann 1963). The North American *I. pini*, *Ips paraconfusus* and *I. avulsus* are the only other *Ips* species known to profit from associated nutritional fungi (for *I. pini*: *Ophiostoma montium* (synonyms *Hyalorhinocladiella ips* and *Ambrosiella ips*, De Beer et al. 2022; for *I. avulsus*: *Ophiostoma ips* and *Entomocorticium sullivanii*, Harrington 2005; Harrington et al. 2021)), but whether they have obligate mutualisms is unclear (reviewed by Harrington 2005); *I. avulsus* and *I. paraconfusus* have a higher fitness when an associated fungus is present (*O. ips* in *I. avulsus*; for *I. paraconfusus* the fungal species is unknown; Harrington 2005). While *I. pini* transmits *O. montium* spores in pouches on the head ('pit mycangia') (Six 2012), no mycetangium was found in *I. avulsus* and *I. paraconfusus*. Pit mycangia are also found in *I. sexdentatus* (Lévieux et al. 1991), but no beneficial fungal role has been found there (Colineau & Lieutier 1994). Interestingly, *I. avulsus* and *I. pini* are found in the same clade, but in a separate one from *I. acuminatus* (Fig. 3); as all three colonize pines it is likely that their putative fungus mutualism evolved convergently, probably in response to similar ecological pressures.

Phytopathogenicity of fungal associates and their role in overcoming host tree defenses

Pathogenicity (defined here as the ability to cause disease) and virulence (described here as the degree or level of pathogenicity) of ophiostomatoid fungi towards their host trees are assessed by inoculations at low densities, where trees receive one or a low number of fungal inoculations, or high densities, i.e., mass inoculations. Mass inoculations aim to mimic bark beetle mass attacks, to evaluate the ability of a fungus to kill host trees and to determine densities when tree mortality occurs (Lieutier et al. 2009; Six and Wingfield 2011).

In a mass inoculation experiment, Guérard et al. (2000) inferred that high densities of inoculation with *O. clavatum* (above 1000 inoculations per m² bark surface) are necessary to severely damage and possibly kill Scots pine trees, which corresponds well with critical densities of 850 natural attacks of *I. acuminatus* leading to tree death. These values

are much higher than those for other bark beetles and their associated fungi, e.g., *I. typographus* (300–500 attacks/m²)-*Endoconidiophora polonica* (400 inoculations/m²) (Christiansen 1985), *T. piniperda* (400 attacks/m²) (Långström et al. 1992)-*Leptographium wingfieldii* (400 inoculations/m²) (Croisé et al. 1998), and suggest a low aggressiveness of *I. acuminatus,* paralleled by a low virulence of its associated fungus *O. clavatum* (Guérard et al. 2000). Inoculation trials on young Scots pine trees and seedlings confirmed that most tested fungal associates of *I. acuminatus* are phytopathogenic but display predominantly only low to moderate virulence towards their host (Table 2; Solheim et al. 2001; Villari et al. 2012; Davydenko et al. 2017; Davydenko 2019; Davydenko & Baturkin 2020a). The most virulent species was *O. minus,* causing the longest necrotic lesions, deepest bluestain and mortality in seedlings (Davydenko et al. 2017).

Fungal associates of *I. acuminatus* might be involved in exhausting tree defense mechanisms. Higher carbon concentrations were measured in reaction zones of Scots pine seedlings inoculated with *O. clavatum* compared to healthy phloem, which reflects an accumulation of phenols, terpenes and tannins in these zones (Guérard et al. 2007). Likewise, wounding as well as inoculation with *O. clavatum* and the nutritionally important *O. macrosporum* (alone and in combination) induced an increase of terpenoids, phenolic compounds and lignin in young Scots pine trees (Villari et al. 2012). The inoculated trees showed a more generic response to both wounding and inoculation, and the only compounds that were significantly more stimulated by fungal inoculation (*O. clavatum* in combination with *O. macrosporum*) than by wounding were pinosylvin monomethyl ether and (+)-α-pinene. These results confirm that fungal associates of *I. acuminatus* induce tree defense mechanisms and can contribute to the exhaustion of tree defenses (Guérard et al. 2007; Villari et al. 2012). Likewise, the example of *O. macrosporum* shows that a bark beetle-associated fungus can have several roles (both providing nutrition and triggering plant defense reactions) to facilitate successful brood establishment (Lieutier et al. 2009; Villari et al. 2012).

One study reported higher frequencies of *O. clavatum* in endemic populations than in epidemic populations of *I. acuminatus* (Villari et al. 2013). The authors suggest that the fungus may play a more significant role in successful brood establishment during endemic population phases than in outbreak populations. During an outbreak, beetle densities might be high enough that the presence of a low virulent fungal associate is no longer critical to overcome tree defenses (Villari et al. 2013). This suggestion is based on a limited number of sites and investigated samples and requires further study.

Ips acuminatus as a potential vector of *Diplodia sapinea*

Diplodia shoot blight, caused by *D. sapinea*, is an emerging disease that has recently occurred in several European countries, frequently on Scots pine, Douglas fir and other host trees (Zlatković et al. 2017; Brodde et al. 2019; Blumenstein et al. 2022; Ritzer et al. 2023; Terhonen et al. 2023). In recent years, it was detected at high frequencies on *I. acuminatus* beetles in Ukraine (Davydenko and Baturkin 2020b) and at lower frequencies in Austria (Elisabeth Ritzer, Martin Schebeck and Thomas Kirisits, unpublished data), which may indicate fungal pathogen transmission by the beetle or even a novel bark beetle–pathogen association. However, the relationship between the fungus and the insect requires further investigation.

Bacterial associates

Information on the bacterial communities of bark beetles is relatively scarce, and they have only been studied in a few species. Bacteria can be found in the galleries, gut, mycetangia and body surface of their insect hosts. The ecological roles of bacteria can be diverse, ranging from pathogenic to neutral to mutualistic (Six 2013; Hofstetter et al. 2015). Bacterial mutualists of bark beetles can be essential for providing nutrients (especially nitrogen), producing antimicrobial substances, helping with the digestion of plant molecules (especially cellulose and hemicellulose), influencing pheromone production and detoxifying host toxins (Six 2013; Hofstetter et al. 2015; Fabryová et al. 2018; García-Fraile 2018; Chakraborty et al. 2020; González-Dominici et al. 2021; Chen et al. 2023). Antimicrobial substances produced by bacteria might also play a significant role in protecting other mutualistic symbionts of bark beetles (Saati-Santamaría et al. 2018; Chen et al. 2023).

A small number of studies focused on the bacterial communities of *I. acuminatus* and its ecological significance. The core bacteriome of *I. acuminatus* consisted of 126 operational taxonomic units from various bacteria groups, like Enterobacteriaceae, Pseudomonadaceae and Xanthomonadaceae (Chakraborty et al. 2020). Compared to the other four studied species (*I. typographus* and *Ips amitinus* on Norway spruce, *Ips cembrae* on European larch and *I. sexdentatus* on Scots pine), *I. acuminatus* had the highest bacterial diversity and richness. The higher diversity might be explained by its phloeomycetophagous lifestyle. Furthermore, certain bacteria might contribute to detoxifying pine defense-related metabolites and enable beetles to colonize relatively healthy trees (Chakraborty et al. 2020).

Other studies assessed the antimicrobial potential of bacterial strains from several bark beetle species, including *I. acuminatus*. Twenty bacteria belonging to *Pseudomonas*, *Micrococcus*, *Arthrobacter*, *Acidiovorax* and *Erwinia* were isolated (Saati-Santamaría et al. 2018; González-Dominici et al. 2021). One particular bacterial strain, i.e., *Arthrobacter ipsi* IA7T, was reported to have important ecological traits. Genomic analyses revealed several genes coding for antimicrobial compounds. In *in vitro* assays, this bacterial strain inhibited several strains of common entomopathogenic fungi infecting *Ips*, e.g., *Beauveria bassiana* and *Metarhizium anisopliae*. Moreover, this strain encodes for genes involved in nitrogen fixation and sulfur metabolism, indicating that the bacteria make those essential nutrients available and enable *I. acuminatus* to convert plant material into energy more efficiently (Gonzáles-Dominici et al. 2021). González-Dominici et al. (2021) also found genes responsible for B-vitamin synthesis and siderophore production important for iron uptake. Another set of genes in this strain seems important for detoxifying pine defense-related metabolites (González-Dominici et al. 2021). Sequencing more bacterial genomes, different 'omics' approaches, and isotope-labeling experiments could provide more insights into bacterial roles for the beetles (Fabryová et al. 2018; García-Fraile 2018).

Natural enemies and their importance for population dynamics

Trophic interactions with natural enemies can affect the population dynamics of bark beetles. Natural enemies comprise parasitoids, predators and pathogens, including numerous arthropods, fungal and nematode species, and microbes (Wegensteiner et al. 2015).

Predators and parasitoids

The natural enemies of *I. acuminatus* and the co-occurring *T. piniperda* have been studied after a population outbreak in France (Herard and Mercadier 1996). Forty-five species (31 predatory and 14 parasitoid species) were detected. The generalists *Thanasimus formicarius, Rhizophagus depressus* and *Medetera* spp. were the three most abundant predators. Especially, *Medetera* spp. larvae were frequently observed in *I. acuminatus* galleries. The main parasitoid species of *I. acuminatus* were all polyphagous, and the most abundant were *Rhopalicus tutela* and *Rhopalicus brevicomis*, *Coeloides melanostigma*, *Dendrosoter middendorfi* and *Dendrosoter hartigii*, and *Spathius rubidus* (Herard and Mercadier 1996). In Poland, 20 species of hymenopteran parasitoids, 17 parasitic and predatory mites, ten predatory insects, one nematode and one entomopathogenic fungus were associated with *I. acuminatus* (Bałazy et al. 1987).

In the south-eastern Alps, six predatory species belonging to Diptera (*Zabrachia* spp. and *Medetera* spp.) and Coleoptera (*Corticeus linearis*, *Rizophagus* spp., one Staphylinidae species and one Nitidulidae species) were found.

Furthermore, 18 hymenopteran species belonging to Pteromalidae (72.2%), Braconidae (17.5%), Eurytomidae (9.7%) and Eupelmidae (0.6%) were associated with *I. acuminatus*. The most common species were *Metacolus unifasciatus*, *D. hartigii*, *Rhopalicus quadratus*, *Ropterocerus xylophagorum*, *Tomicobia acuminati*, *Dinosticus colon* and *Eurytoma arctica*. Some parasitoids are specialists on *I. acuminatus*, like the endoparasitoid *T. acuminati*. A detailed list of parasitoids and predators associated with *I. acuminatus* can be found in Kenis et al. (2004) and Wegensteiner et al. (2015).

Pathogens

Data on the pathogen community, i.e., fungi, bacteria, sporozoa and viruses, of *I. acuminatus,* are relatively scarce (Wegensteiner et al. 2015). A *Chytridiopsis* sp. (Microsporidia, Chytridiopsidae) was found in beetles from Austria, Czechia, Norway (Zitterer 2002), and *Chytridiopsis* cf. *typographi* in Bulgaria (Takov et al. 2007) and Turkey (Algi et al. 2016). These microsporidia develop in the cells of the midgut endothelium and spread throughout the midgut during spore maturation (Zitterer 2002). Other species found in *I. acuminatus* were *Gregarina* sp. (Apicomplexa, Gregrinidae) in Austria and Norway (Zitterer 2002) and *Gregariana* cf. *typographi* in Bulgaria (Takov et al. 2007). These organisms also destroy the midgut cells of their hosts by utilizing cell contents (Zitterer 2002). *Malamoeba scolyti* (Apicomplexa, Leipotrophidae) was also found in the midgut of *I. acuminatus* in Austria; this species destroys the microvilli and masses of cysts close to the tubule (Zitterer 2002). Moreover, a *Mattesia* sp. (Apicomplexa, Leipotrophidae) was reported from Austria (Zitterer 2002) and Turkey (Algi et al. 2016).

Fungal pathogens of *I. acuminatus* belong to the phylum Ascomycota, and most of them are generalists and pathogenic to many different insect species (Wegensteiner et al. 2015). *Beauveria bassiana* was associated with *I. acuminatus* in Poland (Bałazy et al. 1987) and is a common pathogen in many bark beetles (Wegensteiner et al. 2015). *Beauveria bassiana* and *Isaria farinosa* were not effective against *I. acuminatus* in an artificial inoculation experiment; however, these fungi were highly pathogenic to another pine bark beetle, *I. sexdentatus* (Draganova et al. 2007).

To our knowledge, no studies on viruses and pathogenic bacteria associated with *I. acuminatus* have been conducted. Further studies are needed to understand their possible role in the regulation of *I. acuminatus* populations.

Mites

Numerous bark beetle species are associated with various mite species that have different ecological roles. Hofstetter et al. (2015) listed over 250 known phoretic mite species associated with bark beetles. They can decrease health and reproductive success, affect beetle mortality and interact with other microbial symbionts (Hofstetter et al. 2015; Vissa and Hofstetter 2017). Mites can also vector nematodes, protozoa and fungi. Some mite species have a pocket on their exoskeleton for transporting fungal spores (named sporotheca; Hofstetter et al. 2015), which might be relevant for the transmission of bark beetle symbionts.

For *I. acuminatus*, only a few studies assessed the mite community, i.e., three mite species in Turkey (Cilbircioğlu et al. 2021), 17 mite species in Poland (Bałazy et al. 1987) and eight different mite species in China were found (Chang et al. 2017). For example, in Turkey the most abundant mite species in the galleries of *I. acuminatus* was *Proctolaelaps hystericoides,* known to feed on fungal spores. Also, *Dendrolaelaps quadrisetus,* which preys on nematodes (Kinn 1967), was found on the ventral abdomen of *I. acuminatus* (Cilbircioğlu et al. 2021) and was also observed feeding on eggs of *I. typographus* (Khaustov et al. 2018; Cilbircioğlu et al. 2021). *Ereynetes* sp. (also observed on *I. acuminatus* in Turkey) is a predatory mite species that feeds on other mites and nematodes and on eggs and immature stages of different arthropods (Kinn 1967; Cilbircioğlu et al. 2021). Phoretic mites, in combination with their beetle host, play an essential role in the transmission of blue-stain fungi, as described by Chang et al. (2017) in China (Table 2). For example, the ophiostomatoid fungus *Ophiostoma acarorum* was isolated from three mite species from four different bark beetle species, including *I. acuminatus.* This fungus was mostly isolated from mites, indicating that *O. acarorum* is a symbiont of mites rather than of bark beetles (Chang et al. 2017). To date, detailed studies of mite guilds on *I. acuminatus* are lacking. More knowledge about their influence on the life cycle of beetles and other associated organisms would be of high value.

Nematodes

The roles of bark beetle-associated nematodes are diverse and range from mutualism to parasitism. They can occur externally and internally, and some phytophagous nematodes use bark beetles only as vectors for transmission to new habitats (Grucmanova and Holusa 2013; Hofstetter et al. 2015). One putatively beneficial phoretic nematode, feeding on parasitic nematodes, vectored by *I. acuminatus* was mentioned by Rühm (1956) from Germany: *Micoletzkya buetschli acuminati* (Grucmanova and Holusa 2013). *Micoletzkya* species feed on fungi, bacteria or other microorganisms, and parasitic nematodes (Grucmanova and Holusa 2013; Susoy et al. 2013; Susoy and Herrmann 2014). Some of these beneficial nematodes are actively transmitted in specialized transport organs under the beetles' elytra (named

nematangia; Cardoza et al. 2006), but whether these are present in *I. acuminatus* is unknown.

In contrast to *Micoletzkya* spp., most parasitic nematodes of bark beetles are incapable of completing their life cycle only in a free-living state and are obligate parasites. Usually, they do not kill their hosts but reduce their health and modify behaviors, like flight patterns and emergence (Grucmanova and Holusa 2013; Hofstetter et al. 2015). Parasitic nematodes associated with *I. acuminatus* are *Contortylenchus acuminati*, *Cryptaphelenchus macrogaster acuminati*, *Parasitaphelenchus acuminati* and *Parasitorhabditis acuminati* (Rühm 1956; Meirmans et al. 2006; Nedelchev et al. 2008; Grucmanova and Holusa 2013). The severity of parasitism within a beetle population can vary greatly and depends on the geographic region and microclimate inside bark beetle galleries. Nematodes are susceptible to low temperatures and low humidity if they are in a free-living state. During the host's egg-laying period, they emerge from its body to infect the beetle's offspring. Rühm (1956) found that gut nematodes are more susceptible to cold exposure than body cavity nematodes. These results were confirmed for nematodes associated with *I. acuminatus* in Norway. There is no evidence, however, that sexual populations of *I. acuminatus* are more resistant to nematodes than asexual populations (Meirmans et al. 2006). Currently we lack detailed knowledge on the potential positive or negative effects of nematodes on *I. acuminatus* populations.

Evolutionary history

Ips comprises a total of 37 species found in the Northern Hemisphere, covering both North America and Eurasia, utilizing various conifer tree species as hosts (Cognato 2015). The primary host plant genera of *Ips* bark beetles are *Pinus*, *Picea* and *Larix*, although various other conifer genera are also colonized (Pfeffer 1995; Knížek 2011). Here, we analyzed the phylogenetic relationships among nearly all species of the genus *Ips*, i.e., 36 out of 37 species, using up to three molecular markers (COI, 16S and EF-1-alpha; *I. acuminatus*, except from Czechia) and *I. chinensis* only represented by COI (Fig. 3, Supplementary Information 1). Using our comprehensive phylogeny, we aimed to address two central questions on evolutionary trajectories in the whole genus: (i) host plant usage, (ii) ancestral geographic range, (iii) obligate fungal mutualism and (iv) parthenogenesis. Moreover, we use our phylogeny to understand some outstanding life-history traits of the focal species of this article, *I. acuminatus*.

A phylogeny was reconstructed with a Bayesian analysis using MrBayes software (Ronquist et al. 2012). Data were partitioned by codon position and 16S and independently analyzed with GTR + gamma + I model in two independent Monte Carlo runs for 20 million generations. Posterior probabilities were based on 30,002 trees after 25% burn-in. Our results clearly show that the monophyly of *Ips* is well supported with *Orthotomicus* as the sister clade, confirming previous work (Cognato and Vogler 2001; Cognato and Sun 2007; Cognato 2013). Within *Ips,* we recovered five main groups that are well supported with posterior probabilities above 95%. The sister clade to the remaining *Ips* spp. comprises three pine-infesting species, two species native to North America, *Ips emarginatus* and *Ips knausi*, and the European species *I. sexdentatus*. The clade, including all the other species, can be divided into four groups. At the base of this clade are the two pine-utilizing species, *I. acuminatus* and *I. chinensis*. *Ips acuminatus* has a Eurasian range, and *I. chinensis* is found in Asia, for example, in China, Thailand or Laos, but the distribution of the two species likely overlaps in Asia; the species status of *I. chinensis* was just recently confirmed (Knížek and Cognato 2017).

The majority of *Ips* species can be grouped in three clades, which are sister to *I. acuminatus* and *I. chinensis*: (i) a pine-utilizing, North American group (*Ips apache, Ips calligraphus, Ips lectonei, Ips cibricollis, Ips confusus, Ips hoppingi, I. paraconfusus, Ips montanus* and *Ips grandicollis*); (ii) five pine-infesting species native to North America (*I. avulsus, Ips integer, Ips plastographus, I. pini* and *Ips bonanseai*) and the Eurasian spruce bark beetle *Ips duplicatus*; and (iii) a diverse group covering the highest number of species with various spruce- and larch-infesting species from Eurasia (including major forest pests like *I. typographus* or *I. cembrae*; note that the one species not included here, the Asian larch bark beetle, *I. subelongatus*, was confirmed to be sister to *I. cembrae* (Stauffer et al. 2001 Cognato and Sun 2007), a pure spruce-utilizing group from North America (e.g., *I. borealis*) and finally, a diverse group with all three tree genera as primary host from Asia and North America (e.g., *Ips woodi* or *Ips schmutzenhoferi*).

This Bayesian analysis confirmed the relationships among *Ips* species and the level of confidence for each node found in previous studies (Cognato and Vogler 2001; Cognato and Sun 2007). By considering the two traits, i.e., host usage and native range, we propose that the ancestral state of *Ips* bark beetles was a pine-infesting species with a native range in the Holarctic region. The Ipini genera utilizing Pinaceae (*Ips*, *Orthotomicus*, *Pityogenes* and *Pityokteines*) originated from angiosperm-feeding species about 45 million years ago (Jordal and Cognato 2012). *Ips* species most likely started to diverge about 20 million years ago (Cognato 2015), accompanied by geographic expansion and host shifts. During this time, the genus *Pinus* expanded its range, and major diversification within *Ips* might have occurred about 10 million years ago (Keeley 2012; Cognato 2015). Additionally, aggregation pheromone specialization among species was another critical driver for speciation (Cognato et al. 1997;

Cognato 1998, 2015). As various nodes in the phylogeny of the genus *Ips* remain poorly resolved, future research, including genome-wide methods and fossil records, can help elucidate the evolutionary history of this interesting group of bark beetles.

The phylogenetic position of *I. acuminatus* has been recognized in previous studies (Cognato 2013). It formed a separate clade with *I. chinensis*, which is sister to most other species. This phylogenetic position could explain some of the outstanding life-history traits of *I. acuminatus*. For example, as mentioned above, *I. acuminatus* is the only *Ips* species with a prominent internal oral mycetangium, a spore-carrying organ that transports its fungal mutualist, suggesting a strong nutritional dependency (Francke-Grosmann 1952). This strong dependency is reflected by the beetle's performance, as developmental time either increases or the life cycle cannot be completed if the fungal symbiont is not present, which might happen in dry host tissue with unsuitable moisture conditions (Martin Schebeck, Eva Papek and Thomas Kirisits personal observation). This morphological adaptation only evolves in obligate beetle-fungus partnerships (Six and Biedermann 2023), underlining the importance of *O. macrosporum* for nutritional purposes.

The peculiar reproductive biology of *I. acuminatus*, i.e., sexual and asexual reproduction, is not unique to this species. It is also present in *I. tridens*, *I. borealis*, *I. pilifrons* and *I. perturbatus* and has been reported to be related to varying chromosome numbers in females (Lanier and Oliver 1966; Lanier and Kirkendall 1986). This trait most likely evolved independently within the genus at least twice (or might have been secondarily lost in other species).

Finally, future studies on the natural history have to distinguish between *I. acuminatus* and *I. chinensis*, as the status of the latter species has been confirmed only recently (Knížek and Cognato 2017), and some observations might no longer be valid, especially in regions where the two species overlap. Moreover, research on the fungal dependency of *I. chinensis* and the presence of an internal oral mycetangium is required to determine whether these adaptations occur only in *I. acuminatus*. Finally, *I. chinensis* should be tested for the presence of parthenogenesis.

Summary and outlook

Ips acuminatus shares many characteristics with other bark beetle species but is quite unique in certain traits and a lot of biological details still remain unknown. Like many other species in the genus *Ips,* it preferentially colonizes pines whereby it is among the medium aggressive, secondary species, i.e., given high populations it can kill weakened trees. *Ips acuminatus* is a typical polygamous bark beetle with gallery-founding males, but with unusually high harem sizes.

This may be caused by the frequent occurrence of asexual, male-parasitic strains of females, which is only known from *I. acuminatus* and another clade of North American *Ips* species. Within-gallery competition in these big harems might be reduced due to its mutualism with a nutritional fungus that is transmitted within a prominent internal oral mycetangium (unique among *Ips*), which allows offspring to develop on less substrate than other *Ips* without nutritional fungi. Similar to other bark beetles, our understanding of the role played by other symbiotic fungi, bacteria and natural enemies of *I. acuminatus* is limited. Here, we give an outlook on research fields that will contribute to a deeper understanding of this crucial pine bark beetle.

(1) Reproductive biology: Are asexual female strains purely parasitic or are there fitness advantages to sexual and asexual populations? How do sexual and asexual populations in the same spatiotemporal context exist over time? What are the ecological factors that select for the different reproductive modes? Is it true that the frequency of asexuals is higher under harsher temperature conditions and what is the reason for that? How common are asexuals in other species of *Ips*?

(2) Chemical ecology, tree defense mechanisms and host tree quality: Is there no primary attraction to host plants (no kairomone effect) in *I. acuminatus*? Is the common bark beetle anti-aggregation pheromone verbenone irrelevant for the chemical communication of *I. acuminatus*? Are there other anti-aggregation pheromones in this species? In addition, studies on the interactions with hosts will help to understand susceptibility of trees for beetle infestations. Do associated fungi emit volatiles that are relevant for the communication of *I. acuminatus* (as was shown in *I. typographus*; Kandasamy et al. 2023)?

(3) Population dynamics: What are the main drivers of *I. acuminatus* population outbreaks? What are the underlying mechanisms of the spot-like outbreak behavior? What makes some *Ips* species more aggressive than others? What is the relative role of beetles and fungal symbionts in killing trees? Can associated fungi, bacteria as well as natural enemies and pathogens (e.g., viruses, mites, nematodes) affect population dynamics (increase and break-down, particularly during epidemic phases) and how do they respond under different population densities? Do higher beetle densities lead to increased horizontal transmission of symbionts and may this weaken the nutritional beetle-fungus mutualism (as proposed for *I. typographus*; Biedermann et al. 2019)?

(4) Fungal dependency and interactions with other organisms: What species build the core bacterial and fungal community of *I. acuminatus*? What microbes are obli-

gate and what role (e.g., direct nutrition, detoxification, plant pathogenicity, pathogen defense) do they play? Besides *O. macrosporum*, are there other fungal species in the mycetangium of *I. acuminatus*? What species are the main causal agents for blue-staining of the sapwood? Do these microbes help to overcome tree defenses? Is there exchange of microbes among bark beetles colonizing the same tree? What are the main determinants of fungal communities that seem to vary within and between *I. acuminatus* populations? Are these beetles able to shape their fungal communities actively (i.e., promote beneficial over antagonistic species as known for ambrosia beetles; Diehl et al. 2022)?

(5) Abiotic factors affecting the life cycle: Detailed information on temperature, photoperiod and other abiotic environmental drivers for life-cycle regulation will not only be relevant to understand the beetle's spatiotemporal occurrence. It will also be important to develop risk assessment models to predict future outbreaks, under current and future climatic conditions.

Climate change, with a rise in average temperatures, uneven distribution of precipitation patterns and a higher frequency of extreme weather events, e.g., storms, heavy snowfalls and drought, could have positive and negative effects on *I. acuminatus* life history. On the positive side for beetles, due to higher average temperatures, winter mortality and the duration of a beetle generation could be reduced, resulting in higher population densities and higher voltinism. Additionally, more physiologically stressed trees might enable beetles to overcome tree defenses at lower densities leading to reduced intraspecific competition and thus increased fecundity (cf. Biedermann et al. 2019). On the negative side, there might be higher beetle mortality due to heat waves, or a delay of diapause induction could cause mortality in broods established late in the season entering the winter in immature stages (Stange and Ayres 2010; Bentz and Jönsson 2015; Pureswaran et al. 2018; Jactel et al. 2019). In a robust fungal mutualism, *I. acuminatus* may be more vulnerable to climate change compared to other bark beetles. This heightened sensitivity arises from the interdependence between the beetle and its nutritional fungus, *O. macrosporum*, both of which must adapt to altered environmental conditions. Notably, the optimal growth temperature for the nutritional fungus is around 25 °C, with slow growth observed at 30 °C and complete cessation at 35 °C (Dorothea Pöchlauer, Elisabeth Ritzer, Martin Schebeck and Thomas Kirisits, unpublished data). The potential consequences of these temperature-related constraints include a decline in the fitness of the beetle-fungus symbiosis as temperatures increase.

In essence, the repercussions may manifest as range shifts for *I. acuminatus* and its associated organisms, leading to shifts in ecological dynamics. Additionally, the compromised health of host trees, resulting from the diminished fitness of the beetle–fungus partnership, could contribute to altered patterns of tree mortality. This underscores the intricate and interconnected nature of species interactions within ecosystems and highlights the potential ecological consequences of climate-induced changes in a fungal mutualism scenario.

Finally, a deeper understanding of the life history of *I. acuminatus* can help to improve existing management strategies or develop novel ones. For example, data on the effects of abiotic environmental conditions on the beetle's phenology can improve timing of population monitoring or salvage and sanitation logging. Knowledge of beetle performance at different temperatures, including upper and lower limits of development and survival, may be used to assess its population dynamics under current and future climatic conditions. Information on its reproductive biology can inform spatiotemporal development of population densities. Studies on host usage behavior may unravel further insect–plant relationships and may be used in silvicultural planning. Interactions with symbionts of different trophic levels give insights into the performance of *I. acuminatus* but are also of economic relevance in the case of blue-stain fungi. Furthermore, understanding of the community and effectiveness of the beetles' natural enemies may contribute to its sustainable management. Finally, data on the communication within and among species (including olfactory signals) are the basis for a better understanding of the interactions between bark beetles, host plants and other organisms and are the basis for many management measures.

Author contributions Martin Schebeck conceived the structure and content of the article. Eva Papek and Elisabeth Ritzer drafted major parts of the manuscript; Thomas Kirisits led the section on fungal associates. Anthony I. Cognato provided the phylogeny of *Ips* species. Martin Schebeck and Anthony I. Cognato drafted the section on the evolutionary history. Eva Papek, Elisabeth Ritzer, Peter H.W. Biedermann, Anthony I. Cognato, Peter Baier, Gernot Hoch, Thomas Kirisits and Martin Schebeck provided input to the various sections of the manuscript. Martin Schebeck compiled the final draft. All authors revised and approved the final version of the manuscript.

Declarations

Competing interests The authors declare no financial or non-financial conflict of interests.

Consent to participate Not applicable.

Consent to publish Not applicable.

Ethics approval Not applicable.

References

Adams HD, Zeppel MJB, Anderegg WRL, Hartmann H, Landhäusser SM, Tissue DT, Huxman TE, Hudson PJ, Franz TE, Allen CD, Anderegg LDL, Barron-Gafford GA, Beerling DJ, Breshears DD, Brodribb TJ, Bugmann H, Cobb RC, Collins AD, Dickman LT, Duan H, Ewers BE, Galiano L, Galvez DA, Garcia-Forner N, Gaylord ML, Germino MJ, Gessler A, Hacke UG, Hakamada R, Hector A, Jenkins MW, Kane JM, Kolb TE, Law DJ, Lewis JD, Limousin J-M, Love DM, Macalady AK, Martínez-Vilalta J, Mencuccini M, Mitchell PJ, Muss JD, O'Brien MJ, O'Grady AP, Pangle RE, Pinkard EA, Piper FI, Plaut JA, Pockman WT, Quirk J, Reinhardt K, Ripullone F, Ryan MG, Sala A, Sevanto S, Sperry JS, Vargas R, Vennetier M, Way DA, Xu C, Yepez EA, McDowell NG (2017) A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. Nat Ecol Evol 1:1285–1291. https://doi.org/10.1038/s41559-017-0248-x
AFZ (2013) Waldschutz-Übersicht. AFZ-DerWald 7:4–7
AFZ (2014) Waldschutz-Übersicht. AFZ-DerWald 7:4–7
AFZ (2015) Übersicht Waldschutz 2014/15. AFZ-DerWald 7:10–13
AFZ (2016) Übersicht Waldschutz 2015/16. AFZ-DerWald 7:10–13
AFZ (2017) Übersicht Waldschutz 2016/17. AFZ-DerWald 7:12–15
AFZ (2018) Übersicht Waldschutz 2017/18. AFZ-DerWald 7:10–13
AFZ (2019) Übersicht Waldschutz 2018/19. AFZ-DerWald 7:10–13
AFZ (2020) Übersicht Waldschutz 2019/20. AFZ-DerWald 11:12–15
AFZ (2021) Übersicht Waldschutz 2020/21. AFZ-DerWald 9:12–15
AFZ (2022) Übersicht Waldschutz 2021/22. AFZ-DerWald 9:12–15
AFZ (2023) Übersicht Waldschutz 2022/23. AFZ-DerWald 9:12–15
Akbulut S, Stamps WT (2012) Insect vectors of the pinewood nematode: a review of the biology and ecology of *Monochamus* species. For Pathol 42:89–99. https://doi.org/10.1111/j.1439-0329.2011.00733.x

Algi G, Guner BG, Unal S, Yaman M (2016) Survey of pathogens and parasites of the engraver beetle *Ips acuminatus* (Gyllenhal, 1827)(Coleoptera: Curculionidae: Scolytinae) in Turkey. Acta Zool Bulg 68:127–130
Angilletta MJ (2009) Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, New York
Annila E (1969) Influence of temperature upon the development and voltinism of *Ips typographus* L. (Coleoptera, Scolytidae). Ann Zool Fenn 6:161–208
Aoshima K (1965) Studies on wood-staining fungi of Japan. Doctoral thesis, University of Tokyo
Bakke A (1968a) Ecological studies on bark beetles (Coleoptera: Scolytidae) associated with Scots pine (*Pinus sylvestris* L.) in Norway with particular reference to the influence of temperature. Medd Nor Skogforsok 21:441–602
Bakke A (1968b) Field and labratory studies on sex ratio in *Ips acuminatus* (Coleoptera: Scolytidae) in Norway. Can Entomol 100:640–648. https://doi.org/10.4039/Ent100640-6
Bakke A (1978) Aggregation pheromone components of the bark beetle *Ips acuminatus*. Oikos 31:184–188. https://doi.org/10.2307/3543561
Bałazy S, Michalski J, Katajczak E (1987) Contribution to the knowledge of natural enemies of *Ips acuminatus* Gyll. (Coleoptera; Scolytidae). Polish J Entomol 57:735–745
Bale JS (1993) Classes of insect cold hardiness. Funct Ecol 7:751–753
Barnes I, van der Nest A, Granados GM, Wingfield MJ (2022) Dothistroma needle blight. In: Asiegbu FO, Kovalchuk A (eds) Forest microbiology. Academic Press, Amsterdam, pp 179–199
Baturkin D, Davydenko K (2020) Ophiostomatoid fungi colonizing Scots pine (*Pinus sylvestris*) trees infested by *Ips acuminatus* in Sumy region (Ukraine). Belgorod State Technological University: 93–97
De Beer ZW, Seifert KA, Wingfield MJ (2013) A nomenclator for ophiostomatoid genera and species in the Ophiostomatales and Microascales. In: Seifert K, De Beer ZW, Wingfield MJ (eds) The ophiostomatoid fungi: expanding frontiers. CBS-KNAW Fungal Biodiversity Center, Utrecht, pp 245–322
Bentz BJ, Jönsson AM (2015) Modeling bark beetle responses to climate change. In: Vega FE, Hofstetter RW (eds) Bark beetles. Academic Press, San Diego, pp 533–553
Bentz BJ, Logan JA, Amman GD (1991) Temperature-dependent development of the mountain pine beetle (Coleoptera: Scolytidae) and simulation of its phenology. Can Entomol 123:1083–1094. https://doi.org/10.4039/Ent1231083-5
Biedermann PHW, Vega FE (2020) Ecology and evolution of insect–fungus mutualisms. Annu Rev Entomol 65:431–455. https://doi.org/10.1146/annurev-ento-011019-024910
Biedermann PHW, Müller J, Grégoire J-C, Gruppe A, Hagge J, Hammerbacher A, Hofstetter RW, Kandasamy D, Kolarik M, Kostovcik M, Krokene P, Sallé A, Six DL, Turrini T, Vanderpool D, Wingfield MJ, Bässler C (2019) Bark beetle population dynamics in the Anthropocene: challenges and solutions. Trends Ecol Evol 34:914–924. https://doi.org/10.1016/j.tree.2019.06.002
Bigler C, Bräker OU, Bugmann H, Dobbertin M, Rigling A (2006) Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. Ecosystems 9:330–343. https://doi.org/10.1007/s10021-005-0126-2
Blaschke M, Bußler H, Schmidt O (2008) Die Douglasie—(k)ein Baum für alle Fälle. LWF Wissen 59:57–61
Blumenstein K, Bußkamp J, Langer GJ, Schlößer R, Parra Rojas NM, Terhonen E (2021) *Sphaeropsis sapinea* and associated endophytes in Scots pine: interactions and effect on the host under variable water content. Front For Glob Change 4:655769. https://doi.org/10.3389/ffgc.2021.655769

Blumenstein K, Bußkamp J, Langer GJ, Terhonen E (2022) Diplodia tip blight pathogen's virulence empowered through host switch. Front Fungal Biol 3:939007. https://doi.org/10.3389/ffunb.2022.939007

Brattli JG, Andersen J, Nilssen AC (1998) Primary attraction and host tree selection in deciduous and conifer living Coleoptera: Scolytidae, Curculionidae, Cerambycidae and Lymexylidae. J Appl Entomol 122:345–352. https://doi.org/10.1111/j.1439-0418.1998.tb01511.x

Brodde L, Adamson K, Julio Camarero J, Castaño C, Drenkhan R, Lehtijärvi A, Luchi N, Migliorini D, Sánchez-Miranda Á, Stenlid J, Özdağ Ş, Oliva J (2019) Diplodia tip blight on its way to the north: drivers of disease emergence in Northern Europe. Front Plant Sci 9:1818. https://doi.org/10.3389/fpls.2018.01818

Bußkamp J, Blumenstein K, Terhonen E, Langer GJ (2021) Differences in the virulence of *Sphaeropsis sapinea* strains originating from Scots pine and non-pine hosts. For Pathol 51:e12712. https://doi.org/10.1111/efp.12712

Cardoza Y, Paskewitz S, Raffa K (2006) Travelling through time and space on wings of beetles: a tripartite insect–fungi-nematode association. Symbiosis 41:71–79

Chakraborty A, Ashraf MZ, Modlinger R, Synek J, Schlyter F, Roy A (2020) Unravelling the gut bacteriome of *Ips* (Coleoptera: Curculionidae: Scolytinae): identifying core bacterial assemblage and their ecological relevance. Sci Rep 10:18572. https://doi.org/10.1038/s41598-020-75203-5

Chang R, Duong TA, Taerum SJ, Wingfield MJ, Zhou X, de Beer ZW (2017) Ophiostomatoid fungi associated with conifer-infesting beetles and their phoretic mites in Yunnan, China. MycoKeys 28:19–64. https://doi.org/10.3897/mycokeys.28.21758

Chen S, Zhou A, Xu Y (2023) Symbiotic bacteria regulating insect–insect/fungus/virus mutualism. Insects 14(9):741. https://doi.org/10.3390/insects14090741

Chinellato F, Battisti A, Finozzi V, Faccoli M (2014) Better today but worse tomorrow: how warm summers affect breeding performance of a Scots pine pest. Agrochimica-Pisa 58:133–145

Christiansen E (1985) *Ceratocystis polonica* inoculated in Norway spruce: blue-staining in relation to inoculum density, resinosis and tree growth. Eur J For Pathol 15:160–167. https://doi.org/10.1111/j.1439-0329.1985.tb00880.x

Cilbircioğlu C, Kovač M, Pernek M (2021) Associations of phoretic mites on bark beetles of the genus *Ips* in the black sea mountains of Turkey. Forests 12:516. https://doi.org/10.3390/f12050516

Coeln M, Niu Y, Führer E (1996) Entwicklung von Fichtenborkenkäfern in Abhängigkeit von thermischen Bedingungen verschiedener montaner Waldstufen (Coleoptera: Scolytidae). Entomol Gen 21:37–54. https://doi.org/10.1127/entom.gen/21/1996/37

Cognato AI (2013) Molecular phylogeny and taxonomic review of Premnobiini Browne, 1962 (Coleoptera: Curculionidae: Scolytinae). Front Ecol Evol 1:1. https://doi.org/10.3389/fevo.2013.00001

Cognato AI (2015) Biology, systematics, and evolution of *Ips*. In: Vega FE, Hofstetter RW (eds) Bark beetles. Academic Press, San Diego, pp 351–370

Cognato AI, Sun JH (2007) DNA based cladograms augment the discovery of a new *Ips* species from China (Coleoptera: Curculionidae: Scolytinae). Cladistics 23:539–551. https://doi.org/10.1111/j.1096-0031.2007.00159.x

Cognato AI, Seybold SJ, Wood DL, Teale SA (1997) A cladistic analysis of pheromone evolution in *Ips* bark beetles (Coleoptera: Scolytidae). Evolution 51:313–318. https://doi.org/10.2307/2410987

Cognato AI, Vogler AP (2001) Exploring data interaction and nucleotide alignment in a multiple gene analysis of *Ips* (Coleoptera: Scolytinae). Syst Biol 50:758–780. https://doi.org/10.1080/106351501753462803

Cognato AI (1998) Molecular phylogenetics and evolutionary ecology of *Ips* bark beetles (Scolytidae). Doctoral Thesis, Berkeley, USA

Colineau B, Lieutier F (1994) Production of *Ophiostoma*-free adults of *Ips sexdentatus* Boern. (Coleoptera, Scolytidae) and comparison with naturally contaminated adults. Can Entomol 126:103–110. https://doi.org/10.4039/Ent126103-1

Colombari F, Battisti A, Schroeder LM, Faccoli M (2012) Life-history traits promoting outbreaks of the pine bark beetle *Ips acuminatus* (Coleoptera: Curculionidae, Scolytinae) in the south-eastern Alps. Eur J For Res 131:553–561. https://doi.org/10.1007/s10342-011-0528-y

Colombari F, Schroeder ML, Battisti A, Faccoli M (2013) Spatio-temporal dynamics of an *Ips acuminatus* outbreak and implications for management. Agr For Entomol 15:34–42. https://doi.org/10.1111/j.1461-9563.2012.00589.x

Coulson RN (1979) Population dynamics of bark beetles. Annu Rev Entomol 24:417–447. https://doi.org/10.1146/annurev.en.24.010179.002221

Croisé L, Lieutier F (1993) Effects of drought on the induced defence reaction of scots pine to bark beetle-associated fungi. Ann For Sci 50:91–97. https://doi.org/10.1051/forest:19930107

Croisé L, Lieutier F, Dreyer E (1998) Scots pine responses to number and density of inoculation points with *Leptographium wingfieldii* Morelet, a bark beetle-associated fungus. Ann For Sci 55:497–506. https://doi.org/10.1051/forest:19980408

Danks HV (1987) Insect dormancy: an ecological perspective. Biol Surv Canada (Terrestrial Arthropods), Ottawa

Davídková M, Doležal P (2019) Temperature-dependent development of the double-spined spruce bark beetle *Ips duplicatus* (Sahlberg, 1836) (Coleoptera; Curculionidae). Agr For Entomol 21:388–395. https://doi.org/10.1111/afe.12345

Davydenko K, Baturkin D (2020a) Ophiostomatoid fungi vectored by bark beetles and colonizing trees of *Pinus sylvestris* in Sumy region (Ukraine). Proc For Acad Sci Ukr 21:22–29

Davydenko K, Baturkin D (2020b) Pine engraver beetle *Ips acuminatus* as a potential vector of *Sphaeropsis sapinea*. For For Melior 136:149–156. https://doi.org/10.33220/1026-3365.136.2020.149

Davydenko K, Vasaitis R, Menkis A (2017) Fungi associated with *Ips acuminatus* (Coleoptera: Curculionidae) in Ukraine with a special emphasis on pathogenicity of ophiostomatoid species. Eur J Entomol 114:77–85. https://doi.org/10.14411/eje.2017.011

Davydenko K (2019) A comparative characteristic of fungal communities associated with *Ips acuminatus* in different regions of Ukraine. Proc For Acad Sci Ukr 18:118–128. https://doi.org/10.15421/411912

Davydenko K (2021) New insights into the role of phytopathogenic fungi vectored by pine bark beetles in pine decline. Proc Forest Acad Sci Ukr 23:9–16. https://doi.org/10.15421/412122

De Beer ZW, Procter M, Wingfield MJ, Marincowitz S, Duong TA (2022) Generic boundaries in the *Ophiostomatales* reconsidered and revised. Stud Mycol 101:57–120. https://doi.org/10.3114/sim.2022.101.02

Denlinger DL (2022) Insect diapause. Cambridge University Press, Cambridge

Diehl JMC, Kowallik V, Keller A, Biedermann PHW (2022) First experimental evidence for active farming in ambrosia beetles and strong heredity of garden microbiomes. Proc Royal Soc B 289:20221458. https://doi.org/10.1098/rspb.2022.1458

Dobbertin M, Wermelinger B, Bigler C, Bürgi M, Carron M, Forster B, Gimmi U, Rigling A (2007) Linking increasing drought stress to Scots pine mortality and bark beetle infestations. Sci World J 7:231–239. https://doi.org/10.1100/tsw.2007.58

Doležal P, Sehnal F (2007) Effects of photoperiod and temperature on the development and diapause of the bark beetle *Ips typographus*.

J Appl Entomol 131:165–173. https://doi.org/10.1111/j.1439-0418.2006.01123.x

Draganova S, Takov D, Doychev D (2007) Bioassays with isolates of *Beauveria bassiana* (Bals.) Vuill. and *Paecilomyces farinosus* (Holm.) Brown & Smith against *Ips sexdentatus* Boerner and *Ips acuminatus* Gyll. (Coleoptera: Scolytidae). Plant Sci 44:24–28

Eckenwalder JE (2009) Conifers of the world: the complete reference. Timber Press, Portland

EPPO (2023) *Bursaphelenchus xylophilus*. EPPO Bulletin 53:156–183. https://doi.org/10.1111/epp.12915

Fabryová A, Kostovčík M, Díez-Méndez A, Jiménez-Gómez A, Celador-Lera L, Saati-Santamaría Z, Sechovcová H, Menéndez E, Kolařík M, García-Fraile P (2018) On the bright side of a forest pest-the metabolic potential of bark beetles' bacterial associates. Sci Total Environ 619:9–17. https://doi.org/10.1016/j.scitotenv.2017.11.074

Faccoli M, Finozzi V, Colombari F (2012) Effectiveness of different trapping protocols for outbreak management of the engraver pine beetle *Ips acuminatus* (Curculionidae, Scolytinae). Int J Pest Manag 58:267–273. https://doi.org/10.1080/09670874.2011.642824

Ferrenberg S, Kane JM, Mitton JB (2014) Resin duct characteristics associated with tree resistance to bark beetles across lodgepole and limber pines. Oecologia 174:1283–1292. https://doi.org/10.1007/s00442-013-2841-2

Foit J, Čermák V (2014) Colonization of disturbed Scots pine trees by bark- and wood-boring beetles. Agr For Entomol 16:184–195. https://doi.org/10.1111/afe.12048

Francke-Grosmann H (1952) Über die Ambrosiazucht der beiden Kiefernborkenkäfer *Myelophilus minor* Htg. und *Ips acuminatus* Gyll. Medd Stat Skogsforsk 41:1–52

Francke-Grosmann H (1956) Zur Übertragung der Nährpilze bei Ambrosiakäfern. Sci Nat 43:286–287. https://doi.org/10.1007/BF00622498

Francke-Grosmann H (1963) Die Übertragung der Pilzflora bei dem Borkenkäfer *Ips acuminatus* Gyll.: Ein Beitrag zur Kenntnis der Ipiden-Symbiosen. J Appl Entomol 52:355–361. https://doi.org/10.1111/j.1439-0418.1963.tb02046.x

Francke-Grosmann H (1967) Ectosymbiosis in wood-inhabiting insects. Symbiosis 2:141–205. https://doi.org/10.1016/B978-1-4832-2758-0.50010-2

Frühbrodt T, Schebeck M, Andersson MN, Holighaus G, Kreuzwieser J, Burzlaff T, Delb H, Biedermann PHW (2024) Verbenone—the universal bark beetle repellent? Its origin, effects, and ecological roles. J Pest Sci 97:35–71. https://doi.org/10.1007/s10340-023-01635-3

Führer E, Chen ZY (1979) Zum Einfluß von Photoperiode und Temperatur auf die Entwicklung des Kupferstechers, *Pityogenes chalcographus* L. (Col., Scolytidae). Forstwiss Centbl 98:87–91. https://doi.org/10.1007/BF02743103

García-Fraile P (2018) Roles of bacteria in the bark beetle holobiont—how do they shape this forest pest? Ann Appl Biol 172:111–125. https://doi.org/10.1111/aab.12406

Gehrken U (1984) Winter survival of an adult bark beetle *Ips acuminatus* Gyll. J Insect Physiol 30:421–429. https://doi.org/10.1016/0022-1910(84)90100-8

Gehrken U (1985) Physiology of diapause in the adult bark beetle, *Ips acuminatus* Gyll., studied in relation to cold hardiness. J Insect Physiol 31:909–916. https://doi.org/10.1016/0022-1910(85)90024-1

Gehrken U (1989) Supercooling and thermal hysteresis in the adult bark beetle, *Ips acuminatus* Gyll. J Insect Physiol 35:347–352. https://doi.org/10.1016/0022-1910(89)90084-X

Gehrken U (1992) Inoculative freezing and thermal hysteresis in the adult beetles *Ips acuminatus* and *Rhagium inquisitor*. J Insect Physiol 38:519–524. https://doi.org/10.1016/0022-1910(92)90077-Q

Gehrken U (1995) Correlative influence of gut appearance, water content and thermal hysteresis on whole body supercooling point of adult bark beetles, *Ips acuminatus* Gyll. Comp Biochem Physiol Part A Mol Integr Physiol 112:207–214. https://doi.org/10.1016/0300-9629(95)00068-I

Gent CA, Wainhouse D, R. Day K, Peace AJ, J. G. Inward D (2017) Temperature-dependent development of the great European spruce bark beetle *Dendroctonus micans* (Kug.) (Coleoptera: Curculionidae: Scolytinae) and its predator *Rhizophagus grandis* Gyll. (Coleoptera: Monotomidae: Rhizophaginae). Agr For Entomol 19:321–331. https://doi.org/10.1111/afe.12212

González-Dominici LI, Saati-Santamaría Z, García-Fraile P (2021) Genome analysis and genomic comparison of the novel species *Arthrobacter ipsi* reveal its potential protective role in its bark beetle host. Microb Ecol 81:471–482. https://doi.org/10.1007/s00248-020-01593-8

Grégoire J-C, Evans H (2004) Damage and control of BAWBILT organisms an overview. In: Lieutier F, Day KR, Battisti A, Grégoire J-C, Evans HF (eds) Bark and wood boring insects in living trees in Europe, a synthesis. Springer, Dordrecht, pp 19–37

Grucmanova S, Holusa J (2013) Nematodes associated with bark beetles, with focus on the genus *Ips* (Coleoptera: Scolytinae) in central Europe. Acta Zool Bulg 65:547–556

Guérard N, Dreyer E, Lieutier F (2000) Interactions between Scots pine, *Ips acuminatus* (Gyll.) and *Ophiostoma brunneo-ciliatum* (Math.): estimation of the critical thresholds of attack and inoculation densities and effects on hydraulic properties in the stem. Ann For Sci 57:681–690. https://doi.org/10.1051/forest:2000149

Guérard N, Maillard P, Bréchet C, Lieutier F, Dreyer E (2007) Do trees use reserve or newly assimilated carbon for their defense reactions? A 13C labeling approach with young Scots pines inoculated with a bark-beetle-associated fungus (*Ophiostoma brunneo ciliatum*). Ann For Sci 64:601–608. https://doi.org/10.1051/forest:2007038

Hammond WM, Adams HD (2019) Dying on time: traits influencing the dynamics of tree mortality risk from drought. Tree Physiol 39:906–909. https://doi.org/10.1093/treephys/tpz050

Harrington TC (2005) Ecology and evolution of mycophagous bark beetles and their fungal partners. In: Vega FE, Blackwell M (eds) Insect-fungal associations ecology and evolution. Oxford University Press, New York, pp 257–291

Harrington TC, Batzer JC, McNew DL (2021) Corticioid basidiomycetes associated with bark beetles, including seven new *Entomocorticium* species from North America and *Cylindrobasidium ipidophilum*, comb. nov. Antonie Van Leeuwenhoek 114:561–579. https://doi.org/10.1007/s10482-021-01541-7

Hentschel R, Möller K, Wenning A, Degenhardt A, Schröder J (2018) Importance of ecological variables in explaining population dynamics of three important pine pest insects. Front Plant Sci 9:1667. https://doi.org/10.3389/fpls.2018.01667

Herard F, Mercadier G (1996) Natural enemies of *Tomicus piniperda* and *Ips acuminatus* (Col., Scolytidae) on *Pinus sylvestris* near Orleans, France: temporal occurrence and relative abundance, and notes on eight predatory species. Entomophaga 41:183–210. https://doi.org/10.1007/bf02764245

Hernández R, Pérez V, Sánchez G, Castellá J, Palencia J (2004) Ensayos de atracción y captura de *Ips acuminatus* (Coleoptera: Scolytidae). Ecología 18:35–52

Hernández R, Pérez V, Sánchez G, Castellá J, Palencia J, Gil J, Ortiz A (2007) Ensayos de trampeo de escolítidos perforadores subcorticales en pinares mediante el uso de feromonas. Ecología 21:43–56

Hlávková D, Doležal P (2022) Cambioxylophagous pests of Scots pine: ecological physiology of European populations—a review. Front For Glob Change 5. https://doi.org/10.3389/ffgc.2022.864651

Hofstetter RW, Dinkins-Bookwalter J, Davis TS, Klepzig KD (2015) Symbiotic associations of bark beetles. In: Vega FE, Hofstetter RW (eds) Bark beetles. Academic Press, San Diego, pp 209–245

Houston Durrant T, De Rigo D, Caudullo G (2016) *Pinus sylvestris* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz, de Rigo D, Caudullo G, Durrant TH, Mauri A (eds) European atlas of forest tree species. European Union, Luxembourg, pp. e016b094

Hunziker S, Begert M, Scherrer SC, Rigling A, Gessler A (2022) Below average midsummer to early autumn precipitation evolved into the main driver of sudden Scots pine vitality decline in the Swiss Rhône Valley. Front For Glob Change. https://doi.org/10.3389/ffgc.2022.874100

Hytteborn H, Maslov A, Nazimova D, Rysin L (2005) Boreal forests of Eurasia. In: Andersson F (ed) Ecosystems of the World. Elsevier, Amsterdam, pp 23–99

Isberg T, Linnakoski R, Sigurdsson BD, Kasanen R (2022) The pathogenicity of the blue stain fungus *Ophiostoma clavatum* in Scots pine seedlings. Icel Agric Sci 35:33–37. https://doi.org/10.16886/IAS.2022.04

Jactel H, Koricheva J, Castagneyrol B (2019) Responses of forest insect pests to climate change: not so simple. Curr Opin Insect Sci 35:103–108. https://doi.org/10.1016/j.cois.2019.07.010

Jaime L, Batllori E, Margalef-Marrase J, Pérez Navarro MÁ, Lloret F (2019) Scots pine (*Pinus sylvestris* L.) mortality is explained by the climatic suitability of both host tree and bark beetle populations. For Ecol Manag 448:119–129. https://doi.org/10.1016/j.foreco.2019.05.070

Jankowiak R, Solheim H, Bilański P, Marincowitz S, Wingfield MJ (2020) Seven new species of *Graphilbum* from conifers in Norway, Poland, and Russia. Mycologia 112:1240–1262. https://doi.org/10.1080/00275514.2020.1778375

Jankowiak R, Solheim H, Bilański P, Mukhopadhyay J, Hausner G (2022) *Ceratocystiopsis* spp. associated with pine- and spruce-infesting bark beetles in Norway. Mycol Prog 21:61. https://doi.org/10.1007/s11557-022-01808-x

Jankowiak R, Bilánski P, Taerum SJ, Trabka O, Hulbój R (2023) Ophiostomatatoid fungi (Ascomycota) associated with *Ips acuminatus* (Coleoptera) in eastern Poland. Dendrobiology 90:95–110. https://doi.org/10.12657/denbio.090.008

Jordal BH, Cognato AI (2012) Molecular phylogeny of bark and ambrosia beetles reveals multiple origins of fungus farming during periods of global warming. BMC Evol Biol 12:133. https://doi.org/10.1186/1471-2148-12-133

Kandasamy D, Zaman R, Nakamura Y, Zhao T, Hartmann H, Andersson MN, Hammerbacher A, Gershenzon J (2023) Conifer-killing bark beetles locate fungal symbionts by detecting volatile fungal metabolites of host tree resin monoterpenes. PLoS Biol 21:e3001887. https://doi.org/10.1371/journal.pbio.3001887

Keeley JE (2012) Ecology and evolution of pine life histories. Ann For Sci 69:445–453. https://doi.org/10.1007/s13595-012-0201-8

Kenis M, Wermelinger B, Grégoire JC (2004) Research on parasitoids and predators of Scolytidae—a review. In: Lieutier F, Day KR, Battisti A, Grégoire J-C, Evans HF (eds) Bark and wood boring insects in living trees in Europe, a synthesis. Springer, Dordrecht, pp 237–290

Khaustov AA, Klimov PB, Trach VA, Bobylev AN, Salavatulin VM, Khaustov VA, Tolstikov AV (2018) Review of mites (Acari) associated with the European spruce bark beetle, *Ips typographus* (Coleoptera: Curculionidae: Scolytinae) in Asian Russia. Acarina 26:3–79. https://doi.org/10.21684/0132-8077-2018-26-1-3-79

Kim M-S, Heinzelmann R, Labbé F, Ota Y, Elías-Román RD, Pildain MB, Stewart JE, Woodward S, Klopfenstein NB (2022) Armillaria root diseases of diverse trees in wide-spread global regions. In: Asiegbu FO, Kovalchuk A (eds) Forest microbiology. Academic Press, Amsterdam, pp 361–378

Kinn DN (1967) Notes on the life cycle and habits of *Digamasellus quadrisetus* (Mesostigmata: Digamasellidae). Ann Entomol Soc Am 60:862–865. https://doi.org/10.1093/aesa/60.4.862a

Kirisits T (2004) Fungal associates of European bark beetles with special emphasis on the Ophiostomatoid fungi. In: Lieutier F, Day KR, Battisti A, Grégoire J-C, Evans HF (eds) Bark and wood boring insects in living trees in Europe, a synthesis. Springer, Dordrecht, pp 181–236

Kirisits T (2010) Fungi isolated from *Picea abies* infested by the bark beetle *Ips typographus* in the Białowieża forest in north-eastern Poland. For Pathol 40:100–110. https://doi.org/10.1111/j.1439-0329.2009.00613.x

Kirisits T (2013) Dutch elm disease and other *Ophiostoma* diseases. In: Gonthier P, Nicolotti G (eds) Infectious forest diseases. CABI, Wallingford, UK, pp 256–282

Kirkendall LR (1983) The evolution of mating systems in bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae). Zool J Linn Soc 77:293–352. https://doi.org/10.1111/j.1096-3642.1983.tb00858.x

Kirkendall LR (1989) Within-harem competition among *Ips* females, an overlooked component of density-dependent larval mortality. Ecography 12:477–487. https://doi.org/10.1111/j.1600-0587.1989.tb00925.x

Kirkendall LR (1990) Sperm is a limiting resource in the pseudogamous bark beetle *Ips acuminatus* (Scolytidae). Oikos 57:80–87. https://doi.org/10.2307/3565740

Kirkendall LR, Stenseth NC (1990) Ecological and evolutionary stability of sperm-dependent parthenogenesis: effects of partial niche overlap between sexual and asexual females. Evolution 44:698–714. https://doi.org/10.1111/j.1558-5646.1990.tb05949.x

Knížek M (2011) Curculionidae: Scolytinae. In: Löbl I, Smetana A (eds) Catalogue of palaearctic Coleoptera. Apollo Books, Stenstrup, pp 204–251

Knížek M, Cognato AI (2017) Validity of *Ips chinensis* Kurentzov & Kononov confirmed with DNA data. Zool Syst 42:229–235. https://doi.org/10.11865/zs.201712

Knížek M, Liška J (2023) Výskyt lesních škodlivých činitelů v roce 2022 a jejich očekávaný stav v roce 2023. [Occurrence of forest damaging agents in 2022 and forecast for 2023]. Strnady, Výzkumný ústav lesního hospodářství a myslivosti, v. v. i., Zpravodaj ochrany lesa, Supplementum 2023, 86 pp.

Knížek M, Liška J, Véle A, Zahradník P, Lubojacký J (2021) Ochrana borovic e lesní (*Pinus sylvestris* L.) před podkorním a dřevokazným hmyzem. Certifikovaná metodika. Lesnický průvodce 9/2021: 120 pp.

Kohnle U, Kopp S, Francke W (1986) Inhibition of the attractant pheromone response in *Ips acuminatus* (Gyll.) by *I. sexdentatus* (Boerner) (Coleoptera, Scolytidae). J Appl Entomol 101:316–319. https://doi.org/10.1111/j.1439-0418.1986.tb00864.x

Kohnle U, Vité JP, Erbacher C, Bartels J, Francke W (1988) Aggregation response of European engraver beetles of the genus *Ips* mediated by terpenoid pheromones. Entomol Exp Appl 49:43–53. https://doi.org/10.1111/j.1570-7458.1988.tb02475.x

Kolařík M, Hulcr J (2023) *Geosmithia*—widespread and abundant but long ignored bark beetle symbionts. Mycol Prog 22:32. https://doi.org/10.1007/s11557-023-01880-x

Koštál V (2006) Eco-physiological phases of insect diapause. J Insect Physiol 52:113–127. https://doi.org/10.1016/j.jinsphys.2005.09.008

Koštál V, Doležal P, Rozsypal J, Moravcová M, Zahradníčková H, Šimek P (2011) Physiological and biochemical analysis of overwintering and cold tolerance in two central European populations

of the spruce bark beetle, *Ips typographus*. J Insect Physiol 57:1136–1146. https://doi.org/10.1016/j.jinsphys.2011.03.011

Koštál V, Miklas B, Doležal P, Rozsypal J, Zahradníčková H (2014) Physiology of cold tolerance in the bark beetle, *Pityogenes chalcographus* and its overwintering in spruce stands. J Insect Physiol 63:62–70. https://doi.org/10.1016/j.jinsphys.2014.02.007

Kovalchuk A, Wen Z, Sun H, Asiegbu FO (2022) *Heterobasidion annosum* s.l.: biology, genomics, and pathogenicity factors. In: Asiegbu FO, Kovalchuk A (eds) Forest microbiology. Academic Press, Amsterdam, pp 345–359

Krehan H (2011) Bark beetle attack on pines in a steep protection forest in Carinthia. Forstschutz Aktuell 53:2–4

Långström B (1983) Life cycles and shoot-feeding of the pine shoot beetles. Stud For Suec 163:1–29

Långström B, Hellqvist C, Ericsson A, Gref R (1992) Induced defence reaction in Scots pine following stem attacks by *Tomicus piniperda*. Ecography 15:318–327. https://doi.org/10.1111/j.1600-0587.1992.tb00042.x

Lanier GN, Kirkendall LR (1986) Karyology of pseudogamous *Ips* bark beetles. Hereditas 105:87–96. https://doi.org/10.1111/j.1601-5223.1986.tb00646.x

Lanier G, Oliver J Jr (1966) "Sex-ratio" condition: unusual mechanisms in bark beetles. Science 153:208–209. https://doi.org/10.1126/science.153.3732.208

Lee RE (2010) A primer on insect cold-tolerance. In: Denlinger DL, Lee JRE (eds) Low temperature biology of insects. Cambridge University Press, Cambridge, pp 3–34

Legg S (2021) IPCC, 2021: climate change 2021—the physical science basis. Interaction 49:44–450.

Lekander B, Bejer-Petersen B, Kangas E, Bakke A (1977) The distribution of bark beetles in the Nordic countries. Acta Entomol Fenn 32:1–36

Lévieux J, Cassier P, Guillaumin D, Roques A (1991) Structures implicated in the transportation of pathogenic fungi by the European bark beetle, *Ips sexdentatus* Boerner: ultrastructure of a mycangium. Can Entomol 123:245–254. https://doi.org/10.4039/Ent123245-2Lieutier

Lieutier F (2004) Host resistance to bark beetles and its variations. In: Lieutier F, Day KR, Battisti A, Grégoire J-C, Evans HF (eds) Bark and wood boring insects in living trees in Europe, a synthesis. Springer, Dordrecht, pp 135–180

Lieutier F, Garcia J, Yart A, Vouland G, Pettinetti M, Morelet M (1991) Ophiostomatales (Ascomycètes) associées à *Ips acuminatus* Gyll. (Coleoptera: Scolytidae) sur le pin sylvestre (*Pinus sylvestris* L.) dans le Sud-Est de la France et comparison avec *Ips sexdentatus* Boern. Agronomie 11:807–818

Lieutier F, Yart A, Salle A (2009) Stimulation of tree defenses by Ophiostomatoid fungi can explain attack success of bark beetles on conifers. Ann For Sci 66:801–801. https://doi.org/10.1051/forest/2009066

Linnakoski R, De Beer ZW, Niemelä P, Wingfield MJ (2012) Associations of conifer-infesting bark beetles and fungi in Fennoscandia. Insects 3:200–227. https://doi.org/10.3390/insects3010200

Linnakoski R, Jankowiak R, Villari C, Kirisits T, Solheim H, de Beer ZW, Wingfield MJ (2016) The *Ophiostoma clavatum* species complex: a newly defined group in the Ophiostomatales including three novel taxa. Antonie Van Leeuwenhoek 109:987–1018. https://doi.org/10.1007/s10482-016-0700-y

Liška J, Knížek M, Véle A (2021) Evaluation of insect pest occurrence in areas of calamitous mortality of Scots pine. Cent Eur For J 67:85–90. https://doi.org/10.2478/forj-2021-0006

Lobinger G (1994) Die Lufttemperatur als limitierender Faktor für die Schwärmaktivität zweier rindenbrütender Fichtenborkenkäferarten, *lps typographus* L. und *Pityogenes chalcographus* L. (Col., Scolytidae). J Pest Sci 67:14–17. https://doi.org/10.1007/bf01906563

Løyning MK (2000) Reproductive performance of clonal and sexual bark beetles (Coleoptera: Scolytidae) in the field. J Evol Biol 13:743–748. https://doi.org/10.1046/j.1420-9101.2000.00227.x

Løyning MK, Kirkendall LR (1996) Mate discrimination in a pseudogamous bark beetle (Coleoptera: Scolytidae): male *Ips acuminatus* prefer sexual to clonal females. Oikos 77:336–344. https://doi.org/10.2307/3546074

Masuya H, Kaneko S, Yamaura Y, Yamaoka Y (2009) Ophiostomatoid fungi isolated from Japanese red pine and their relationships with bark beetles. Mycoscience 50:212–223. https://doi.org/10.1007/s10267-008-0474-9

Mathiesen A (1950) Über einige mit Borkenkäfern assoziierte Bläuepilze in Schweden. Oikos 2:275–308. https://doi.org/10.2307/3564798

Mathiesen A (1951) Einige neue *Ophiostoma*-Arten in Schweden. Sven Bot Tidskr 45:203–232

Mathiesen-Käärik A (1953) Eine Übersicht über die gewöhnlichsten mit Borkenkäfern assoziierten Bläuepilze in Schweden und einige für Schweden neue Bläuepilze. Medd Stat Skogsforsk 43:1–74

Matías L, Jump AS (2012) Interactions between growth, demography and biotic interactions in determining species range limits in a warming world: the case of *Pinus sylvestris*. For Ecol Manag 282:10–22. https://doi.org/10.1016/j.foreco.2012.06.053

Mayers C, Harrington T, Biedermann P (2022) Mycangia define the diverse ambrosia beetle–fungus symbioses. In: Schultz TR, Gawne R, Peregrine PN (eds) The convergent evolution of agriculture in humans and insects. The MIT Press, Cambridge, pp 105–142

McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytol 178:719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x

Meirmans S, Skorping A, Løyning M, Kirkendall L (2006) On the track of the red queen: bark beetles, their nematodes, local climate and geographic parthenogenesis. J Evol Biol 19:1939–1947. https://doi.org/10.1111/j.1420-9101.2006.01153.x

Mota MM, Braasch H, Bravo MA, Penas AC, Burgermeister W, Metge K, Sousa E (1999) First report of *Bursaphelenchus xylophilus* in Portugal and in Europe. Nematology 1:727–734. https://doi.org/10.1163/156854199508757

Nedelchev S, Takov D, Pilarska D (2008) Parasitic and associated nematodes of bark beetles in Bulgaria. Acta Zool Bulg 1(2):83–91

Pérez G, Sierra J (2006) Eficacia de cebos atrayentes y trampas en el control de "Ips acuminatus" Coleoptera: Scolytidae. Boletín De Sanidad Vegetal Plagas 32:259–266

Pfeffer A (1995) Zentral-und westpaläärktische Borken-und Kernkäfer (Coloptera: Scolytidae, Platypodidae). Pro Entomologia, Naturhistorisches Museum Basel, Basel, Switzerland

Pineau X, David G, Peter Z, Sallé A, Baude M, Lieutier F, Jactel H (2017) Effect of temperature on the reproductive success, developmental rate and brood characteristics of *Ips sexdentatus* (Boern.). Agr For Entomol 19:23–33. https://doi.org/10.1111/afe.12177

Plewa R, Mokrzycki T (2017) Occurrence, biology, and economic importance of the sharp-dentated bark beetle *Ips acuminatus* (Gyllenhal, 1827) (Coleoptera, Curculionidae, Scolytinae) in Poland. Sylwan 161:619–629

Postner M (1974) Scolytidae (=Ipidae), Borkenkäfer. In: Schwenke W (ed) Die forstschädlinge Europas. Paul Parey, Hamburg, pp 334–482

Pureswaran DS, Roques A, Battisti A (2018) Forest insects and climate change. Curr For Rep 4:35–50. https://doi.org/10.1007/s40725-018-0075-6

Ragland GJ, Armbruster PA, Meuti ME (2019) Evolutionary and functional genetics of insect diapause: a call for greater integration. Curr Opin Insect Sci 36:74–81. https://doi.org/10.1016/j.cois.2019.08.003

Rebaudo F, Rabhi V-B (2018) Modeling temperature-dependent development rate and phenology in insects: review of major developments, challenges, and future directions. Entomol Exp Appl 166:607–617. https://doi.org/10.1111/eea.12693

Rennerfelt E (1950) Über den Zusammenhang zwischen dem verblauen des Holzes und den Insekten. Oikos 2:120–137. https://doi.org/10.2307/3564666

Ritzer E, Schebeck M, Kirisits T (2023) The pine pathogen *Diplodia sapinea* is associated with the death of large Douglas fir trees. For Pathol 53:e12823. https://doi.org/10.1111/efp.12823

Romeralo C, Botella L, Santamaría O, Diez JJ, Laflamme G (2023) *Gremmeniella abietina*: a loser in the warmer world or still a threat to forestry? Curr For Rep 9:332–349. https://doi.org/10.1007/s40725-023-00193-2

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst Biol 61:539–542. https://doi.org/10.1093/sysbio/sys029

Rühm W (1956) Die Nematoden der Ipiden. Veb Gustav Fischer Verlag, Jena, Parasitologische Schriftenreihe

Ryan K, Hurley BP (2012) Life history and biology of *Sirex noctilio*. In: Slippers B, de Groot P, Wingfield M (eds) The sirex woodwasp and its fungal symbiont. Springer, Dordrecht, pp 15–30

Saati-Santamaría Z, López-Mondéjar R, Jiménez-Gómez A, Díez-Méndez A, Větrovský T, Igual JM, Velázquez E, Kolarik M, Rivas R, García-Fraile P (2018) Discovery of phloeophagus beetles as a source of *Pseudomonas* strains that produce potentially new bioactive substances and description of *Pseudomonas bohemica* sp. nov. Front Microbiol 9:913. https://doi.org/10.3389/fmicb.2018.00913

Salt RW (1963) Delayed inoculative freezing of insects. Can Entomol 95:1190–1202. https://doi.org/10.4039/Ent951190-11

Sauvard D (2004) General biology of bark beetles. In: Lieutier F, Day KR, Battisti A, Grégoire J-C, Evans HF (eds) Bark and wood boring insects in living trees in Europe, a synthesis. Springer, Dordrecht, pp 63–88

Schebeck M, Schopf A (2017) Temperature-dependent development of the European larch bark beetle, *Ips cembrae*. J Appl Entomol 141:322–328. https://doi.org/10.1111/jen.12351

Schebeck M, Hansen EM, Schopf A, Ragland GJ, Stauffer C, Bentz BJ (2017) Diapause and overwintering of two spruce bark beetle species. Physiol Entomol 42:200–210. https://doi.org/10.1111/phen.12200

Schebeck M, Krumböck S, Schuler H, Stauffer C (2019) Are bacterial endosymbionts reproductive manipulators in the bark beetle *Ips acuminatus*? Mitt Dtsch Ges Allg Angew Ent 22:119–201

Schebeck M, Dobart N, Ragland GJ, Schopf A, Stauffer C (2022) Facultative and obligate diapause phenotypes in populations of the European spruce bark beetle *Ips typographus*. J Pest Sci 95:889–899. https://doi.org/10.1007/s10340-021-01416-w

Schebeck M, Schopf A, Ragland GJ, Stauffer C, Biedermann PHW (2023) Evolutionary ecology of the bark beetles *Ips typographus* and *Pityogenes chalcographus*. Bull Entom Res 113:1–10. https://doi.org/10.1017/S0007485321000353

Schüler S, Chakraborty D (2021) Limitierende Faktoren für den Douglasienanbau in Mitteleuropa im Klimawandel. Schweiz Z Forstwes 172:84–93. https://doi.org/10.3188/szf.2021.0084

Siitonen J (2014) *Ips acuminatus* kills pines in southern Finland. Silv Fenn 48(4):1145. https://doi.org/10.14214/sf.1145

Sinclair BJ, Coello Alvarado LE, Ferguson LV (2015) An invitation to measure insect cold tolerance: methods, approaches, and workflow. J Therm Biol 53:180–197. https://doi.org/10.1016/j.jtherbio.2015.11.003

Six DL (2012) Ecological and evolutionary determinants of bark beetle —fungus symbioses. Insects 3:339–366. https://doi.org/10.3390/insects3010339

Six DL (2013) The bark beetle holobiont: why microbes matter. J Chem Ecol 39:989–1002. https://doi.org/10.1007/s10886-013-0318-8

Six DL, Biedermann PHW (2023) Fidelity or love the one you're with? Biotic complexity and tradeoffs can drive strategy and specificity in beetle–fungus by-product mutualisms. Ecol Evol 13:e10345. https://doi.org/10.1002/ece3.10345

Six DL, Wingfield MJ (2011) The role of phytopathogenicity in bark beetle–fungus symbioses: a challenge to the classic paradigm. Annu Rev Entomol 56:255–272. https://doi.org/10.1146/annurev-ento-120709-144839

Six DL, Klepzig KD (2021) Context dependency in bark beetle-fungus mutualisms revisited: assessing potential shifts in interaction outcomes against varied genetic, ecological, and evolutionary backgrounds. Front Microbiol. https://doi.org/10.3389/fmicb.2021.682187

Solheim H, Krokene P, Långström B (2001) Effects of growth and virulence of associated blue-stain fungi on host colonization behaviour of the pine shoot beetles *Tomicus minor* and *T. piniperda*. Plant Pathol 50: 111–116 doi https://doi.org/10.1046/j.1365-3059.2001.00541.xStange

Stange EE, Ayres MP (2010) Climate change impacts: insects. eLS. https://doi.org/10.1002/9780470015902.a0022555

Stauffer C, Kirisits T, Nussbaumer C, Pavlin R, Wingfield JC (2001) Phylogenetic relationships between the European and Asian eight spined larch bark beetle populations (Coleoptera, Scolytidae) inferred from DNA sequences and fungal associates. Eur J Entomol 98:99–105

Stenseth NC, Kirkendall LR, Moran N (1985) On the evolution of pseudogamy. Evolution 39:294–307. https://doi.org/10.1111/j.1558-5646.1985.tb05667.x

Steyrer G, Cech TL, Furst A, Hoch G, Perny BR (2020) Waldschutzsituation 2019 in Österreich: Schaden durch Borkenkäfer weiter extrem hoch. Forstschutz Aktuell 64:33–44

Susoy V, Herrmann M (2014) Preferential host switching and codivergence shaped radiation of bark beetle symbionts, nematodes of *Micoletzkya* (Nematoda: Diplogastridae). J Evol Biol 27:889–898. https://doi.org/10.1111/jeb.12367

Susoy V, Kanzaki N, Herrmann M (2013) Description of the bark beetle associated nematodes *Micoletzkya masseyi* n. sp. and *M. japonica* n. sp. (Nematoda: Diplogastridae). Nematology 15:213–231. https://doi.org/10.1163/15685411-00002672

Takov DI, Doychev DD, Linde A, Atanasova Draganova S, Kirilova Pilarska D (2007) Pathogens of bark beetles (Curculionidae: Scolytinae) and other beetles in Bulgaria. Biologia 67:966–972. https://doi.org/10.2478/s11756-012-0086-x

Tauber MJ, Tauber CA, Masaki S (1986) Seasonal adaptations of insects. Oxford University Press, New York

Terhonen E, Hytönen T, Leino K, Ylioja T, Sutela S (2023) First report of *Diplodia sapinea* causing Diplodia tip blight on *Juniperus communis* subsp. *communis* in Finland. New Dis Rep 47:e12149. https://doi.org/10.1002/ndr2.12149

Thomas F, Rzepecki A, Werner W (2022) Non-native Douglas fir (*Pseudotsuga menziesii*) in central Europe: ecology, performance and nature conservation. For Ecol Manag 506:119956. https://doi.org/10.1016/j.foreco.2021.119956

Trägårdh I (1939) The forest insects of Sweden. Hugo Gebers Förlag, Stockholm

Tubby K, Adamčikova K, Adamson K, Akiba M, Barnes I, Boroń P, Bragança H, Bulgakov T, Burgdorf N, Capretti P, Cech T, Cleary M, Davydenko K, Drenkhan R, Elvira-Recuenco M, Enderle R, Gardner J, Georgieva M, Ghelardini L, Husson C, Iturritxa E, Markovskaja S, Mesanza N, Ogris N, Oskay F, Piškur B, Queloz V, Raitelaitytė K, Raposo R, Soukainen M, Strasser L, Vahalík P, Vester M, Mullett M (2023) The increasing threat to European forests from the invasive foliar pine pathogen *Lecanosticta acicola*. For Ecol Manag 536:120847. https://doi.org/10.1016/j.foreco.2023.120847

Vallet E (1981) Etude du dépérissement du pin sylvestre en région Centre et des principaux ravageurs scolytides associés: *Tomicus piniperda*, *Ips sexdentatus* et *Ips acumunatus* (Coleoptera, Scolytidae). Doctoral Thesis, Orléans, France

Villari C, Battisti A, Chakraborty S, Michelozzi M, Bonello P, Faccoli M (2012) Nutritional and pathogenic fungi associated with the pine engraver beetle trigger comparable defenses in Scots pine. Tree Physiol 32:867–879. https://doi.org/10.1093/treephys/tps056

Villari C, Tomlinson JA, Battisti A, Boonham N, Capretti P, Faccoli M (2013) Use of loop-mediated isothermal amplification for detection of *Ophiostoma clavatum*, the primary blue stain fungus associated with *Ips acuminatus*. Appl Environ Microbiol 79:2527–2533. https://doi.org/10.1128/aem.03612-12

Vissa S, Hofstetter RW (2017) The role of mites in bark and ambrosia beetle-fungal interactions. In: Shields VDC (ed) Insect physiology and ecology. InTech, Rijeka, pp 135–156

Vité JP, Bakke A, Renwick JAA (1972) Pheromones in *Ips* (Coleoptera: Scolytidae): occurence and production. Can Entomol 104:1967–1975. https://doi.org/10.4039/Ent1041967-12

Waalberg ME (2015) Fungi associated with three common bark beetle species in Norwegian Scots pine forest. Master Thesis, Ås, Norway

Wegensteiner R, Wermelinger B, Herrmann M (2015) Natural enemies of bark beetles: predators, parasitoids, pathogens, and nematodes. In: Vega FE, Hofstetter RW (eds) Bark beetles. Academic Press, San Diego, pp 247–304

Wermelinger B (2004) Ecology and management of the spruce bark beetle *Ips typographus*—a review of recent research. For Ecol Manag 202:67–82. https://doi.org/10.1016/j.foreco.2004.07.018

Wermelinger B, Seifert M (1998) Analysis of the temperature dependent development of the spruce bark beetle *Ips typographus* (L.) (Col., Scolytidae). J Appl Entomol 122:185–191. https://doi.org/10.1111/j.1439-0418.1998.tb01482.x

Wermelinger B, Seifert M (1999) Temperature-dependent reproduction of the spruce bark beetle *Ips typographus*, and analysis of the potential population growth. Ecol Entomol 24:103–110. https://doi.org/10.1046/j.1365-2311.1999.00175.x

Wermelinger B, Rigling A, Schneider Mathis D, Dobbertin M (2008) Assessing the role of bark- and wood-boring insects in the decline of Scots pine (*Pinus sylvestris*) in the Swiss Rhone valley. Ecol Entomol 33:239–249. https://doi.org/10.1111/j.1365-2311.2007.00960.x

Wermelinger B, Epper C, Kenis M, Ghosh S, Holdenrieder O (2012) Emergence patterns of univoltine and bivoltine *Ips typographus* (L.) populations and associated natural enemies. J Appl Entomol 136:212–224. https://doi.org/10.1111/j.1439-0418.2011.01629.x

Werren JH, Baldo L, Clark ME (2008) *Wolbachia*: master manipulators of invertebrate biology. Nat Rev Microbiol 6:741–751. https://doi.org/10.1038/nrmicro1969

Wilsterman K, Ballinger MA, Williams CM (2021) A unifying, eco-physiological framework for animal dormancy. Funct Ecol 35:11–31. https://doi.org/10.1111/1365-2435.13718

Yvon A, Wegensteiner R (2015) Studies on the development of *Tomicus piniperda* and *Tomicus minor* (Coleoptera, Curculionidae) depending on temperature. Mitt Dtsch Ges Allg Angew Ent 20:275–278

Zitterer P (2002) Antagonists of *Ips acuminatus* (Gyllenhall) with special consideration of pathogens. Diploma thesis, Vienna, Austria

Zlatković M, Keča N, Wingfield MJ, Jami F, Slippers B (2017) New and unexpected host associations for *Diplodia sapinea* in the Western Balkans. For Pathol 47:e12328. https://doi.org/10.1111/efp.12328

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.