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REVIEW
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Cambioxylophagous Pests of Scots Pine: Ecological Physiology of European Populations—A Review

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Climatic extremes have been gathering momentum since the 1880s and are believed to be a long-term factor increasing the mortality of Scots pine trees, *Pinus sylvestris* (L.) in Europe. Weather monitoring over the past 120 years shows that, in Central Europe, surface air temperatures grow at a rate of 0.18°C per decade. Many changes due to these abiotic stressors are already visible in the forests' canopy and biodiversity. But the influence of the rise in temperature and in precipitation deficiency brings one more player into this die-back scheme. Bark beetles, and their increasing outbreaks, are further agents acting to accelerate and expand the impacts of weather on trees. While *P. sylvestris* react to abiotic stressors by decreasing functions of the hydraulic system, mainly the defense system, for bark beetles, warming is a profitable condition. Various bionomy processes are modified: vegetation seasons prolong, larval growth and development rates accelerate, reproductive potential rises, and overwintering success increases. Thus, the insect populations grow, and the infestation pressure on weakened hosts intensifies. Finally, even species of small ecologic importance can cause extensive losses of forest cover. Furthermore, international trade and intercontinental transportation support the potential threat of spreading forest pests far away from their original geographic range. Together with climatic amelioration, pests may adapt to new conditions, establish new prosperous populations, disperse rapidly, and cause prodigious losses. However, detailed information about cambioxylophagous pests on *P. sylvestris* in Central Europe is still missing. The purpose of our review is to map the bionomy and behavior of six bark beetle species—in particular, the sharp-dentated bark beetle, *Ips acuminatus* (Gyllenhal, 1827), the six-toothed bark beetle, *Ips sexdentatus* (Börner, 1767), the common pine shoot beetle, *Tomicus piniperda* (Linnaeus, 1758), the lesser pine shoot beetle, *Tomicus minor* (Hartig, 1834), the pine shoot beetle, *Tomicus destruens* (Wollaston, 1865), the Mediterranean pine engraver, *Orthotomicus erosus* (Wollaston, 1857) (Coleoptera: Curculionidae: Scolytinae), and the steel-blue jewel beetle, *Phaenops cyanea* (Fabricius, 1775) (Coleoptera: Buprestidae)—on *P. sylvestris* in Central Europe, to compare and summarize the available data on European populations, and to try to propose ideas and directions for future research.

Keywords: Scots pine, bark beetles, bionomy, ecological physiology, climate change

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INTRODUCTION

The negative effects of climate change on forests have increased tree mortality and caused a global decline of forest cover worldwide in the last decade (Logan et al., 2003; Raffa et al., 2008; Allen et al., 2010, 2015; Lindner et al., 2010; Das et al., 2013). Overall global temperatures have increased between 1880 and 2012 by an average of 0.85°C (range 0.65–1.06°C). That means the temperature has risen about 0.08°C per decade since 1880 (Lindsey and Dahlman, 2022; Noaa, 2022). However, in the past 40 years, since 1981, respectively, the warming rate has doubled to 0.18°C per decade (Lindsey and Dahlman, 2022; Noaa, 2022). The IPCC (2007) has projected that total global increases to 2100 will be 1.8–4.0°C, while Walsh et al. (2014) suggest that warming for the same period in the US will be 3.0–9.0°C. Such changes may result in a shift in the hydroclimatic regime and extensive climate variability with intensive weather extremes, including a higher risk of flood, drought, fire, and pest breakouts (Schelhaas et al., 2003; Trenberth et al., 2003; Field and Barros, 2014).

The Scots Pine, *Pinus sylvestris* (L.)

The distribution area of *Pinus sylvestris* in Europe spans from Portugal to the Northern Arctic Circle, where this tree species covers an approximate area of 28 million hectares (Mátyás et al., 2004; Houston Durrant et al., 2016). In the United States, Scots pines are cultivated specifically for use as Christmas trees (Houston Durrant et al., 2016), or as erosion control elements (Sullivan, 1993). *P. sylvestris* is forgiving to the site and water supply, as its drought resistance is high (Cech and Perny, 1998; Vertui and Tagliaferro, 1998; Rigling and Cherubini, 1999; Houston Durrant et al., 2016). Nevertheless, since the 1990s a decline in *P. sylvestris* cover has been observed throughout its range (Martínez-Vilalta and Piñol, 2002; Hódar et al., 2003; Galiano et al., 2010). The dieback is mainly explained as a complex imbalance between trees and secondary pathogens induced by drought and groundwater shortage (Logan et al., 2003; Dobbertin et al., 2007; Wermelinger et al., 2008; Krams et al., 2012). The seriousness of the situation is evidenced by more than 150 million m^3 of pine wood harvested in Austria (Cech and Perny, 1998), Italy (Vertui and Tagliaferro, 1998; Vacchiano et al., 2011), Switzerland (Dobbertin et al., 2005; Bigler et al., 2006; Wermelinger et al., 2008), Southern France (Thabeet et al., 2009), Spain (Galiano et al., 2010), and Czechia (Lubojacký et al., 2019).

The Cambioxylophagous Pest Species Spectrum and Their Aggressivity

Weakened trees are most frequently attacked by species from the family Curculionidae, subfamily Scolytinae, and genera *Ips* and *Tomicus* (Lieutier et al., 2004). However, other pests from the family Buprestidae (the steelblue jewel beetle, *Phaenops cyanea,* Fabricius, 1775) and Cerambycidae may also cause significant damage (Wermelinger et al., 2008; Foit and Čermák, 2014).

The aggressivity potential is characterized by developmental rate, voltinism, fecundity, and host tree defoliation status. Species with an aggregation pheromone and whose above-named parameters are high usually have the capability to attack and kill healthy trees, and thus are considered primary pests. Conversely, species utilizing the products of wood decaying processes will most likely be secondary pests, preferring weakened trees (Escherich, 1914; Lieutier et al., 2004, 2009; Wermelinger et al., 2008; Foit and Čermák, 2014). However, climate warming invigorates the bark beetles' aggressivity, which means that previously harmless or economically unimportant species are becoming more aggressive and causing serious damage to their hosts (Gaylord et al., 2013; Netherer et al., 2015; Pešková et al., 2016).

The Effect of Temperature and Drought on Trees and Insects

Tree decline is a process during which abiotic and biotic factors cause gradual disintegration of forest cover (Manion, 1981; Thomas et al., 2002; Ostry et al., 2011). Basically, three factors operating progressively play a role at different spatio-temporal scales (Manion, 1981). Firstly, long-term abiotic stressors (e.g., extreme droughts and high temperatures) weaken the trees (Manion, 1981; Dobbertin et al., 2007; Anderegg et al., 2015), which causes cavitation, xylem dysfunction, a limitation of some metabolic processes, and reduces the natural defense of trees against pests through resin channels (Sperry and Tyree, 1988; Hanson and Weltzin, 2000; McDowell et al., 2011; Kelsey et al., 2014; Sangüesa-Barreda et al., 2015). Further decline is influenced by short-term abiotic or biotic factors working synergistically (Anderegg et al., 2015; Gea-Izquierdo et al., 2019). Trees suffering from the action of these stressors accumulate and produce volatile substances, mainly ethanol and terpenoids, which in combination with aggregation pheromones, might attract opportunistic insect species and further weaken host trees (Pitman et al., 1975; Schroeder and Lindelöw, 1989; Gallego et al., 2008; Miller and Rabaglia, 2009; Lingren et al., 2012; Kolb et al., 2016). The third and final contributor to tree mortality is generally some biotic factor (Oliva et al., 2013; Gea-Izquierdo et al., 2019).

Drought also contributes substantially to the link between host and pest. In principle, drought stress actively modulates tree physiology on basic chemical levels. Alterations in trees' metabolic pathways may take different forms (e.g., regulation of carbon fixation and storage, fatty acid biosynthesis, level and overall composition of secondary metabolites) (Farquhar et al., 1982; Ferrio et al., 2003; Flexas et al., 2007; Moreira et al., 2009; Sampedro et al., 2011; Moreno-Gutiérrez et al., 2012; Fox et al., 2018; López-Goldar et al., 2018; Suárez-Vidal et al., 2019). In addition, alterations might be induced by trees to fight the drought (Carmona et al., 2011; Suárez-Vidal et al., 2019): for example, changes in nutrient content, lignification, thickening of resin canal density, cavitation, hydraulic conductivity (narrowing tracheids or creating pits), or decreases in water content (Gaylord et al., 2013; Hereş et al., 2014; Camarero et al., 2015; Anderegg and HilleRisLambers, 2016; Suárez-Vidal et al., 2019). The water deficit reduces tree plasticity and their ability to respond to pest attacks (Suárez-Vidal et al., 2019). Therefore, host survival is highly dependent on the intensity and duration of the stresses occurring together (Ramegowda and Senthil-Kumar, 2015), as well as species-specific resistance ability (Arango-Velez et al., 2016; Lusebrink et al., 2016).

Insects further profit from climate change as growing season temperatures largely affect all of their life processes, including metabolism and reproduction, developmental rate, mortality of progeny, and voltinism. Temperature also synchronizes spring emergence, and thus the mass attack, which contributes to successful infestation of host trees (Régnière and Bentz, 2007; Powell and Bentz, 2009; Bentz et al., 2010; Weed et al., 2013). The Mediterranean and North-Eastern Europe are considered primary hot spots, where global warming will advance the positive feedback response to pest populations' behavior (Giorgi, 2006). Moreover, the combination of beneficial conditions with an ample supply of susceptible, and nutritionally optimal food sources often helps to shift the aggressivity of bark beetle species from the endemic to epidemic threshold (Raffa et al., 2008; Gaylord et al., 2013). Based on future climate predictions, an increase in the extent, severity, and frequency of insect outbreaks, as well as the magnitude of tree mortality events, is expected (Allen et al., 2010). Pest range has usually been defined as either "primary-secondary" or "epidemic-endemic," in connection to aggressivity and ability to multiply (Furniss and Carolin, 1977; Manion, 1981). This type of characterization includes the effect of drought stress only peripherally. A more suitable range definition seems to be the "stress compounders-stress confounders" spectrum (Trugman et al., 2021). This scope better characterizes the interactions between species and biotic agents, as it is based on a wider range of factors (i.e., drought stress, stress physiology, pest activity, and preferences) contributing to tree mortality. While most of the reviewed species act as stress compounders and kill the most stressed trees, *Dendroctonus spp.* bark beetles act as stress confounders that attack the largest hosts regardless of their physiological conditions (Trugman et al., 2021).

Climate changes may also shift the distribution areas of numerous insect species (Parmesan et al., 2011). Shifting of an area's characteristic temperature limits and the beetles' prompt reaction to the climatic amelioration might facilitate their migration to new ecosystems, higher latitudes, and higher elevations (MacLean, 1983; Ayres and Scriber, 1994; Ayres and Lombardero, 2000; Thuiller et al., 2008; Netherer and Schopf, 2010; Parmesan et al., 2011; Buotte et al., 2017; Lantschner et al., 2017).

Studies that have delt with bark beetles in relation to *P. sylvestris* predominantly include topics like voltinism (e.g., Vité et al., 1974; Hernández Hernández et al., 2004; Pérez and Sierra, 2006; Sarıkaya, 2008; Özcan, 2011; Colombari et al., 2012), development (e.g., Jactel and Lieutier, 1987; Özcan, 2011; Péter, 2014), diapause and cold hardiness (e.g., Bakke, 1968; Gehrken, 1984, 1985, 1989, 1995; Hernández Hernández et al., 2004; Pérez and Sierra, 2006; Colombari et al., 2012), and olfactory communication (e.g., Bakke, 1978; Byers et al., 1985; Lanne et al., 1987; Kohnle, 2004; Romón et al., 2017). Novel methods of forest protection and pest management have been rarely tested (e.g., Colombari et al., 2012, 2013; Faccoli et al., 2012; Chinellato et al., 2014). Unfortunately, our current knowledge of the behavior, migration pathways, and pest status of many species is gradually changing due to global climate changes. Therefore, the aim of this review is to provide an overview of the available information on the most harmful pests of Scots pines with regard to differences between their populations, and to point out the gaps in our knowledge of their bionomy. The above-named species with considerable ecological and economical influence, include the sharp-dentated bark beetle *Ips acuminatus* (Gyllenhal, 1827), the six-toothed bark beetle, *Ips sexdentatus* (Börner, 1767), the common pine shoot beetle, *Tomicus piniperda* (Linnaeus, 1758), the lesser pine shoot beetle, *Tomicus minor* (Hartig, 1834), the pine shoot beetle, *Tomicus destruens* (Wollaston, 1865), and the steel-blue jewel beetle, *Phaenops cyanea* (Fabricius, 1775).

Cambioxylophagous Pests

This group unites pests that can be characterized by feeding on the inner bark, destroying the cambial tissues, or even boring deeply into the sap- and heartwood (Bouget et al., 2005; Sallé et al., 2014). Typical representatives belong in the families Curculionidae (Scolytinae), Buprestidae, and Cerambycidae (Bouget et al., 2005; Sallé et al., 2014).

The Sharp-Dentated Bark Beetle, Ips acuminatus (Gyllenhal, 1827)

According to the BAWBILT (Bark and Wood Boring Insects in Living Trees in Europe) database, *I. acuminatus* is one of the most aggressive species in Europe, as the damage caused by its outbreaks between 1990–2000 reached almost 13 million m^3 of wood (Grégoire and Evans, 2004; Gilbert and Sauvard, 2007; Foit and Čermák, 2014). Beetles develop in the thin bark of the crown or branches of *P. sylvestris* and other pine species, and transfer blue stain fungi from the genus *Opisthostoma,* causing growth disorders, crown thinning, and ultimately, death of the host tree (Mathiesen, 1950; Lieutier et al., 1991; Villari, 2012). Consequently, an enormous decline of *P. sylvestris* monocultures has been recorded throughout Europe (Bakke, 1968; Lieutier et al., 1991; Villari, 2012; Siitonen, 2014).

Distribution. This species extends from Northern Spain through the Fenno-Scandinavian region, from Siberia to China, and through the Korean peninsula to Japan (Wood and Bright, 1992; Bright and Skidmore, 2002; Siitonen, 2014). However, reproductive success is affected by low temperatures, limiting the distribution area (Bakke, 1968). Destructive outbreaks of this species have recently been reported from Slovakia, Germany, Switzerland, Romania, Spain, the Italian and Swiss Alps, Finland, and Czechia (Švestka and Wiesner, 1997; Grégoire and Evans, 2004; Wermelinger et al., 2008; Colombari et al., 2013; Siitonen, 2014). Since this species is well-adapted to cold conditions, the rise in temperature thresholds might enable this beetle to spread northerly. Additionally, survival ability will increase, supporting the growth of hot spots, which will cause extensive damage.

Life Cycle and Reproduction. *Ips acuminatus* emerges in temperatures above 14°C (Bakke, 1968; Colombari et al., 2012), and the optimum temperature for spring swarming is 18°C (Bakke, 1968; Lekander et al., 1977; Hernández Hernández et al., 2007). Males colonize the upper parts of trunks and branches with thin, smooth bark and phloem thickness about 2-3 mm (Bakke, 1968). After creating a frass-free nuptial chamber, about 0.25 cm^2 in size, males produce aggregation pheromone to attract both sexes to the tree (Bakke, 1968). Polygynous males usually mate with 1–7 females, but it can be up to 12 females (Bakke, 1968; Kirkendall, 1990; Løyning and Kirkendall, 1996; Colombari et al., 2012). Unmated females, 10–20% of the population, colonize uninfested trees where they bore maternal galleries. Mated females bore maternal galleries radially from the nuptial chamber and parallel to the trunk (Kirkendall, 1990). Males protect the entrance hole against other males until mid-June (Bakke, 1968). The length of maternal galleries is significantly correlated with population density and reaches 1–11 cm (Colombari et al., 2012). First, eggs are laid at a distance shorter than 1 cm, alternating on either side of the maternal gallery. On average, each female deposits 4-16 eggs (Colombari et al., 2012). Newly hatched larvae bore larval galleries perpendicular to the maternal ones. Colombari et al. (2012) recorded low survival of sub-imaginal stages, and only around 41% of larvae, 21% of pupae, and 65% of young progeny finished the development to adulthood. However, up to 94% of the progeny successfully completed development in Norway (Kirkendall, 1989).

Two types of female genotypes were recorded in the *I. acuminatus*–sexually mating diploids and pseudogamous triploids. Pseudogamous females reproduce parthenogenetically, but they require mating with males as an initial trigger for embryogenesis. Thus, males' genetic information isn't transmitted to the genome of their offspring, and they produce exclusively female progeny. Since triploid offspring have up to 47.3% higher survival than the offspring of sexual mating, pseudogamous females may contribute considerably to the population density in newly colonized areas (Løyning, 2000).

Voltinism. While the Scandinavian populations of *I. acuminatus* are univoltine (Bakke, 1968), the Central and Southern European ones are bivoltine (Hernández Hernández et al., 2004; Colombari et al., 2012). Although Kirkendall (1990) experiments showed that 23–56% of galleries are nuptial chamber- and male-free, some authors believe that females do not re-emerge to establish sister broods (Pérez and Sierra, 2006). In multivoltine populations, reproductive development continues until the shortening of daylength in late summer induces facultative diapause (Gehrken, 1985).

Diapause and Overwintering. Once the photoperiodic signal is perceived at the edge of the vegetation season, adults start to prepare for overwintering. Flight activity decreases, metabolism slows down, reproduction and ovarian development is ceased, and beetles actively search for a suitable overwintering microhabitat (Gehrken, 1985). The majority of beetles overwinter under the bark of standing trees. Univoltine populations stay in the substrate where they developed; whereas individuals from multivoltine populations may change hosts and infest new trees in the surroundings. However, callow beetles cannot reproduce at the end of the season, as their mating organs are immature (Gehrken, 1985). Overwintering in soil litter under infested trees or in fallen branches has been reported in some Central and Southern European populations (Bakke, 1968; Gehrken, 1985; Hernández Hernández et al., 2004; Pérez and Sierra, 2006; Colombari et al., 2012).

During autumn, facultative diapause intensifies, and ovary development is suspended at the level of germ cells in germarium (Doležal and Sehnal, 2007). In December, previtellogenesis and ovary development is restored. Later, during January, metabolism increases, and diapause is terminated. Post-diapause quiescence gradually terminates with rising spring temperatures and lasts until the end of April (Gehrken, 1985).

Diapause development is tightly connected with mechanisms that increase cold hardiness. Starting in autumn, *I. acuminatus* accumulates energetic reserves and cryoprotectants, decreases water content, and empties the guts. Increased amounts of trehalose, and cryoprotective compounds such as ethylene glycol, mannitol, sorbitol, dulcitol, and anti-freeze proteins are synthesized to protect body tissues from ice crystal formation causing lethal injuries (Gehrken, 1984, 1985, 1989, 1992, 1995). Moreover, a sophisticated exoskeleton structure with pores of only about $6.19*10^{-22}$ mm in diameter, shields the body from ice crystals penetrating through the body surface (Gehrken, 1992). All these adaptations lower the risk of freezing and increase the chance of successful overwintering. Studies of the supercooling point (SCP—the temperature when body liquids freeze) in *I. acuminatus* report very low temperatures of −35°C (Gehrken, 1984, 1985, 1995).

The Six-Toothed Bark Beetle, Ips sexdentatus (Börner, 1767)

Ips sexdentatus is an example of a secondary pest that prefers weakened or disturbed pines, even though occurrences of local outbreaks after abiotic disturbances followed by spread to healthy stands have recently increased (Etxebeste et al., 2013).

Their preferred hosts are various species of pines (*Pinus* spp.) as well as spruces (*Picea* spp.) in Asia. Some authors have also reported attacks of firs (*Abies* spp.) and larches (*Larix* spp.) (Chararas, 1962). In Turkey and Georgia, *I. sexdentatus* causes extensive dieback of the Caucasian spruce [*Picea orientalis* (L.)] (Schimitschek, 1944; Lozovoj, 1966; Özcan, 2011).

Distribution. The distribution area of this Eurasian species spans from Portugal through Central and Northern Europe, from the Balkans to Turkey, Russia, China, South-Eastern Asia, and Japan (Jonášová and Prach, 2004; Knížek et al., 2020). Rising temperatures in Europe facilitate the occurrence of natural disturbance and create suitable living conditions for *I. sexdentatus,* which might lead to an increase in the generation number or extra sister broods.

Life Cycle and Reproduction. Spring swarming starts in late April or early May when temperatures reach 20°C (Özcan, 2011, 2017). Males of *I. sexdentatus* colonize weakened trees and prefer sections where bark thickness reaches 5–15 mm (Bouhot et al., 1987; Markalas, 1997). Males create a nuptial chamber and produce an aggregational pheromone (ipsdienol) to attract 1–5 females to copulate with (Vité et al., 1974; Francke et al., 1986; Kohnle et al., 1992; Etxebeste and Pajares, 2011). Maternal galleries are oriented parallel to the trunk axis, and their length can reach up to 1 m. Each female deposits ∼40 eggs on both sides of the maternal gallery at a density of around 2 eggs/cm (Jactel and Lieutier, 1987). Infestation density is negatively correlated with the length of maternal galleries (Jactel and Lieutier, 1987).

After hatching, larvae feed on the phloem and build galleries perpendicular to the maternal gallery. The sex ratio of offspring is 1:1, and more than 80% of females re-emerge to establish sister broods (Jactel and Lieutier, 1987).

Voltinism. Voltinism of *I. sexdentatus* is largely temperature dependent (Vité et al., 1974; Sarıkaya, 2008; Özcan, 2011). While populations in Northern Europe are univoltine, Central European populations are bivoltine and in the areas with hot, long summers (e.g., the Mediterranean), 4–6 generations may occur (Chararas, 1962; Vallet, 1981; Sierra and Martín, 2005; Péter, 2014).

Overwintering. Adults of *I. sexdentatus* overwinter under the bark of standing or fallen trees (Chararas, 1962; Lévieux et al., 1985). Their limits for successful winter survival are relatively high, as the average SCP in adults is −19°C. Sub-adult stages rarely overwinter and suffer higher mortality. The SCP of larvae was −9°C, and the only stage reported to finish development the next spring were pupae (Chararas, 1962; Bakke, 1968; Lévieux et al., 1985).

The Common Pine Shoot Beetle, Tomicus piniperda (Linnaeus, 1758)

Tomicus piniperda is a secondary pest of standing weakened pine trees and a primary pest of annual young shoots, causing substantial disturbance to the photosynthetic apparatus (Långström and Hellqvist, 1991; Långström et al., 2001; Foit and Čermák, 2014). Extensive feeding during outbreaks can lead to disruption or complete cessation of growth, and rarely, even to the host's death (Långström and Hellqvist, 1991; Långström et al., 2001). Regeneration after defoliation is a long-lasting process accompanied by higher sensitivity to other pathogens (Långström et al., 1990).

Tomicus piniperda prefers the lower parts of trunks, with thicker bark and phloem, of trees stressed by drought or fungal infections (Annila et al., 1999; Långström et al., 2001; Sikström et al., 2011). Its main host tree is *P. sylvestris*. Their occurrence has also been recorded on other pine species, such as black pine [*Pinus nigra* (J. F. Arnold)], maritime pine [*Pinus pinaster* (Aiton)], white pine [*Pinus strobus* (L.)], red pine [*Pinus resinosa* (Aiton)], and Jack pine [*Pinus banksiana* (Lamb.)], as well as Douglas firs [*Pseudotsuga menziesii* (Mirb.) Franco], spruces (*Picea* spp.), and larches (*Larix* spp.) (Browne, 1968; Bright and Skidmore, 1997; Siegert and McCullough, 2001).

Distribution. The distribution range of *T. piniperda* reaches from Portugal through Europe to Asia and Japan. Its northern border copies the range of *P. sylvestris*, and in the south, it spans to north Africa (Browne, 1968; Lekander et al., 1977). Climate change not only allowed for continental population mixing and re-colonizations during the postglacial age, resulting in high genetic divergence among European populations, but also allowed for intercontinental moves. The increasing abundance of common shoot pine beetle has been closely monitored in North America, where this species was introduced in the 1990s and became an invasive pest (Czokajlo et al., 1997; Annila et al., 1999; Borkowski, 2001; Öhrn et al., 2018). Moreover, their high adaptability to regional conditions alters the populations' bionomy (Horn et al., 2009). Based on this information, prediction models of potentially endangered areas have been made (Horn et al., 2012). The enormous versatility and life cycle divergence of this species has strongly influenced opinions on their relationship with *Tomicus destruens* (Carle, 1973; Gallego and Galián, 2001). The invasive potential of *T. piniperda* is augmented by its enormous spreading potential and adaptability to new conditions. In future, therefore, this species could become a serious pest worldwide.

Life Cycle and Reproduction. This monogamous bark beetle emerges from overwintering habitats, in thick bark near the base of the trunk, in early spring (Eidmann, 1965, 1974; Bakke, 1968). Adults are active when temperatures exceed 5°C and first flights have been recorded at 10–12°C during early March and April (Långström, 1983). Females initiate the attack and males follow them later (Saarenmaa, 1983). Fertilized females bore maternal galleries about 4–10 cm long (Saarenmaa, 1983) and lay up to 70 eggs on both sides (Šrot, 1968; Schroeder, 1999). Fecundity is positively correlated with female body weight and negatively correlated with infestation density (Schroeder and Weslien, 1994; Schroeder, 1997; Hui and Xue-Song, 1999; Amezaga and Garbisu, 2001). During oviposition, males clean the frass from the galleries (Šrot, 1968), then both sexes emerge and undergo maturation feeding to replenish their energetic reserves (Šrot, 1968). Larval development is temperature dependent (Yvon and Wegensteiner, 2015) and pupation occurs within 7–10 weeks (Šrot, 1968). Young adults emerge from June to mid-July in Sweden (Långström et al., 2002), and from July to August (Knížek, 1998) in Central Europe; they follow parental beetles into the tree crowns to infest 1–3-year-old pine shoots (Långström, 1983; Långström et al., 2002). Feeding starts near the branches whorl and continues apically for a few millimeters up to 7 cm. One tunnel may be occupied by 2–3 individuals (Haack et al., 2001). During outbreaks, intensive regeneration feeding may cause 80–98% defoliation of the crown (Haack et al., 2001).

Voltinism. Tomicus piniperda has so far been considered a univoltine species with hibernation before establishment of a new generation. However, emergence and sister brood occurrence, indicate possible continuous reproduction (Ryall and Smith, 2000) and the potential to become multivoltine (Poland and Haack, 2000).

Overwintering. In Northern Europe, the shoot feeding period is terminated by sub-zero temperatures, usually in the second half of October, when adults migrate to the base of the trunk and bore into the thick bark located 25 cm below the soil litter (Petrice et al., 2002). In China and Southern Europe, populations may overwinter under the bark at higher sections of the trunk or even in shoots on the ground (Masutti, 1969; Långström et al., 2002).

The Pine Shoot Beetle, Tomicus destruens (Wollaston, 1865)

The taxonomic relationship of *T. piniperda* and *T. destruens* has long been unclear. In the beginning, these species were considered only diverse ecotypes (Carle, 1973; Schwerdtfeger, 1981; Faccoli et al., 2005b), but gradually doubts about the group's uniformity have arisen (Lekander, 1971; Wood and Bright, 1992; Pfeffer, 1995). Genetic analyses have revealed divergences typical for distant relatives (Gallego and Galián, 2001; Kerdelhué et al., 2002; Kohlmayr et al., 2002; Faccoli et al., 2005a,b). Subsequently, a sympatric relationship was supported by morphological studies (Faccoli, 2006) and the ecological and climatic requirements based on distribution area (Vasconcelos et al., 2003; Faccoli et al., 2005b).

Tomicus destruens is considered a serious pest of 1-year old pine shoots. The typical hosts are pine species of coastal areas: for example, maritime pine (*P. pinaster*), stone pine [*Pinus pinea* (L.)], and Aleppo pine [*Pinus halapensis* (Mill.)] (Vasconcelos et al., 2003; Faccoli et al., 2005b; Chakali, 2007; Pernek et al., 2012). Infestations have also been recorded on Turkish pine [*Pinus brutia* (Ten.)], Canary Island pine [*Pinus canariensis* (C. Smith)], and black pine (*Pinus nigra*) (Kerdelhué et al., 2002; Gallego et al., 2004, 2008; Faccoli, 2007; Sarıkaya and Avci, 2010). Like *T. piniperda*, *T. destruens* colonizes the thick bark in lower sections of the trunk (Chakali, 2007). Its outbreaks frequently turn up in the healthy trees surrounding fire disturbed forests (Branco et al., 2010).

Distribution. Their distribution area includes Macaronesia, the Southern coast of Portugal, Spain, France, the Italian peninsula and Sardinia, Dalmatia, Turkey, Cyprus, and Northern Africa (Chararas, 1962; Lekander, 1971; Mendel et al., 1985; Chakali, 1992, 2007, 2008; Monleón et al., 1996; Ben Jamaa et al., 2000; Kohlmayr et al., 2002; Vasconcelos et al., 2003, 2005; Ciesla, 2004; Gallego et al., 2004; Faccoli et al., 2005b; Horn et al., 2006, 2012; Sarıkaya and Avci, 2010; Pernek et al., 2012; Lentini et al., 2015). *Tomicus destruens* is a Mediterranean species distributed in lowlands with an elevation maximum of approximately 1,000 m and with a dry, warm climate (Gallego et al., 2004). If the minimum temperature thresholds rise, this bark beetle will be able to spread north of its territory. High adaptability and the ability to develop in *P. nigra*, which covers the Mediterranean area, could mean immense damage resulting from this species in southern Europe.

Life Cycle. Tomicus destruens adults are active at temperatures around 5°C. The timing of flight activity differs by location and elevation (Sarıkaya and Avci, 2010). Generally, there are two phases, the stronger one, which occurs in October and November, is followed by a second one from mid-November to January (Sabbatini Peverrieri et al., 2008). In Italy, flight starts at 12°C (Faccoli et al., 2005a; Chakali, 2007, 2008; Sabbatini Peverrieri et al., 2008; Lentini et al., 2015), in Sardinia at 14°C (Lentini et al., 2015), and in Algiers, Tunisia and Israel at 6–8°C (Mendel et al., 1985; Ben Jamaa et al., 2000; Chakali, 2008).

Fertilized females bore 3-15 cm long maternal galleries vertically toward the tree crown (Faccoli, 2007, 2009; Chakali, 2008; Gallego et al., 2008; Sarıkaya and Avci, 2010) and oviposit 80–95 eggs on both sides. Every egg chamber is clogged with frass (Chakali, 2008; Lentini et al., 2015). Maternal gallery length, female fertility, and egg hatchability are negatively correlated with attack density (Faccoli, 2007; Sarıkaya and Avci, 2010; Lentini et al., 2015). Larval development is temperature dependent and lasts 50–200 days. Low temperatures substantially increase sub-imaginal mortality (Faccoli et al., 2005a; Horn et al., 2006; Sabbatini Peverrieri et al., 2008; Lentini et al., 2015).

Young adults emerge from the end of May until June (Sabbatini Peverrieri et al., 2008; Pernek et al., 2012) and undergo maturation feeding on young shoots (Chakali, 2007, 2008; Sabbatini Peverrieri et al., 2008; Sarıkaya and Avci, 2010; Lentini et al., 2015). Adults tend to select the same host tree species in which they developed (Tiberi et al., 2009).

Voltinism. Tomicus destruens populations are univoltine or bivoltine (Masutti, 1969; Dajoz, 1980; Mendel et al., 1985; Monleón et al., 1996; Sarıkaya and Avci, 2010; Horn et al., 2012; Lentini et al., 2015). Females continuously replenish energetic reserves, so that they do not need to undergo another cycle of regeneration feeding (Fernández Fernández et al., 1999b; Lentini et al., 2015) and can re-emerge and continue laying eggs up to four times (Lentini et al., 2015).

Overwintering. Tomicus destruens has summer dormancy in all developmental stages including eggs (Nanni and Tiberi, 1997; Pernek et al., 2012). Adults undergo dormancy inside the shoots, where regeneration feeding takes place, or in maternal galleries under the bark of infested trees (Russo, 1940; Masutti, 1969; Triggiani, 1984; Santini and Prestininzi, 1991; Monleón et al., 1996; Nanni and Tiberi, 1997), just like the juvenile stages (Triggiani, 1984; Santini and Prestininzi, 1991; Monleón et al., 1996; Faccoli et al., 2005a).

The Lesser Pine Shoot Beetle, Tomicus minor (Hartig, 1824)

The *Tomicus minor* beetle is a pest of several pine species (*Pinus* spp.): most commonly *P. sylvestris* in Europe, and Yunnan pine [*Pinus yunnanensis* (Franchet)] in China. These beetles generally prefer weakened hosts (Annila et al., 1999; Fernández Fernández et al., 1999a), but some authors consider this species a secondary aggressive, able to colonize and kill even healthy trees (Fernández Fernández et al., 1999a; Foit and Čermák, 2014).

Distribution. Except for North America, the distribution area of *T. minor* is similar to that of *T. piniperda* (Lungren, 2004), i.e., from Portugal through Europe, and copying the North African coast to Asia and Japan (Browne, 1968; Lekander et al., 1977). As its bionomy is not monitored in much detail, it is difficult to predict its future distribution. Due to climate change, a move toward northern territories might be expected. Furthermore, optimal conditions might support an increase in aggressivity, which would probably cause a greater occurrence of hot spots and a larger amount of damage.

Life Cycle. Overwintered *T. minor* adults first fly at temperatures of about 10°C, and flight peaks at temperatures of about 12°C (Långström, 1983), i.e., March to April in Central Europe and April to May in Scandinavia (Långström, 1983).

Females infest the trees and males follow them. European populations prefer trees with smooth bark or shaded, windthrown, and wind-broken trees (Långström, 1984), while populations in China prefer the thick bark near the trunk base (Ye and Ding, 1999). Fertile females bore "V" shaped maternal galleries transversely with the trunk axis. Usually, galleries are two-armed, with a mating chamber in the middle; however, 10% of the galleries are one-armed (Fernández Fernández et al., 1999a). Females oviposit alternately in both arms (Långström, 1983). Males keep the galleries frass free (Fernández Fernández et al., 1999a) and secure the entrance hole against predators and other males (Långström, 1983). Shortly before the end of ovipositing, males emerge and migrate into the tree crown for regeneration feeding (Långström, 1983), or search for other females to mate with (Fernández Fernández et al., 1999a). In reaction to repeated mating, females extend maternal galleries by about 7 cm and oviposit again. The overall gallery length may reach up to 20 cm and is negatively correlated with attack density. One female oviposits approximately 100 eggs (Fernández Fernández et al., 1999a). Their hatchability is low, with only 26% of progeny reaching maturity (Långström, 1983). Larvae feed on phloem, but low nutrition quality drives feeding into the wooden part, where the fungi inoculated by parental beetles are consumed (Francke-Grosmann, 1951; Fernández Fernández et al., 1999a). Total development lasts about 105 days in Northern Europe (Långström, 1983), 135 days in Southern Europe, and 125 days in China (Lieutier et al., 2015). Re-emergence and sister brood establishment has been observed in Swedish, Spanish and Chinese populations (Långström, 1983; Fernández Fernández et al., 1999a; Långström et al., 2002).

Regeneration Feeding and Overwintering. Regeneration feeding takes place during summer months in the lower part of the tree crown, where beetles feed on 3–4 mm thick young shoots (Långström, 1983). It continues until low autumn temperatures and shortening daylength induces hibernation. The Southern European and Chinese populations hibernate in mined shoots in tree crowns. Conversely, Scandinavian populations migrate to the soil litter and cracks in bark close to the trunk base (Långström, 1983; Fernández Fernández et al., 1999b).

Mediterranean Pine Engraver, Orthotomicus erosus (Wollaston, 1857)

Orthotomicus erosus is considered a secondary pest of recently fallen, windthrown, or fire-injured trees (Mendel and Halperin, 1982; Mendel, 1983; Arias et al., 2005; Lieutier and Paine, 2016; Sarıkaya and Şen, 2017). Although extensive damage to Turkish pine (*P. brutia*) and Aleppo pine (*P. halapensis*) has been reported in its natural distribution area of Israel and Iran (Mendel, 1983), these beetles can feed and reproduce in a broad range of coniferous species found in Mediterranean and Aegean coastal regions. The dominant hosts belong to pines and damage has been reported on Turkish pine (*P. brutia*), Caribbean pine [*Pinus caribaea* (Morelet)], Canary Island pine (*P. canariensis*), shortleaf pine [*Pinus echinata* (Mill.)], Afghan pine [*Pinus elderica* (Medw)], Aleppo pine (*P. halapensis*), black pine (*P. nigra*), stone pine (*P. pinea*), maritime pine (*P. pinaster*), Monterey pine [*Pinus radiata* (D. Don)], red pine (*P. resinosa*), and Scots pine (*P. sylvestris*) (Atkinson, 1921; Chararas, 1964; Carle, 1973; Mendel and Halperin, 1982; Walter et al., 2009; Sarıkaya et al., 2013). Less suitable hosts, in which development or maturation feeding has been recorded, include white spruce [*Picea glauca* ([Moench.] Voss)], Caucasian spruce (*P. orientalis*), balsam fir [*Abies balsamea* ([L.] Mill.)], Nordmann fir [*Abies nordmanniana* (Steven)], Spanish fir [*Abies pinsapo* (Boiss)], eastern hemlock [*Tsuga canadensis* ([L.] Carrière)], tamarack [*Larix laricina* ([Du Roi] K. Koch)], Mediterranean cypress [*Cupressus sempervirens* (L.)], Arizona cypress [*Cupressus arizonica* (Greene)], Lebanese cedar [*Cedrus libani* (A.Rich.)], and Douglas fir (*Pseudotsuga menziesii*) (Mendel and Halperin, 1982; Gil Sanchéz and Pajares Alonso, 1986; Wood and Bright, 1992; Arias et al., 2005; Walter et al., 2009; Sarıkaya et al., 2013; Pernek et al., 2019). The wide host range of this species and its high mobility (Sarıkaya and Şen, 2017), together with the invasions promoted by international timber transportation (Brockerhoff et al., 2006a; Haack, 2006), have resulted in this species' recent massive spread into new environments (Sarıkaya et al., 2013; Pernek et al., 2019).

Orthotomicus erosus prefers medium stem parts with thicker bark (diameter up to 90 cm) and main branches (diameter above 5 cm) (Mendel and Halperin, 1982; Seybold and Downing, 2007; Pernek et al., 2019), and often occurs together with *I. sexdentatus* (Paiva et al., 1988), *Hylastes angustatus* (Herbst, 1793), *Hylurgus ligniperda* (Fabricius, 1787), *Pissodes nemorensis* (Germar, 1824) (Tribe, 1990), *Pityogenes calcaratus* (Eichhoff, 1878), and *T. destruens* (Mendel and Halperin, 1982).

Distribution. The native range of *O. erosus* spans from the Middle East to the Mediterranean countries, Southern and Central Europe, England, Northern Africa, Caucasus and Crimea, as well as to China and Central Asia (Atkinson, 1921; Schimitschek, 1944; Balachowsky, 1949; Chararas, 1964; Lozovoj, 1965; Chararas and M'Sadda, 1970; Carle, 1973; Chararas et al., 1978; Anon, 1981; Mendel and Halperin, 1982; Mendel, 1983, 1988a,b; Yin et al., 1984; Mendel et al., 1986; Wood and Bright, 1992; Paiva, 1994; Pfeffer, 1995; Eglitis, 2000; Lieutier et al., 2002; Haack, 2004, 2006; Henin and Pavia, 2004; Arias et al., 2005; Lee et al., 2005; Brockerhoff et al., 2006a; Ben Jamaa et al., 2007; Seybold and Downing, 2007; Sarıkaya and Avci, 2010; Amini et al., 2013; Gómez and Martínez, 2013). Nonetheless, due to international trade, *O. erosus* has invaded North and South America (Haack, 2004; Ruiz and Lanfranco, 2008), South Africa, and Fiji (Wood and Bright, 1992; Eglitis, 2000).

Orthotomicus erosus reacts rapidly to changing local temperatures, and within months can switch from endemic to epidemic status in a locality. After an outbreak, the vast range of possible hosts simplifies its spread into near or far surroundings. Taken together, it is possible to assume that the shift in low-temperature limits might enable *O. erosus* to continue conquering the European continent. On top of that, *O. erosus* seems to be a perfect candidate for introduction by cargo trade into new niches worldwide.

Life Cycle and Reproduction. The first individuals emerge when temperatures exceed 7–9°C (Tribe, 1990; Sarıkaya et al., 2013), and swarming peaks at temperatures of around 12–15°C (Tribe, 1990; Mendel et al., 1991). Males colonize the substrate and bore into the phloem to excavate a nuptial chamber (Mendel and Halperin, 1982; Giesen et al., 1984). Conspecifics of both sexes are then attracted by an aggregation pheromone. Males usually mate with 1–3 females, but rarely up to even six (Atkinson, 1921; Chararas, 1964; Chararas and M'Sadda, 1970; Carle, 1973; Mendel and Halperin, 1982; Tribe, 1990). Oviposition in the absence of males is not uncommon as a certain percentage of females can be inseminated during the autumnal maturation feeding (Mendel, 1983). Females bore 12–120 mm long maternal tunnels longitudinal to the tree axis in cambium and outer xylem (Mendel and Halperin, 1982), and lay around 75 eggs (maximum 170 eggs) into the egg niches on both sides of the tunnels (Mendel and Halperin, 1982; Eglitis, 2000; Haack, 2004). Perpendicular larval galleries end with a pupation chamber in the inner bark, or more deeply in the sapwood in cases of insufficient bark thickness (Mendel and Halperin, 1982). To reach sexual maturity, young adults undergo maturation feeding and emerge when their cuticle is fully sclerotized (Eglitis, 2000). Total development lasts from 30 to 75 days under optimal temperature conditions (Mendel, 1983).

Orthotomicus erosus has a minimum temperature limitation, as the threshold for oviposition and development of immature stages is 14°C, which supports rapid offspring production and a quick switch from endemic to epidemic status (Mendel and Halperin, 1982; Mendel, 1983; Mendel et al., 1985).

Voltinism. The voltinism in *O. erosus* depends on temperature and host phloem quality; up to seven generations per year may occur (Mendel, 1983; Mendel et al., 1985; Lieutier and Paine, 2016). European populations are usually bivoltine, while 3–4 generations occur in North and South America and Africa, 4–5 in the Middle East, and up to six in the Mediterranean region (Carle, 1973; Mendel, 1983; Lee et al., 2005; Seybold and Downing, 2007; Sarıkaya, 2008; Sarıkaya et al., 2013; Pernek et al., 2019).

Overwintering. In the fall, *O. erosus* adults aggregate to overwinter under the bark of host trees (Mendel, 1983; Haack, 2004; Sarıkaya et al., 2013). Generally, dozens of adults penetrate to the phloem through a single entrance hole and then spread in all directions and bore irregular overwintering tunnels (Mendel, 1983).

Adults are the only overwintering stage in populations located close to the northern distribution limit and at high elevations (Mendel, 1983), while immature stages successfully overwinter in regions with mild winters, e.g., Turkey and the United States (Schimitschek, 1944; Seybold and Downing, 2007).

The Steelblue Jewel Beetle, Phaenops cyanea (Fabricius, 1775)

Habitats with sparsely distributed *P. sylvestris* and a warmer microclimate create optimal conditions for the occurrence of *P. cyanea* (Sierpiński, 1965; Perz and Ciesielski, 1993). The host tree spectrum also includes white pine (*P. strobus*), European larch [*Larix decidua* (Mill.)], European silver fir [*Abies alba* (Mill.)], and Norway spruce [*Picea abies* (L.)]. *Phaenops cyanea* is considered a secondary pest of old, weakened, and damaged trees (Bettag, 1979; Gutowski et al., 1992; Perz and Ciesielski, 1993; Łabêdzki, 1993; Gutowski and Królik, 1996; Luterek, 1996). Under suitable conditions, *P. cyanea* attack intensity and aggressivity increase, making the species a primary pest that causes damage to healthy forests (Zahradník, 1999; Foit and Čermák, 2014). According to the BAWBILT database, damage to eight million hectares and 12 million m^3 were recorded in Slovakia and Poland during the 1990s (Grégoire and Evans, 2004). Vast losses have also been recorded in Germany, Czechia, Hungary, and Romania (Templin, 1962; Hellrigl, 1978; Apel, 1988; Wiegard and Amarell, 1994; Majunke, 1995; Apel et al., 1999; Knížek et al., 2020).

Distribution. Phaenops *cyanea* occurs almost throughout the Palearctic region, except in the extreme northern and Atlantic areas—i.e., Northern Africa, the Caucasus, Siberia, and Northern Mongolia (Gutowski et al., 1992; Mühle, 1993; Gutowski and Królik, 1996). In Central Europe, their distribution area predominantly includes lowlands up to 800 m.a.s.l. (Templin, 1962; Gabryel, 1967; Gfeller, 1985; Gutowski et al., 1992; Szujecki, 1995), although their ability to cope with temperature fluctuations allows them to spread into mountains at around 1,400 m.a.s.l., where sudden species abundance has been recorded (Gfeller, 1985; Del Pozo et al., 1995; Sowińska, 2006). Their abundance is lower in Southern Europe and in the north-western part of the continent (Templin, 1962; Hellrigl, 1978; Apel, 1988; Wiegard and Amarell, 1994; Majunke, 1995; Apel et al., 1999). In future, increases in the low-temperature thresholds might mean the distribution area will extend into highlands or even into the mountains. Also, areas with low abundance could suffer from significant damage as the life cycle might speed up.

Life Cycle. In Central Europe, flight activity starts in May and June, peaking 1 month later when temperatures reach 20°C (Stumpf, 1999; Zahradník, 1999). Mating takes place on the trunk surface and males repeatedly mate with females. Fertilized females then search for sunlit cracks in the bark to lay their eggs (Dengler, 1975; Gutowski et al., 1992; Zahradník, 1999; Bílý, 2002; Sowińska, 2006). Larvae hatch 3–4 days later and bore through the bark to the phloem (Filippenkova, 1971; Apel, 1991). Larval tunnels are irregular, flat or oval in the transverse cross-section, and 15–30 cm long (Gutowski et al., 1992; Zahradník, 1999; Bílý, 2002; Sowińska, 2006). Larval development lasts approximately 3 months, but detailed information about the factors influencing larval maturation, number of instars, and pupation are missing (Zahradník, 1999; Bílý, 2002). Larval abundance is significantly impacted by natural enemies and other species of cambioxylophagous insects (Gutowski et al., 1992; Szujecki, 1995). Another important factor in larval mortality are host tree defensive mechanisms, especially resin ducts (Gutowski et al., 1992) and the ability to avoid them (Weissbecker et al., 2006). The pupation process takes place in pupal chambers in the bark (Sierpiński, 1965; Bílý, 2002) or in the sapwood of trees with thin bark (Sierpiński, 1965). The length of the life cycle varies from a typical annual to an extended biennial or an exceptional 3-years cycle (Sierpiński, 1965; Szujecki, 1995; Apel et al., 1999; Zahradník, 1999).

Maturation Feeding and Overwintering. Adults undergo regeneration and maturation feeding on pine needles throughout the vegetation season from May to September (Gutowski et al., 1992; Zahradník, 1999; Bílý, 2002; Sowińska, 2006), which may lead to a considerable loss of the photosynthetic apparatus (Bílý, 2002).

Phaenops cyanea adults are short-living beetles. Males die within 3 or 4 days after copulation (Filippenkova, 1971; Apel, 1991), while females live up to 36 days (Bílý, 2002). During September and October, mature larvae and prepupae bore overwintering chambers 2–3 cm deep under the bark, or in the case of thin bark, 1–1.5 cm deep in the sapwood (Bílý, 2002). Pupation occurs in April and May and adults emerge 2–3 weeks later (Bílý, 2002). Young instar larvae overwinter in their tunnels and continue development the following spring (Gutowski et al., 1992; Zahradník, 1999; Bílý, 2002).

DISCUSSION

The global climate is continuously warming (Field and Barros, 2014), and weather models predict significant changes in temperature conditions by the end of the twenty first century (IPCC, 2007; Kolb et al., 2016). Even though temperature fluctuations represent an ordinary phenomenon in the world's climate millennia, the current unprecedented warming is likely to act as a powerful agent affecting the relationship between trees and subcortical insects. While forest ecosystems possess a long restoration time and their flexibility to react to climate changes is a little bit slow (Lindner et al., 2010), the cambioxylophagous insects rapidly react to any temperature increase, which ultimately results in the pest having higher fitness and reproductive success (Bakke, 1968).

Insects respond to climate warming in multiple ways, according to Lehmann et al. (2020); the monitored modifications are 55% related to voltinism and phenology and 62% to population dynamics. As ectotherms, active and post-diapause insects are primarily sensitive to environmental temperatures (Forrest, 2016), and thus optimal weather conditions early in spring result in an immediate response (Bartolomeus et al., 2011; Roy et al., 2015; Sato and Sato, 2015; Thomsen et al., 2016), for example, the earlier onset of spring swarming in bark beetles (Faccoli, 2009). A warm and dry vegetation season supports a shortening of the developmental period for all immature insect stages and shifts univoltine populations to multivoltine or adds one more generation in bivoltine populations (Jönsson et al., 2009; Mitton and Ferrenberg, 2012; Hlásny et al., 2021). Temperature influences such as these were recently confirmed in species causing several infestations of spruce and larch in Central Europe—e.g., European spruce bark beetle *Ips typographus* (Linnaeus, 1758), double-spined bark beetle *Ips duplicatus* (Sahlberg, 1836), and large larch bark beetle *Ips cembrae* (Heer, 1836)—either in laboratory experiments (Wermelinger and Seifert, 1998; Schebeck and Schopf, 2017; Davídková and Doležal, 2019), in laboratory cultures (Pfeffer and Knížek, 1995), or under field conditions (Mrkva, 1995; Wermelinger et al., 2012). A similar trend can also be observed in several bark beetle pests of *P. sylvestris*—e.g., *I. sexdentatus*, *T. piniperda*, and *T. destruens* (Šrot, 1968; Jactel and Lieutier, 1987; Horn et al., 2006; Sabbatini Peverrieri et al., 2008; Özcan, 2011; Péter, 2014; Yvon and Wegensteiner, 2015). Furthermore, increasing autumn temperatures bring a significant prolongation of the vegetation season (Bartolomeus et al., 2011; Diamond et al., 2011; Karlsson, 2014; Kharouba et al., 2014; Roy et al., 2015), which enables completion of development to most chilling tolerant stage prior to the onset of the harsh winter season and increases the probability of successful overwintering (e.g., Gallinat et al., 2015; Raffa et al., 2015; Rosenberger et al., 2017a; Schebeck and Schopf, 2017; Štefková et al., 2017). Together, these factors result in an enormous increase in pest population density (Wermelinger et al., 2008), an extensive dieback of host trees (e.g., Allen et al., 2010; IPCC, 2014; Senf et al., 2018; Hlásny et al., 2021; Marqués et al., 2022), and a shift in pest aggressivity. Under the influence of a changing climate, several species with minor economic importance in the past—e.g., *I. acuminatus*, *T. piniperda*, *T. destruens*, *T. minor*, and *P. cyanea*—have recently become more aggressive, causing severe environmental and economic losses (Gaylord et al., 2013; Netherer et al., 2015; Pešková et al., 2016).

An insects' response to a warming environment may include shortening of its life cycle, and thus reaching epidemic levels in a shorter time (Bradshaw and Holzapfel, 2006). However, different life traits were recorded in two species of North American bark beetles, *Dendroctonus ponderosae* (Hopkins, 1902) and *Dendroctonus rufipennis* (Kirby, 1837). In the semivoltine species *D. rufipennis*, rising temperatures together with a longer growing season may result in finishing the development of callow adults in 1 year (Hansen et al., 2001; Hansen and Bentz, 2003; Schebeck et al., 2017). This shift from semi- to univoltinism has been predicted and recently also observed in some parts of *D. rufipennis* range (Régnière and Bentz, 2007; Schebeck et al., 2017; Bentz et al., 2019). A further shift to bivoltinism is highly improbable due to the occurrence of obligatory diapause that conditions the sexual maturation of progeny (Schebeck et al., 2017; Bentz et al., 2019). In the case of univoltine *D. ponderosae*, the shift to bivoltinism is conditioned by extreme temperature increases (Bentz et al., 2019), and thus only extreme climate change scenarios would be powerful enough to initiate a shift toward bivoltinism in its natural range (Bentz et al., 2019). However, expansion to Mexico and the southeast United States as well as lower latitudes in Europe might result in bivoltinism (Bentz et al., 2019). The species' survival in a changing climate will depend on its physiological plasticity and possible mechanisms that might result in bivoltine populations of *Dendroctonus* bark beetles in future cannot be excluded completely (Bentz et al., 1991, 2019; Powell and Bentz, 2014; Bentz and Hansen, 2017).

The above-mentioned immediate responses of insects to high temperatures predominantly include short-term changes. Long-term effects of a changing climate can be demonstrated by shifts in the distribution area of species, regardless of the latitude and altitude (Gallego et al., 2004; Thuiller et al., 2008; Netherer and Schopf, 2010), as numerous species pioneer previously uncolonized territories (Buotte et al., 2017; Lantschner et al., 2017). It was estimated that up to 90% of insect species react to temperature changes by widening their geographic range (Lehmann et al., 2020). That has already been monitored for different kinds of pests like the larch bud moth, *Zeiraphera diniana* (Hübner, 1799), gypsy moth, *Lymantria dispar* (Linnaeus, 1758), pine processionary moth, *Thaumetopoea pityocampa* (Denis and Schiffermüller, 1775), emerald ash borer, *Agrilus planipennis* (Fairmaire, 1888), orpine bark beetles *O. erosus*, *H. ligniperda, Hylurgus micklitzi* (Wachtl, 1881), and *Hylastes linearis* (Erichson, 1836), etc. (Turchin et al., 2003; Toffolo et al., 2006; Liebhold et al., 2013; Faccoli et al., 2020). Thus, it can be assumed that sooner or later pine pests may spread their territories. Species expansions are a natural phenomenon and a dynamic process shaped by variations in climatic conditions that have occurred constantly for millions of years (Liebhold et al., 1995). Usually, the distribution range of species is determined by suitable ecological conditions, which support population viability (Liebhold et al., 1995). Therefore, the essential factors controlling species spread are climate, as well as the natural biological and geographical barriers (Bentz et al., 2010; Lantschner et al., 2017). At first, climate change promotes species dominance and spread within a domestic area (Bradley et al., 2012). Later, the former insurmountability of the natural barriers is dwindled due to extreme climatic deviations. Further spread into new, unexploited areas is supported by growing international trade (Mayr, 1963; Liebhold et al., 1995; Seebens et al., 2017), and new migration pathways into untapped food resources are loosed (Allee et al., 1949; Odum, 1971; Fox and Fox, 1986; Williamson and Brown, 1986; van Lenteren et al., 1987; Pimentel, 1993; Erbilgin et al., 2014; Cooke and Carroll, 2017; Rosenberger et al., 2017b). The introduction of forest pests is usually unnoticeable, but over time, some of them become a threat to the forest (Liebhold et al., 1995; Niemelä and Mattson, 1996). Typical prominent invasive representatives are the wood borers and bark beetles (Brockerhoff et al., 2006b; Liebhold et al., 2017). Even though pest density and distribution in the invaded area might be low, the seriousness of the damage inflicted could be economically high, as documented for the white pine weevil, *Pissodes strobi* (Say, 1831) on *P. strobus* in North America (Pimentel, 1993).

It seems that the phenotypic plasticity of bark beetles is elevated due to their ability to assimilate to new conditions. So, in time, there is a possibility that the selection pressure triggered by climate changes will play a role in reinforcing pre-adapted features or provoking genetic changes for preferential features, which would allow the native insects to be faster and more successful in their expansions. On top of that, the ability to utilize non-native tree species, causing damage or even their death, might also be positively affected (Carroll et al., 2004; Bentz et al., 2010; Wingfield et al., 2010; Paine et al., 2011; Branco et al., 2015; Lantschner et al., 2017; Liebhold et al., 2017). An example case might be the possible dispersion of *T. destruens,* which typically attacks coastal pine species, with an ability to evolve in inland species like *P. nigra* (Faccoli, 2007). The threat lies in the fact that *P. nigra* refuges are scattered around Southern Europe and cover Mediterranean mountains (Vidaković, 1991). If bark beetle populations from contact zones successfully breed in a new host, enormous devastation of southern European pine forests would occur.

During the last century, Central Europe experienced many epidemic outbreaks and migrations of the bark beetle pests. These have had a significant impact on an extensive area of boreal and temperate forests (Raffa et al., 2008; Økland et al., 2011). Spruce, pine, and larch stands were affected. Climate change brings many alterations to forest ecosystems, and the mechanisms and stimuli that trigger pest expansion beyond range borders are still not well-comprehended (Økland et al., 2019). The main problem is the complexity of interactions between beetles' bionomy, climate, and environment dispositions (Økland et al., 2019). Therefore, in the near future, a higher expansion rate of forest pests like *I. typographus*, *I. cembrae*, *I. duplicatus*, *Ips mannsfeldi* (Wachtl, 1879), *I. acuminatus*, and *Ips aminitus* (Eichhoff, 1871) is to be expected (Lekander et al., 1977; Grodzki, 2003; Vakula et al., 2007; Holuša et al., 2010; Olenici et al., 2010; Aakala et al., 2011; Økland et al., 2011; Lindelöw et al., 2015; EFSA PLH, 2017).

Even though rising thermic limits and extension of the growing season support changes in voltinism, multivoltinism persists until beetles perceive the shortening daylength (Annila, 1969; Schopf, 1985, 1989; Doležal and Sehnal, 2007; Schroeder and Dalin, 2017). Therefore, after the summer solstice, the shortening of day length accompanied by the drop in night temperature induce diapause development in many temperate-zone species (Doležal and Sehnal, 2007; Saunders, 2014). Based on the latitude and altitude, a slow adjustment of reproduction, development, and stress resistance to local conditions occurs (Schebeck et al., 2021). This evolutionary adaptation reduces pre-imaginal mortality during the harsh season, and thus reduces population losses (Baier et al., 2007). Diapause is terminated during the period of low mid-winter temperatures (Doležal and Sehnal, 2007) and the following post-diapause quiescence is solely temperature dependent (DeWilde, 1970; Gehrken, 1985), which shifts insect emergence from hibernation sites until favorable conditions occur in the following spring (Dobart, 2006; Doležal and Sehnal, 2007). However, intraspecific differences in photoperiodic threshold have been recorded in several species of bark beetles, including *I. typographus* (Schopf, 1985, 1989; Doležal and Sehnal, 2003, 2007; Baier et al., 2007; Faccoli, 2009; Schroeder and Dalin, 2017; Schebeck et al., 2021). In northern populations of this species, diapause development occurred even during long day conditions (Schroeder and Dalin, 2017; Schebeck et al., 2021). Thus, it seems that the photoperiod threshold is, at least for now, an important driver influencing the voltinism of local populations. Nevertheless, the hidden danger of climate change might be a general increase in night temperatures. Long-lasting constant temperature below 5°C (at least 2 months) induces diapause development in *I. typographus* (Doležal and Sehnal, 2007), but these conditions in Central Europe and Southern Scandinavia have already stagnated. Additionally, climate models predict that the frequency of years with chill conditions will decrease by more than 50% by the end of this century (Jönsson et al., 2011). Consequently, long and warm periods at the end of the vegetation season may eventually cease diapause development, as was confirmed by laboratory research of *D. rufipennis.* In a recent study, lack of cold stimulation produced active non-diapausing adults that laid viable eggs (Davenport, 2020). Such a situation may result in prompt temperature-mediated emergence in early spring followed by rapid population growth (Jönsson et al., 2011; Davenport, 2020). Therefore, studies of photoperiodic response and its temperature modifications in populations of bark beetles across their geographic range represent a crucial area of investigation for understanding changes in bionomy, predicting future trends, and finally, for adjusting forest management (Jönsson et al., 2011).

CONCLUSION

In summary, climate change, especially temperature increases, significantly impacts insect pests of *P. sylvestris* in multiple ways, including behavioral details, population dynamics, voltinism, distribution, and epigenetic features such as diapause development and overwintering strategies. Unfortunately, empirical data on relationships between temperature conditions and phenological traits in those bark beetle species are still scarce, which complicates effective management of pest species. Detailed research on species and population levels are crucial to evolve new, and improve existing, methods of forest protection and pest management.

AUTHOR CONTRIBUTIONS

DH contributed to the content of the study and wrote the first draft of the manuscript. PD contributed to the content and wrote and controlled sections of the manuscript. Both authors contributed to manuscript revision, read, and approved the submitted version.

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