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Bark beetle outbreaks in coniferous forests – a review of climate change effects

Luciana Jaime[1], Enric Batllori[1,2], and Francisco Lloret[1,3].

[1]Centre de Recerca Ecològica i Aplicacions Forestals (CREAF), 08193 Cerdanyola del Vallès, Barcelona, Spain.

[2]Unitat de Botànica i Micologia, Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Universitat de Barcelona, 08028 Barcelona, Spain.

[3]Unitat d'Ecologia, Departament de Biologia Animal, Biologia Vegetal i Ecologia, Universitat Autònoma Barcelona (UAB), 08193 Cerdanyola del Vallès Barcelona, Spain.

Correspondence:

Luciana Jaime, CREAF, Cerdanyola del Vallès, Spain.

ORCID ID: https://orcid.org/0000-0002-2452-6790

E-mail: lujaimegonzalez@gmail.com

Abstract

Extreme weather episodes related to anthropogenic climate change have enhanced the frequency and magnitude of bark beetle disturbance, causing worldwide mortality of forests in the last decades. Changes in temperature and precipitation regimes are altering the relationships between host tree populations and associated bark beetle species, as these insect-host systems are highly sensitive to climate extremes. However, it is not fully understood how climate interacts with the different components of bark beetle-host systems, and thus the existing knowledge is still insufficient to face the challenges of understanding the system response to changing environmental conditions. Here, we review the most important findings of the influence of climatic factors on the dynamics of bark beetle and host tree populations at different spatiotemporal scales. Future research should integrate how the effects of climate on individual tree responses to beetle attack scale up to outbreak patterns at regional scale. Recent advances in plant physiology, disturbance ecology, ecological niche modelling, and remote sensing can further our understanding of the risks of bark beetle disturbance in forest ecosystems under changing climate.

Key words: forest mortality, biotic disturbance, heatwaves, extreme drought, host tree resistance, outbreak dynamics.

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Conflicts of interest/Competing interests

I declare that the authors have no competing interests as defined by Springer, or other interests that might be perceived to influence the results and/or discussion reported in this paper.

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L.J. wrote the original draft. E.B. and F.L. supervised, reviewed and edited the manuscript.

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CONTENTS

1. Introduction

During the last decades of anthropogenic-driven changes in temperature and precipitation regimes (IPCC 2019), mortality in forests has been increasing due to abiotic and biotic disturbances such as bark beetle outbreaks (Weed et al. 2013; Seidl and Rammer 2017; McDowell et al. 2020). An important feature of the systems composed of host trees and the bark and wood boring insects colonizing these tree species is that they are highly sensitive to climatic variability, particularly to extreme weather episodes (Lehmann et al. 2020). Therefore, understanding the response of such bark beetle-host systems to changing climate is necessary to assess the risk of current and future outbreaks and their consequences for forest dynamics and resilience.

Bark beetles are among the most important biotic agents affecting forests dynamics. First, bark beetles inhabit both natural and managed forests over the globe (Hulcr et al. 2015). Second, the dynamics of these bark beetle-host systems can become irruptive, undergoing natural intermittent outbreaks that cause tree mortality at landscape extent (Raffa et al. 2015). Third, in the context of climate change, some bark beetle species are currently showing altered outbreak dynamics within their historical ranges, and many of them are expanding their latitudinal and elevational distribution (Cudmore et al. 2010; Georgiev et al., 2022) and even their host tree preferences (Cullingham et al. 2011). Fourth, bark beetles strongly impact the structure and functioning of forest ecosystems, affecting size class distribution, species composition, successional dynamics and disturbance regimes (e.g., wildfires), carbon stocks, nutrient cycling, and hydrology (Morris et al. 2017). Bark beetle disturbance can have, therefore, important consequences to the maintenance of ecosystem services into the future (Hlásny et al., 2019; McDowell et al., 2020). Yet, the role of climate and its variability on the dynamics of bark beetle-host systems is not completely understood.

Given the relevance of bark beetle disturbance to forest dynamics in the current context of climate change, we review the existing scientific knowledge of the influence of climatic factors on bark beetle-host tree dynamics. Particularly, we focus on bark beetle species that have the potential to kill coniferous forests trees due to their ecological and economical relevance. First, we explain the bark beetle biology and particularities of species-specific life cycle, the effect of temperature on bark beetles and the transition from endemic to epidemic stage. Then, we present a brief overview of the mechanisms of host tree resistance and its relationship with changing climatic conditions. These aspects provide the conceptual basis for assessing the drivers of current outbreak dynamics in North America and Europe and of those that may promote the transition from endemic to outbreak stages under future climates. Finally, we identify major research needs and priorities.

2. Biology of bark beetles

Bark beetles are a group of small cylindrical insects classified in the subfamily Scolytinae (Latreille 1804), within the diverse family Curculionidae, order Coleoptera (Linnaeus 1758; Latreille 1802). Within the subfamily Scolytinae, there are currently ca. 6000 identified species belonging to 247 genera distributed in all biogeographic regions, excluding the Antarctic (Hulcr et al. 2015). Less than 1% of the Scolytinae species are able to colonize and kill healthy trees. However, tree-killing species such as those breeding in temperate coniferous forests can cause important ecological and economic impacts (Lindgren and Raffa 2013; Hicke et al. 2016; Morris et al. 2017; Sommerfeld et al. 2018). This review is focused on this group of conifer tree-killing species, particularly well-studied species of *Dendroctonus*, *Ips* and *Tomicus* genera in North American and European forests.

2.1. Life cycle

Bark beetles, *sensu stricto,* live, breed and feed in galleries inside plant tissues, except during dispersal periods in the adult stage (Raffa et al. 2015) and for some species that can overwinter in forest litter (Schebeck et al. 2017). Each generation of bark beetles is organized around a common life cycle that includes three main stages: attack and establishment in host tree for reproduction, larval development, and maturation and dispersal (Sauvard 2004). However, there are many variations among bark beetle species at each stage of the life cycle, in addition to different reproductive strategies (i.e., monogamous or polygamous), voltinism (i.e., number of generations per year), and host preferences, that can influence dispersal, host tree colonization behaviours and their potential risk of developing into outbreak populations.

The attack and establishment in the host tree for reproduction generally begin when pioneer beetles locate a new susceptible host, bore through the bark into the phloem, and excavate chambers or galleries to recruit mating partners. In monogamous species, the females are typically the pioneers, as in the genera *Dendroctonus* and *Tomicus* (Lieutier et al. 2015; Six and Bracewell 2015), whilst in polygamous species, it is usually the males, as in the genus *Ips* (Cognato 2015). Conspecific recruitment for mating on the new host is promoted by aggregation pheromones or attractant compounds produced by the pioneer beetles (Blomquist et al. 2010). After mating, females excavate oviposition galleries in the phloem to deposit eggs along them for brood production.

For mass attacking bark beetle species, like *Dendroctonus ponderosae*, *Dendroctonus rufipennis,* and *Ips typographus*, the use of aggregation pheromones is also a mechanism to deplete host tree defences (Seybold et al. 2000; Blomquist et al. 2010). Pioneer beetles initiate and coordinate mass attacks using combinations of pheromones and host tree volatiles released by damaged tissues (Krokene 2015). The success or failure of the attack relies on the beetle's population density and the defensive capacity of the affected tree, which vary among alternative host species and tree individuals (Christiansen et al. 1987; Boone et al. 2011). Although tree-killing bark beetle species are capable of incurring host tree mortality alone, associated microorganisms and fungi may be critical for detoxifying or exhausting tree defences (Raffa 2014; Six and Wingfield 2011; Chiu et al. 2019). When tree defences are overwhelmed, bark beetles release inhibitory compounds or anti-aggregation pheromones to prevent subsequent infestations and minimize conspecific competition (Wood 1982). A tree is typically available for one or, in certain cases, two beetle generations each year, depending on host size, host nutritional quality, and the infesting bark beetle species (Raffa et al. 2016).

During the development stage, larvae usually bore individual galleries more or less perpendicular to the maternal gallery and feed on phloem or fungi which have invaded phloem. Then, pupation takes place in individual pupal chambers excavated in the phloem, as in *Ips sexdentatus* (Sauvard 2004), or in outer bark, as in *Tomicus piniperda* (Lieutier et al. 2015). Upon the emergence from the pupa, beetles need a maturation period prior be able to reproduce. In most species, maturation feeding takes place in the phloem of the natal host tree, as in *Dendroctonus* and *Ips* species (Sauvard 2004; Six and Bracewell 2015). Once mature, beetles emerge from the natal host to find a new susceptible tree for brood production. However, in *Tomicus* species maturation feeding occurs in the shoots or twigs of healthy trees. In this case, beetles emerge from natal hosts to disperse for maturation feeding and then disperse again to find susceptible trees for reproduction (Lieutier et al. 2015).

The dispersal distance to new host trees is influenced by beetles' fitness (e.g., lipid reserves, flight muscles), biotic environmental factors (e.g., population dynamics, stand density and composition), and abiotic environmental factors (e.g., wind, temperature) (Kautz et al. 2016; Jones et al. 2019). The average dispersal of most bark beetles is from a few hundred meters to a few kilometres (Jactel, 1991; Werner and Holsten, 1997; Poland et al. 2000; Doležal et al. 2016). However, beetles have the potential for long-distance dispersal when flight is aided by wind. Individuals of *D. ponderosae* have been recorded more than 24 km from their natal tree (Evenden et al. 2014) and individuals of *I. sexdentatus* and *I. typographus* over 40 km (Nilssen 1984, Jactel and Gaillard 1991).

2.2. Bark beetles responses to temperature

As poikilotherms, bark beetles' life cycles are directly influenced by temperature (see Fig. 1) (Sauvard 2004, Bentz et al. 2010). Temperature affects the different stages of beetle development$^{\mathrm{Fig.1A;(1)}}$, overwintering survival $^{\mathrm{Fig.1;A(2)}}$, and number of generations $^{\mathrm{Fig.1;A(3)}}$, but also activities such as gallery construction, mating, oviposition, maturation, emergence and dispersal flight. Also, it influences the development of associated microorganisms and fungi $^{\mathrm{Fig.1;A(4)}}$ and bark beetle natural enemies$^{\mathrm{Fig.1;A(5)}}$ (Six and Wingfield 2011; Wegensteiner et al. 2015). In general, rising temperatures accelerate the rates of life processes, increasing winter survival and population density$^{\mathrm{Fig.1;C(13)}}$, and thus the attack pressure$^{\mathrm{Fig.1;A(6)}}$ on host trees. However, the effect of temperature on developmental processes is not linear. This effect varies according to species-specific thermal tolerances, species geographical distribution, and in relation to the species strategy to maintain life-cycle timing (i.e., diapause or direct temperature control) (Bentz et al. 2010).

High temperatures can promote development rate$^{\mathrm{Fig.1;A(1)}}$ from eggs to adults accelerating reproduction, larval development and maturation, as well earlier emergence in spring. However, temperatures that surpass species-specific thermal tolerance, as experienced during heatwaves, can have negative effects on beetle development and lifespan (Rouault et al. 2006). In *I. sexdentatus*, development rate and productivity can increase with temperature, as result of enhanced oviposition rates and reduced larval developmental time, allowing for two instead of one generation per year (Pineau et al. 2017). In *Tomicus* species, warmer temperatures at the end of the winter allow for early emergence, maturation feeding on shoots and dispersal, thereby promoting the synchronization of adult emergence in spring (Lieutier et al. 2015). For species with a diapause strategy, such as *I. typographus* and *D. rufipennis,* the effect of temperature depends on the life stage in which diapause occurs (Bentz et al. 2010; Schebeck et al. 2017). For instance, in *D. rufipennis*, their facultative diapause during the prepupal stage may be averted by warm summer temperatures, resulting in a univoltine life cycle as opposed to two years when diapause is invoked. On the other hand, higher minimum temperatures could disrupt the obligatory adult diapause of this species which is initiated by low temperatures (Schebeck et al. 2017).

Temperature during the cold season (i.e, late fall, winter, and early spring) influences the survival rate $^{\mathrm{Fig.1;A(2)}}$ of beetle populations. Larvae and pupae, in general, are especially vulnerable to mortality by freezing. In *D. ponderosae* and *D. frontalis*, very low winter temperatures contribute to larvae mortality whilst warmer winters increase brood survival (Ungerer et al. 1999; Creeden et al. 2014). For that, most species overwinter as adults inside the natal host tree during their maturation stage waiting for spring to emerge (Sauvard 2004), although individuals of some species can temporarily emerge to overwinter in the forest litter, as in *I. typographus* (Schebeck et al. 2017). In the case of *Tomicus* species, adults usually overwinter in maturation shoots or the base of healthy trees (Lieutier et al. 2015). For species with diapause to survive the cold temperatures, such as *D. rufipennis* and *I. typographus*, temperature and photoperiod play a primary role in the induction, maintenance and termination of diapause during overwintering (Schebeck et al. 2017). In this case, high temperatures can be critical for *I. typographus* when diapause induction must occur, as they can suppress this process and increase the risk of winter mortality (Doležal and Sehnal 2007).

Temperature also largely influences the number of beetle generations and sister broods $^{\text{Fig.1;A(3)}}$ (i.e., new brood(s) produced by re-emerged parental beetles in the same year), which in turn determine population density and attack pressure in the current and following season. In species with a multivoltine cycle, such as *I. acuminatus*, *I. sexdentatus* and *I. typographus,* and *D. frontalis*, high summer temperatures can promote the emergence of more than one generation per year and increase the number of sister broods (Ungerer at al. 1999; Colombari et al. 2012; Pineau et al. 2017; Netherer and Hammerbacher 2022). In the case of *D. ponderosae* and *D. rufipennis* species, the development of beetle populations at high elevations or northern latitudes can be limited by cold temperatures, needing more than one year to complete a generation (i.e., semi-voltine cycle). However, high summer temperatures reduce beetle development time, and prevent facultative prepupal diapause in *D. rufipennis*, allowing it to shift from semi- to univoltine cycles (Six and Bracewell 2015). In addition, the adaptive seasonality in *D. ponderosae* species, allows northern beetles to develop rapidly enough, and southern beetles slowly enough, to maintain univoltine life cycles (Safranyik and Caroll 2006). For *Tomicus* species, all populations have one generation per year, but the number of sister broods may be positively influenced by high summer temperatures (Sauvard 2004, Lieutier et al. 2015).

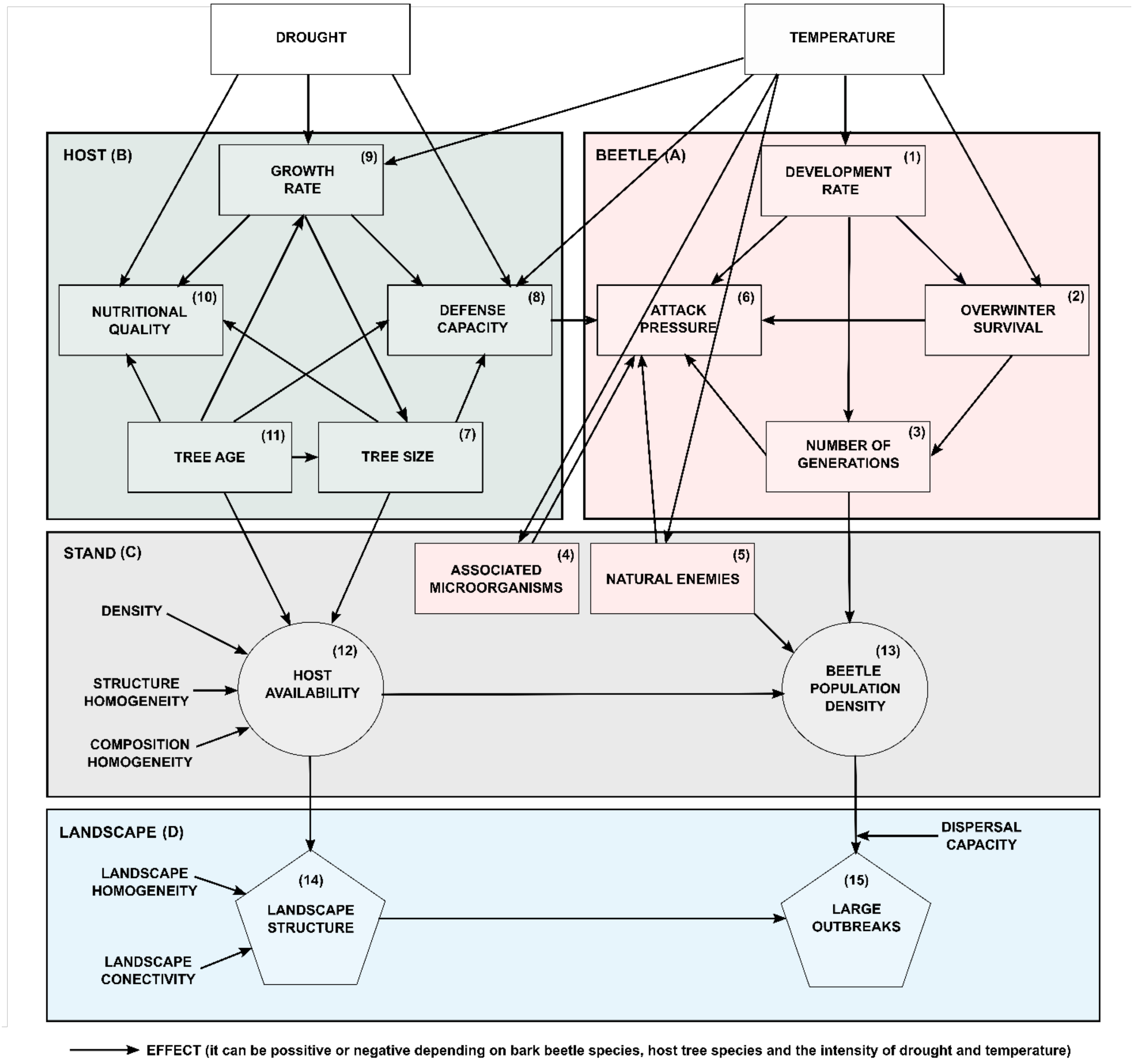

Figure 1. Network of relationships among the different components of the bark beetle-host system, operating from the beetle (A) and individual host trees (B), to the stand (C), and the landscape scale (D) under drought and temperature conditions. The effect among components can be positive or negative depending on bark beetle species, host tree species and the intensity of drought and temperature (see the

main text for a more detailed explanation about each particular effect). Numbers in brackets correspond to superscripts in the main text.

2.3. Transition from endemic to epidemic stage

In most forests, tree-killing bark beetle species are typically found in endemic stage (i.e., low-density populations), which may evolve into an outbreak in case conditions for development become highly favourable (Lantschner and Corley 2023). During the endemic stage, beetles can only overcome the defensive mechanisms of trees weakened by suppression, disease, mechanical damage, or attacked by other insects (Carroll et al. 2006; Boone et al. 2011; Smith et al. 2011; Hroššo et al. 2020). These trees tend to have a smaller diameter with thinner phloem and low nutritional quality, which restricts brood production and limits beetle population, maintaining it at low densities (Bleiker et al. 2014). From this endemic stage, incipient-epidemic beetle populations can develop when large-diameter host trees are successfully attacked due to a local decline in host resistance, which increases beetle population density (Safranyik and Carroll 2006). In *D. ponderosae*, this transition from endemic to incipient-epidemic stage at stand level can be triggered by a combination of preceding biotic and abiotic stressors and high tree density, which promote the spatial aggregation of attacks (Howe 2022). Then, the incipient-epidemic stage is characterized by clumps of infested trees, in which the bark beetle-host system lays at a critical threshold between the transition of beetle populations from an incipient-epidemic stage to an epidemic stage (i.e., outbreaks). Climatic factors such as drought and warm temperatures may promote this transition, such as in *D. ponderosae*, *D. rufipennis* and *I. typographus* (Creeden et al. 2014; Kolb et al. 2016; Marini et al. 2017; Netherer et al. 2019). Importantly, climatic conditions including extreme drought and temperature can disrupt the positive and negative relationships that regulate the dynamics of bark beetle-host systems from their individual components to landscape scale (see Fig. 1). These effects include the alteration of (i) host tree characteristics such as growth rate, defence capacity, and nutritional quality, (ii) beetle characteristics such as life cycle, development rate, and dispersal capacity, (iii) presence of beetle-associated microorganisms and beetle natural enemies, (iv) stand structure and composition, and (v) landscape structure (Wallin and Raffa 2004; Raffa et al. 2005; Simard et al. 2012; Seidl et al. 2016; Howe et al. 2022).

As result of the growth and expansion of local incipient-epidemic populations at the scale of forest stands, the epidemic stage occurs at landscape level. Once the epidemic stage has started, their high population density allows beetles to begin to attack larger and healthier trees that provide more nutritional quality for brood development, although they have a better defence capacity. At endemic levels, trees with higher concentrations of defensive compounds are less likely to be attacked, however, this relationship is reversed during the incipient and epidemic stage (Boone et al. 2011). When the beetle population attacking a given tree surpasses a critical "threshold of attack density," the defensive capacity of the host is exhausted, declining its resistance to subsequent brood development, leading to tree death (Raffa and Berryman 1983; Christiansen et al. 1987). Therefore, as the beetle population grows, the insects can kill more vigorous trees regardless of their stress level (Stephenson et al. 2019). In this situation, the outbreak can be sustained by positive density-dependent feedbacks (Raffa et al. 2008). Another factor to consider is that new beetle generations can develop a higher tolerance to host chemical defences and overcome them even in well defended trees, as has been seen in *D. rufipennis* (Wallin and Raffa 2004). In addition to positive density-dependent feedbacks, the heritability of traits that increase tolerance could explain why some outbreaks continue several years after cessation of a drought and heat event (Ryan et al. 2015). Finally, the collapse of outbreaks occurs during the post-epidemic stage (Safranyik and Carroll 2006) when many trees have been killed and host availability is reduced, and the beetle population declines at densities low enough that insects cannot overwhelm the defences of the remaining healthy trees (Biedermann et al. 2019). Unsuitable weather conditions, such as extremely cold temperatures during the dispersal period, can also play an important role in the collapse of outbreaks, such as in *D. ponderosae* (Sambaraju et al. 2012), as well as predation and parasitism by natural enemies.

3. Host tree resistance

3.1. From tree to regional scale

During the co-evolution of the host tree and bark beetle species, conifers have developed different defence mechanisms against bark beetle attack and their associated microorganisms, such as ophiostomatoid fungi (Raffa 2014; Krokene 2015). These mechanisms are based on constitutive (i.e., preformed) and inducible (i.e., newly-produced under attack) defences comprising mechanical and chemical barriers, which are combined through one to four successive stages (Franceschi et al. 2005; Kolosova and Bohlmann 2012; Celedon and Bohlmann 2019). The first stage of defence reaction is focused on repelling and inhibiting the initial attack using constitutive mechanisms. These include bark anatomical structures difficult to bore and consume by the insects, and chemical compounds such as oleoresin which can flush, repel and seal bark beetle entry. If constitutive mechanisms fail, a second stage based on inducible defences is activated to kill or compartmentalize the beetles that successfully penetrate the host tree. Following the attack, trees respond by increasing the concentration of semiochemicals with inhibitory and toxic effects on attacking beetles and associated fungi and, anatomically, changing the cell structure around the injured tissue to create a necrotic area. The necrotic area is impregnated with defence compounds such as terpenoid and phenolic substances to restrain the infestation and prevent the development of beetle galleries and the growth of associated fungi (Christiansen et al. 1987). In a third stage, the damage tissues are sealed and repaired to limit opportunistic or subsequent infestations

(Franceschi et al. 2005). Finally, once an invading organism is identified, a fourth stage based on acquired or systemic defence can be induced, including the capacity of synthetizing more specialized defence responses, such as gene-for-gene, to inhibit future attacks (Franceschi et al. 2005; Eyles et al. 2010).

Properties of individual trees, such as size, tree age, or phenology can determine tree resistance to bark beetle attacks (see Fig. 1). With regard to tree size$^{\text{Fig.1;B(7)}}$, beetles can easier overcome the resistance mechanisms of smaller trees as they are less effectively defended compared to large trees (Raffa et al. 2016). This is due to host resistance might be influenced by tree age$^{\text{Fig.1;B(11)}}$ (Christiansen et al. 1987). Previous studies have found that chemical defences increased with age in *Pinus contorta*, *Pinus ponderosa* and *Pinus flexilis* (Ferrenberg et al. 2017), while others report that older stems are less chemically defended than younger ones in trees of *P. contorta* (Goodsman et al. 2013). Likewise, the production of bark compounds can vary with tree age, such as volatile organic compounds in *P. abies* that act as repellents of *I. typographus* and have been shown to decrease with age under laboratory conditions (Blažytė-Čereškienė et al. 2015). Smaller trees might therefore be preferred as hosts during endemic stage, for instance by in *D. ponderosae* (Boone et al. 2011). Conversely, species such as *D. rufipennis* and *I. typographus* prefer large-diameter trees, despite they are better defended, because their thicker and more nutritional phloem$^{\text{Fig.1;B(10)}}$ supports the development of larger broods (Reid and Robb 1999; Jenkins et al. 2014; Hroššo et al. 2020). Hence, during epidemic stage, both large and small trees can be attacked successfully.

Tree phenology also influences tree resistance, since trees can be more susceptible to infestation during their growth season, which often coincides with the emergence of adult beetles for reproduction, if more resources are invested into growth than into defense (Rossi et al. 2006;

Krokene 2015). Defence compounds are costly to produce, so periods of fast growth$^{\text{Fig.1;B(9)}}$ could reduce carbon allocation to defences$^{\text{Fig.1;B(8)}}$ (Stamp 2003; Matyssek et al. 2012; Cooper et al. 2018). Indeed, in some *Pinus* species, higher resistance to bark beetle attack has been documented in those trees that invested more resources in the production of resin ducts than in fast growth (Kane and Kolb 2010; Ferrenberg et al. 2014, 2015; Hood and Sala 2015; Kichas et al. 2020). Consistently, in Norway spruce (*Picea abies*), higher levels of constitutive and inducible defences have been found in slow-growing trees (Baier et al. 2002). But this is not a general relationship, since in some cases, such as *Pinus taeda*, higher levels of induced defences were found in fast-growing trees. Allocation of carbon and water into resin production might become a priority only after wounding (Lombardero et al. 2000). In the case of *P. contorta* and *P. albicaulis* such trade-offs between tree growth and defense (e.g., formation of new resin ducts) have not been observed (Mason et al. 2019). In addition to variations between tree species, carbon allocation to growth and defence may differ among populations due to phenotypic variation (Ferrenberg et al. 2023).

Stand-level characteristics including structure (e.g., basal area, stem density, stand density index, stand age, and spatial distribution) and species composition can also influence the resistance to bark beetle infestation according to host availability$^{\text{Fig.1;C(12)}}$ (see Fig. 1) (Fettig et al. 2007). Furthermore, in stands with high basal area or tree density (e.g., stem), high levels of among-tree competition and an associated reduction in tree vigour are expected (Fettig et al. 2014; Kichas et al. 2021). Competition for water, nutrients, and sunlight may limit resource allocation to produce defences against bark beetle attack (Raffa and Berryman 1983; Christiansen et al. 1987).

In terms of species composition and structure, bark beetles' olfactory recognition of host trees is easier in monospecific and even-aged aggregations of trees (Byers 2004; Raffa et al. 2016). Therefore, there is a higher likelihood of increased beetle population density $^{\text{Fig.1;C(13)}}$ (i.e., transition from endemic to epidemic stage) in monospecific, high-density stands with host trees distributed in a clustered pattern (Akkuzu et al. 2017; Aoki et al. 2018), as bark beetle dispersal is favoured among nearby host trees. On the contrary, in mixed forests, the chemical stimuli from non-host trees can produce a “chemical barrier” disrupting host tree recognition by beetles (see "semiochemical diversity hypothesis", Zhang and Schlyter 2004), thus host trees located in mixed stands could go unnoticed (Jactel and Brockerhoff 2007). In addition, bark beetles can avoid areas with non-host volatiles since some bark volatiles and aromatic compounds may indicate the presence of trees that are not suited as hosts (Byers et al. 1998; Schiebe et al. 2011). However, Berthelot et al. (2021) recently reported that the risk of bark beetle infestation of less preferred, host tree genera in mixed forests may increase due to spillover from preferred hosts. Lastly, at landscape and regional scales, the homogeneity and connectivity of the landscape$^{\text{Fig.1;D(14)}}$ can favour beetle dispersal and the development of large outbreaks$^{\text{Fig.1;D(15)}}$ (Chapman et al. 2012). Such epidemics are often driven by drought and high temperatures, which can modulate the cessation or spread of outbreaks across time and space (Aukema et al. 2008; Marini et al. 2012; Preisler et al. 2012; Kolb et al. 2016; Seidl et al. 2016; Howe et al. 2011, 2022).

3.2. Resistance and climate change

Extreme temperatures (i.e., heatwaves) can accelerate the susceptibility of host trees to bark beetle attacks due to their negative effects on tree defence capacity $^{\text{Fig1;B(8)}}$ (see Fig. 1) (Huang et al. 2020). Excessive temperatures influence many tree physiological and biochemical processes, for instance, leading to an increased emission of volatile organic compounds (Holopainen et al. 2018) that bark beetles can detect as a stress signal (Raffa et al. 2016), increased evapotranspiration, and declined photosynthesis (McDowell et al. 2022). Stress physiology is reflected by an increased use of carbohydrates for the maintenance of tree basal metabolism, decreased growth$^{\text{Fig.1;B(9)}}$, and an increment of foliar damage, reducing tree performance and investment in defence (Teskey et al. 2015; McDowell et al. 2022). Therefore, temperatures experienced during heatwaves can lead to weakened trees with less defence capacity to resist bark beetle attacks.

Drought stress, in many cases concomitant with high temperatures, also affects the resistance of host trees (see Fig. 1). Its effects on constitutive and induced tree defences can be negative, neutral, or even positive depending on the intensity and duration of the dry event and tree recovery time (Ayres and Lombardero 2000; Gaylord et al. 2013; Netherer et al. 2015; Kolb et al. 2019; Trowbridge et al. 2021). Moderate water stress might stimulate the production of tree defences, while severe water stress might decrease tree resistance (Lorio 1968). Different tree defence responses are due to the fact that carbon allocation in trees is affected by drought in several ways (Matyssek et al. 2012; McDowell et al. 2022). During moderate drought, tree growth$^{\mathrm{Fig.1;B(9)}}$ is more limited than photosynthesis due to the negative effects on turgor-driven cell growth (McDowell et al. 2022); that might lead to an increase of carbon allocation in secondary metabolites for both constitutive and induced defences$^{\mathrm{Fig.1;seB(8)}}$ (Huang et al. 2020) improving, in turn, tree resistance to bark beetle attack and their associated fungi (Lombardero et al. 2000; Rissanen et al. 2021). On the contrary, extreme and/or long-lasting drought stress induces stomatal closure to reduce transpiration, which diminishes photosynthesis and carbon assimilation, and can eventually lead to a depletion of carbohydrates reserves (McDowell et al. 2008; Mitchell et al. 2013; Choat et al. 2018). Thus, water and carbon scarcity compromise both growth$^{\mathrm{Fig.1;B(9)}}$ and production of secondary metabolites$^{\mathrm{Fig.1;\ B(8)}}$, eventually resulting in slow-growing trees without enough defensive capacity to cope with bark beetle attack and their associated fungi (Rolland and Lempérière 2004); but also potentially reducing the host tree acceptance by bark beetles, as it has been seen in *P. abies* by *I. typographus* (Netherer et al. 2015). However, the threshold at which drought stress constrains tree defence remains uncertain, mainly due to a scarcity of enough evidence linking carbohydrates, hydraulics mechanisms and defensive compounds in field experiments of host mature trees (Huang et al., 2020; McDowell et al. 2022).

4. Changes in patterns of bark beetle outbreaks related to observed climate change

As explained above, warm temperatures and drought conditions influence the dynamics of bark beetle-host systems and have facilitated, to some extent, past outbreaks (Berg et al. 2006; Hebertson and Jenkins 2008; Sambaraju et al. 2019; Negrón and Huckaby 2020). However, current patterns of bark beetle outbreaks documented in North America and Europe appear to be different from past observations (i.e., mid- to late 20th century), suggesting that changes in some key factors such as climate are responsible for these emerging new patterns (Raffa et al. 2008; Bentz et al. 2010; Pureswaran et al. 2018; Fettig et al. 2022). First, outbreaks are more frequent, severe, and their duration is longer (Berg et al. 2006; Werner et al. 2006; Marini et al. 2012; Hlásny et al. 2021) This may result from warming temperatures which could be enhancing the number of beetle generations per year of multivoltine bark beetle species (Colombari et al. 2012; Siitonen 2014; Marini et al. 2017; Netherer and Hammerbacher 2022). Second, the spatiotemporal synchronicity between outbreaks may be increasing. Outbreaks of several bark beetle species are occurring simultaneously at regional scales (Økland et al. 2005; Aukema et al. 2006; Sherriff et al. 2011). Third, some bark beetle species are extending their distribution beyond their historical range, spreading geographically (Carroll et al. 2004; Weed et al. 2013; Siitonen 2014) and with the risk of behaving as invasive species, such as *D. ponderosae* (Cudmore et al. 2010). Finally, some bark beetle species are infesting new and previously non-recorded coniferous species, suggesting expansions in host tree preferences (Logan et al. 2010; Cullingham et al. 2011; Raffa et al. 2013).

The global trade of wood products can increase the risk of beetle invasive species and host preference switches (Lantschner et al. 2017).

4.1. North America

In the last two decades, a dramatic number of coniferous trees have been killed by bark beetles across millions of hectares from Mexico to Canada (Fettig et al. 2022). Only in the western United States, during 2000-2018, more than 36 million forest ha were affected by outbreaks of tree-killing species belonging to *Dendroctonus* and *Ips* genera (Hicke et al. 2020; USDA 2020). Particularly, *D. ponderosae* and *D. rufipennis* caused much of the tree mortality over major forested areas (Bentz and Klepzig 2014). For instance, in British Columbia (Canada), *D. ponderosae* outbreaks have resulted in the mortality of mature *P. contorta* trees over 14 million ha (Woods et al. 2010), converting the forest from a net carbon sink to a carbon source (Kurz et al. 2008). Although the mechanisms that contribute to such widespread outbreaks are complex, there is strong evidence that climate change is amplifying the joint influence of insect disturbances and tree stress induced by warming conditions and extreme drought events, leading to devastating effects on forests (Bentz et al. 2010; Preisler et al. 2012; Seidl and Rammer 2017).

Some studies suggest that irruptive bark beetle outbreaks across North America are primarily being driven by the influence of warming on beetle life cycles, whereas drought-induced reduction of host defences appear to be a secondary driver, such as for *D. rufipennis* outbreaks in *Picea engelmannii* forests (Pettit et al. 2020). This has been seen in south-central Alaska and Yukon Territory since the 1990s, where consecutive years of warmer temperatures have promoted massive and spatiotemporally synchronized *D. rufipennis* outbreaks (Berg et al. 2006; Sherriff et al. 2011). For other bark beetle species, the effects of drought conditions on the host tree appear to be the most determinant in driving recent outbreaks, as in *D. rufipennis* (Hart et al. 2014, 2017) and *Ips confusus* infestation in western North America (Breshears et al. 2005; Kleinman et al. 2012; Kolb et al. 2019). For *D. ponderosae* and *D. frontalis*, both warming and drought conditions greatly influence ongoing impact and expansion (Preisler et al. 2012; Weed et al. 2013; Sidder et al. 2016; Cooper et al. 2018; Lombardo et al. 2023). This reveals that climate change effects on beetle outbreaks and the response of host populations vary both regionally and among different bark beetle-host systems, likely due to differences in bark beetles life cycles and critical feedbacks loops that coordinate host tree species responses (Reed and Hood 2021).

The response of host tree populations under the interacting effects of drought and bark beetle disturbances have also varied across species' distribution ranges. For instance, stands of *Pinus edulis* with historically suitable climatic conditions for tree populations were more damaged by bark beetle outbreaks concurrent with a recent severe drought event (Kleinman et al. 2012; Lloret and Kitzberger 2018). Similar patterns were observed for *P. engelmannii* forests attacked by *D. rufipennis* in the Southern Rocky Mountains (Jaime et al. 2022b). In addition, warming temperatures can facilitate range shifts of bark beetle species by turning climatically unsuitable habitats for these insects into suitable ones, or vice versa (Ungerer et al. 1999; Williams and Liebhold 2002; Sambaraju et al. 2019). In *D. ponderosae*, its evolutionary potential (e.g., selection for cold tolerance) to adapt to novel habitats and the removal of climatic constraints (Samarasekera et al. 2012) has allowed its range expansion to northern areas in Canada, where the number of attacks has increased in regions that were not climatically suitable in the past (Carroll et al. 2004; Cudmore et al. 2010; de la Giroday et al. 2012). Moreover, the range expansion of this beetle species could allow it to infest other coniferous species, such as *Pinus banksiana*, throughout zones in which this tree species hybridizes with lodgepole pine at its western range edge in north-central Alberta (Cullingham et al. 2011).

4.2. Europe

Bark beetle outbreaks - mostly caused by tree-killing species belonging to *Ips* and *Tomicus* genera are an important driver of the recently doubled tree mortality across Europe, in combination with other disturbances and stressors (Lieutier et al. 2004; Senf et al. 2018; Pattaca et al. 2022). The most injurious species is *I. typographus*, which has attacked a large part of the European spruce forests in the last decades (Seidl et al. 2014; Georgiev et al. 2022). Only in the Czech Republic, more than 23 million m^3 of *P. abies* trees were killed by *I. typographus* beetles during 2017-2019 (Hlásny et al. 2021). In central and eastern Europe, the transition of bark beetle populations from an endemic to an epidemic stage has been typically triggered by windthrows, which damage host trees and provide large amounts of breeding material (Schelhaas et al. 2003; Mezei et al. 2017; Seidl et al. 2017; Hroššo et al. 2020). However, the severity of recent outbreaks and the decline of host tree resistance also appear to be modulated by increased climatic variability, waves of hotter-droughts, and synchronicity of extreme weather events across European landscapes (Rouault et al. 2006; Seidl et al. 2016; Senf and Seidl 2018; Neumann et al. 2017; Netherer et al. 2019). The spatio-temporal synchronicity of these weather factors can promote the increase of bark beetle populations, according to the Moran effect (Tobin et al. 2023).

Unprecedented events of extreme drought concomitant with very high temperatures in 2003, 2015, and 2018 (Hanel et al. 2018) have promoted bark beetle attack and beetle populations' growth over Central European forests (Rouault et al. 2006; Schuldt et al. 2020; Jaime et al. 2022a). Notably, regional summer droughts and prolonged water stress are triggering infestation pulses of *I. typographus* on spruce tree populations (Seidl et al. 2016). Severe water-limiting conditions decrease *P. abies* resistance to bark beetle attack due to impaired constitutive defence traits, such as resin flow (Netherer et al. 2015). Similarly, recent drought events are weakening the resistance of *Pinus sylvestris* populations to bark beetle attacks (Rebetez and Dobbertin 2004; Krams et al. 2012; Jaime et al. 2022a), particularly in locations with historically suitable climatic conditions (Jaime et al. 2019). Moreover, warmer temperatures are promoting population increases of the most frequent bark beetle species that attack this pine: *T. piniperda*, *T. minor*, *I. sexdentatus*, and *I. acuminatus* (Lieutier et al. 2004; Dobbertin et al. 2007; Wermelinger et al. 2008).

Warming temperatures can also shift the voltinism of beetles from one to two or even three generations per year, allowing the increase of population size and the likelihood of outbreaks (Bentz and Jönsson 2015). Multivoltinism has been observed in the last decades in populations of *I. typographus* in northern Europe (Jönsson et al. 2009, 2011) and *I. acuminatus* in the south-eastern Alps (Colombari et al. 2012). Further, dry summers are also altering the distribution and aggressiveness (i.e., capacity to kill healthy trees) of secondary bark beetle species, such as *I. acuminatus*, with increased attack levels on *P. sylvestris* trees in southern Finland (Siitonen 2014).

5. Outbreak predictions under climate change scenarios

The observed changes in historical bark beetle-host dynamics foreshadow extensive modifications in forest ecosystems as climate change accelerates. Global warming is predicted to dramatically affect the frequency, magnitude, and distribution of bark beetle outbreaks (Bale et al. 2002; Biedermann et al. 2019). In North America, increases in mean temperature will increase the risk of *D. ponderosae* outbreaks in higher elevations and northern latitudes (Sambaraju et al. 2012). By contrast, at lower elevations and latitudes, further warming could reduce the current climatically suitable habitat for this beetle species (Williams and Liebhold 2002; Evangelista et al. 2011; Sidder et al. 2016) by disrupting its adaptive seasonality (Logan and Powell 2001). For *D. rufipennis*, warming will also promote expansions to higher altitudes, mediated by alterations in spruce forests susceptibility (DeRose et al. 2013). Accordingly, simulations under climate change scenarios predict a drought- and beetle-induced reduction of large *P. engelmannii* trees, which may trigger a shift in forest composition and structure (Temperli et al. 2015; Foster et al. 2018). For other *Dendroctonus* species, such as *D. frontalis*, climatically suitable habitat will continue to increase over time towards northern latitudes and higher elevations (Evangelista et al. 2011; Lesk et al. 2017).

In Europe, cumulative forest growing stock affected by *I. typographus* could be strongly amplified into the future, with projected increases between 59%, under a moderate climate scenario (RCP 4.5), to 205%, under a hot climate scenario (RCP 8.5) (Kausrud et al. 2012; Sommerfeld et al. 2020), as result of the development of more beetle generations per year (Jönsson et al. 2011). Such increase in beetle abundance and attack pressure will reduce the dominance of *P. abies* in the forested landscape of many European countries (Sommerfeld et al. 2020). For other *Ips* species, such as *I. sexdentatus*, more generations per year are also expected to increase beetle population levels, triggering more frequent outbreaks under future climate scenarios (Pineau et al. 2017). However, warmer temperatures could alter the interactions between bark beetles and their natural enemies adding complexity to future predictions (Wermelinger et al., 2021).

Despite the accelerated beetle population development and the drought-induced decline in host resistance associated with climate change, the emerging forest composition and landscape structure could be less susceptible to subsequent infestation in both North America and Europe. Empirical and simulation studies revealed that past bark beetle outbreaks exerted negative feedbacks on subsequent ones (Kashian et al. 2011; Hart et al. 2015; Temperli et al. 2015), mainly due to shifts in tree species composition and the reduction of host availability. Accordingly, future predictions indicate that ongoing beetle-induced changes in forest structure and composition could dampen future outbreak dynamics (Thom et al. 2017; Honkaniemi et al. 2020). However, other studies indicate that such negative feedbacks may not fully compensate favourable outbreak conditions in areas where host trees are still abundant (Sommerfeld et al. 2020) or are recovered over time, evidencing the complexity of predicting the effects of climate change on bark beetle-host systems.

Changing climatic conditions will also affect the habitat suitability and, in the long-term, the distribution of host tree species (McKenney et al. 2007; Fei et al. 2017; Dyderski et al. 2018; Kelsey et al. 2018). Under warmer and highly fluctuating environmental conditions, coniferous species could locally disappear, potentially migrating to other areas, or persist by adapting to new conditions. Species-specific responses will depend on multiple factors such as phenotypic variation and plasticity, acclimation capacity, fecundity, dispersal ability, and biotic interactions (Aitken et al. 2008). For instance, range contractions of major host tree species are predicted at low latitudes, such as *P. sylvestris* in Europe and *P. engelmannii* in North America (Rehfeldt et al. 2006; Matias et al. 2017; Dyderski et al. 2018), whereas range expansions are predicted towards higher altitudes and latitudes. Since shifts in host trees' distribution will determine, in turn, range shifts of their attacking bark beetle species (Temperli et al. 2013, 2015), further attention will be needed to study the combined behaviour of bark beetle and conifers distribution under climate change scenarios.

6. Research needs and priorities

As outlined in the previous sections, multiple factors govern beetle infestation and current and future patterns of beetle activity. Therefore, understanding the response of components of different bark beetle-host systems to climate change requires addressing a multiplicity of issues.

(1) Given that the components of the bark beetle-host system and their complex interactions are not equally affected by climate changes, it is essential to better discern how the bark beetle-

host system's temperature- and water-dependent processes will be affected (Anderegg et al. 2015; Ryan et al. 2015). This question demands additional studies to specifically assess the performance of the different relationships of bark beetle-host systems and increasing drought and temperature (Fig. 1). For instance, long-term field studies designed to measure the climate change effects on the complex interactions between host trees, bark beetles, microorganisms associated, and natural enemies are needed (Wermelinger et al. 2021; Hofstetter et al. 2022). Since climate-induced responses may vary among different bark beetle-host systems (Reed and Hood 2021), the analysis of their influence on host tree physiology and beetle life cycle dynamics should be analysed for each specific system. The quantification of the net effects of climatic parameters on species-specific bark beetle and host tree populations may be suitable for this purpose, in which net effects could result from different functions to assess the change of bark beetle and host tree traits in relation to climate parameters. The integration of this information into modelling approaches will enhance predictions of host tree resistance and infestation trends under more frequent and extreme weather events.

(2) Development of additional methods to scale up from tree- to stand-level susceptibility are needed. At stand scale, no consistent patterns have been identified to explain why some host tree populations are more susceptible to outbreaks, while others maintain beetle populations at an endemic stage. It has been shown how drought weakens individual host trees and makes them more susceptible to bark beetle attack (Gaylord et al. 2013; Kolb et al. 2019; Netherer et al. 2015). However, the translation from individual trees to stand susceptibility is not straightforward, and in some cases, it is more determined by warming conditions that promote beetle development than by the effects of drought stress on trees (Pettit et al. 2020). Indeed, similar climatic conditions may be experienced distinctly by different beetle and host tree species. Therefore, the application of

standardized indices across species, such as species climatic suitability or the location of populations within the species' climatic niche obtained from ecological modelling, could be useful to assess the response patterns of both host tree and insect populations and to anticipate stand mortality episodes driven by bark beetles under increasingly frequent extreme weather events (Lloret and Kitzberger 2018; IPCC 2019; Jaime et al. 2019, 2022b).

(3) Early detection of bark beetle attack in which trees have yet to show visual signs of infestation stress will be crucial to relate the point in time of infestation with weather data, particularly under extreme climatic periods. In addition to supporting management actions aiming to minimize outbreak's impacts, this would allow a better understanding of the effects of climate change on outbreak emergence and to identify host tree populations that are more susceptible to be affected. New technologies such as satellite-derived data or LiDAR have shown potential to develop tools for early detection of beetle activity and parametrize spatiotemporal models of outbreak dynamics (Meddens and Hicke 2014; Hart and Veblen 2015; Hais et al. 2016; Abdullah et al. 2019; Rodman et al. 2021). Moreover, chemical-based techniques such as using trained dogs or drones with gas sensor arrays could allow optimizing the early detection of beetle-attacked trees (Johansson et al. 2019; Paczkowski et al. 2021).

(5) Characterizing thresholds of change in forest ecosystems to anticipate regime shifts (i.e., sudden changes to a new system state) is a pressing scientific issue. At landscape scale, more frequent and extensive bark beetle outbreaks can exceed the historical boundaries of the resilience of forest ecosystems, causing long-term impacts on ecosystem structure and community dynamics (Raffa et al. 2008; Bentz et al. 2010; Thom et al. 2017). Importantly, ecosystem legacies of previous climatic, biotic, and human-induced disturbances may also determine forest resistance to subsequent outbreaks (Johnstone et al. 2016; Kannenberg et al. 2020; Sommerfeld et al. 2020).

Additional research fully integrating the climatic and legacy effects on both beetle and host tree historical distribution ranges could better estimate forest resilience to ongoing and future outbreaks.

(5) Risk assessment considering insect invasiveness into new areas, the potential for tree hybridization under changing tree species distribution, and tree susceptibility to native and invasive bark beetle species is crucial to anticipate future invasions and derived impacts. Climate change, international trade, and land use are leading to an increase in the number of invasive plant and insect species with important ecological and economic impacts (Marini et al. 2011; Lantschner et al. 2020). Many bark beetle species have already been established in regions outside their native range (Faccoli et al. 2020), with potentially far-reaching impacts on the dynamics of native host trees (Lantschner et al. 2017). Similarly, homogeneous plantations of exotic conifers offer excellent opportunities to previously, non-aggressive native bark beetles to extend their distribution range, resulting in increased damage and, in some cases, becoming significant pests (Bertheau et al. 2009; Branco et al. 2015; Howe et al. 2021). The integration of the bark beetle-host species climatic niche (Jaime et al. 2022a) would allow more accurate predictions of the expected patterns of species distribution changes under climate change scenarios.

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