Universitat Autònoma de Barcelona

Role of the species climatic niche on the insect-host system under drought episodes

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Role of the species climatic niche on the insect-host system under drought episodes

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Abstract

In the last decades, extreme weather episodes related to anthropogenic climatic change have enhanced the frequency and magnitude of biotic disturbances, causing worldwide mortality of forests. Particularly, changes in temperature and precipitation regimes are altering the relationships between host tree populations and their attacking insects as insect-host systems are highly sensitive to climate variation. Nevertheless, it is still not largely understood how climate interacts with the different components of the insect-host system and determines its response at different spatiotemporal scales.

In this thesis, I aim to address whether the species climatic niche explains the response of coniferous host tree populations to major abiotic and biotic disturbances, such as drought and bark beetles. For this purpose, I used niche modeling tools to standardize the climatic conditions experienced by host trees and their attacking insects, obtaining different indices and measures to explore their relevance in determining: host tree mortality and infestation at tree- and stand-scale (Chapter 2); outbreak dynamics at regional scale (Chapter 3); and forest resistance to bark beetle attack considering different insect-host systems (Chapter 4).

Specifically, in Chapter 2, I assessed whether the climatic suitability of both host tree and bark beetle species, together with tree and stand attributes, explained the tree mortality and stand infestation of Scots pine populations that experienced drought and bark beetle attack in the northeast of the Iberian Peninsula. At tree-level, I found that mortality was determined by tree size and intensity of beetle attack, smaller trees being more susceptible to die. At stand-level, infestation was negatively associated with tree density and basal area, and positively associated with tree richness. Notably, host tree populations located in historically suitable climatic areas were more susceptible to infestation, particularly when such locations were also suitable for bark beetle species. However, the relationships found with tree and stand attributes suggested that the studied host populations were attacked by beetle populations at an endemic phase (i.e.,

low-density). Such results highlighted the need to examine whether infestation patterns across species' climatic suitability ranges were maintained when beetle populations transitioned to an epidemic phase (i.e., outbreak) and how the climatic variability experienced prior and during the outbreak episode influence the response of the insect-host system. Therefore, in Chapter 3, I analyzed the role of different indices of tree and beetle climatic suitability, together with forest attributes, in the dynamics of spruce beetle outbreak on Engelmann spruce populations during 14 years at the Southern Rocky Mountains. I estimated the host and insect historical climatic suitability, its variability, and the climatic suitability during the outbreak episode. Three spatiotemporal approaches were considered to analyze outbreak dynamics, from the cumulative overall response to the year-to-year patterns of outbreak initiation and spread. Similar to the results obtained in Chapter 2, host tree populations living in historically suitable climatic areas were more susceptible to experience an outbreak. The analyses also revealed that during the outbreak episode, especially for outbreak initiation, the occurrence of suitable climatic conditions for beetle populations was more important than a severe loss of climatic suitability for the host trees. This fact was also reflected in year-to-year patterns. Low levels of outbreak initiation and spread were mainly determined by host climatic suitability, while massive amounts of outbreak initiation and spread were determined by beetle climatic suitability during the episode together with forest attributes. Such results emphasized the importance of including different temporal scales to unravel the major drivers underpinning the dynamics of insect-host systems. Finally, in Chapter 4, I used species niche characterization within a common environmental space of different insect-host systems to assess the resistance of European coniferous forests to bark beetle disturbance. Specifically, I analyzed the overall and species-specific forest resistance to bark beetle attack and subsequent tree mortality in relation to the distance to species climatic niche optimum, drought conditions, and forest attributes. The results showed that a confluence of predisposing and promoting factors determined the overall forest resistance to beetle attack. Particularly, I found that monospecific forests close to both host

tree and beetle climatic optimums were less resistant to beetle attack, especially when such forests experienced long-lasting moderate droughts. However, factors determining forest resistance to beetle attack varied among insect-host systems, likely due to critical feedbacks driving the dynamics of the attacking bark beetle species involved. Contrastingly, once attacked, forest resistance to subsequent tree mortality was driven by the occurrence of previous drought events of long duration and intensity. These results highlight the need to consider the particularities of different insect-host systems as different predisposing and promoting factors might determine their response to climatic alterations.

This Thesis exposes important insights from a species climatic niche perspective about how climate determines the susceptibility patterns of host tree populations to be affected by bark beetle disturbance. Notably, the position of tree populations within the species' climatic niche is relevant to explain these patterns across different insect-host systems and study scales. Additionally, the combination of analyzing both host tree and bark beetle species climatic niche gains importance under the influence of extreme weather conditions. These insights have important implications to better anticipate the response of forests to beetle disturbance under the ongoing global climate change.

Para Allegra

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  Jaime, Luciana; Batllori, Enric & Lloret, Francisco. Effects of climatic change on the insect-host system: the case of bark beetles. To be submitted to *Landscape Ecology.*

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Other articles as a result of collaborative research during my Ph.D. period.

- 2021. Elvira, Nuria J; Lloret, Francisco; **Jaime, Luciana**; Margalef-Marrase, Jordi; Pérez Navarro, M. Ángeles & Batllori, Enric. Species climatic niche explains post-fire regeneration of Aleppo pine (Pinus halepensis Mill.) under compounded effects of fire and drought in east Spain. *Science of The Total Environment* 798. https://doi.org/10.1016/j.scitotenv.2021.149308

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Chapter 1

Introduction

1.1. Scientific framework.

During the last decades of anthropogenic-driven changes in temperature and precipitation regimes (IPCC, 2019), worldwide forests have been increasingly dying due to biotic disturbances such as insect outbreaks (McDowell et al., 2020; Seidl et al., 2017; Weed et al.2013). The systems composed of a host tree and its attacking insect are highly sensitive to climatic variability, particularly to extreme weather episodes (Lehmann et al., 2020). Therefore, understanding the response of such insect-host systems to changing climate is necessary to assess current and future outbreaks and their consequences to forests' dynamics and resilience.

Bark beetles are among the most important biotic agents affecting forests dynamics. First, bark beetles inhabit natural and managed forests over the globe (Hulcr et al., 2015). Second, the dynamics of these insect-host systems may become eruptive, undergoing natural outbreaks and extensive tree mortality, which can scale up from local to regional extent (Raffa and others, 2015a). 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 distribution geographically and even their host tree preferences (Weed et al., 2013). Fourth, bark beetles strongly impact forest ecosystems' processes and structure, affecting size classes distribution, species composition, successional dynamics and disturbance regimes (e.g., wildfires), carbon stocks, nutrient cycling, and hydrology (Morris et al., 2017). Bark beetle disturbance has, therefore, important consequences on ecosystem services that pose great challenges for the future.

Given the great relevance of bark beetle disturbance in the current context of climate change and the need to better understand the role of climate on bark beetle-host systems (insect-host systems, hereafter), I review the existing evidence of the influence of climatic factors on insect-host dynamics. First, I explain the general bark beetle biology and the relationship between beetles' life cycle and climatic factors. Then, I examine the mechanisms of host tree resistance and its relationship with changing climatic conditions. These aspects provide the conceptual basis for assessing the factors characterizing current outbreak dynamics and those that may promote the transition from endemic to outbreak phases under future climates. Finally, I identify present major research needs and priorities to contextualize the aims and scope of this thesis.

1.2. General biology of bark beetles.

Bark beetles are a group of insects classified in the subfamily Scolytinae (Latreille, 1804) within the diverse family Curculionidae, order Coleoptera (Latreille, 1802, Linnaeus, 1758). 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 conifer forests can cause important ecological and economic impacts (Hicke et al., 2016; Lindgren & Raffa, 2013; Morris et al., 2017; Sommerfeld et al., 2018). This review is focused on this group of conifer tree-killing species, with particular emphasis on *Dendroctonus*, *Ips,* and *Tomicus* genera.

Bark beetles have a small body size and live in tunnels built inside plant tissues, excepting a short period during their imago stage. Larvae mostly feed on the phloem situated between the bark and the wood (bark beetles *sensu stricto*) or upon fungi in the sapwood (ambrosia beetles) of the host tree species. Imagoes of bark beetles *sensu stricto* excavate galleries into the phloem for brood production, in which several parts of the tree can be used: main trunk, branches, cones, and roots. However, each genus and even many species are usually restricted to a particular part of the tree. This habitat differentiation may permit the coexistence of different bark beetle species in the same host tree (Amezaga & Rodríguez, 1998; Ayres et al., 2001; Schlyter & Anderbrant, 1993).

In general, bark beetles emerge as imagoes from their brood galleries in spring or summer to disperse, seek a mate, and find a new susceptible host tree when the natal host is depleted (Raffa et al., 2015). Beetles' flight capacity determines their dispersal distance, which varies among species, but usually does not exceed a few hundred meters (Jactel, 1991; Werner & Holsten, 1997; Williams et al., 2008). In addition, the success of these flights can be determined by the beetle's fitness, the distribution of susceptible new hosts, and weather conditions (Jones et al., 2019; Kautz et al., 2016). For instance, long-distance dispersal is favored by wind (Nilssen, 1984), as it has been seen in *Dendroctonus ponderosae* (de la Giroday et al., 2011).

Once pioneer beetle individuals, either males or females depending on the species, find a susceptible new host, they produce aggregation pheromones to promote conspecific recruitment and mediate a mass attack (Blomquist et al., 2010). The success or failure of the mass attack relies on the beetle's population density and the defensive capacity of the affected tree (Boone et al., 2011). Although tree-killing bark beetle species are capable of incurring host tree mortality alone, in some cases, associated phytopathogenic fungi may be critical for detoxifying or exhausting tree defenses (Hofstetter et al., 2015; Six & Wingfield, 2011). When tree defenses are overwhelmed, bark beetles release anti-aggregation pheromones to prevent subsequent infestations and minimize conspecific competition (Wood, 1982). A tree is typically available for one or two beetle generations each year, depending on host size, host nutritional quality, and the infesting bark beetle species (Raffa et al., 2016).

As poikilotherm insects, temperature highly determined beetles' life cycle (Bale et al., 2002; Logan et al., 2003). Warm temperatures can favor beetle development$^{\text{Fig.1.1; A(1)}}$, increasing reproduction rates$^{\text{Fig.1.1; A(2)}}$, and reducing the duration of their life cycle (Preisler et al., 2012; Rouault et al., 2006; Sherriff et al., 2011). Likewise, high temperatures in winter can increase the survival rates of overwintering beetle populations$^{\text{Fig.1.1; A(3)}}$ (Ayres & Lombardero, 2000; Miller & Werner, 1987) and promote the emergence of more than one generation per year, especially in those species with a multivoltine cycle (Colombari et al., 2013; Pineau et al., 2017; Schebeck et al., 2017). In addition, temperature influences phenological timing$^{\text{Fig.1.1; A(4)}}$, which determines the degree of synchrony of bark beetle emergence and mass attack (Bentz et al., 2010), and the development of associated microorganisms and bark beetle predators[Fig.1.1; A(5)] (Six & Wingfield, 2011; Wegensteiner et al., 2015). Consequently, the positive effects of temperature on the beetle life cycle increase the attack success[Fig.1.1; A(6)] and the beetle population density[Fig.1.1; A(13)]. However, this success can be limited under extreme temperatures experienced during heatwaves due to negative effects on beetle development[Fig.1.1; A(1)], reproduction[Fig.1.1; A(2)], and lifespan when species-specific temperature thresholds are surpassed (Jactel et al., 2019; Rouault et al., 2006).

1.3. Host tree resistance.

From tree to regional scale

During the co-evolution of the host tree and bark beetle species, conifers have developed two major defense mechanisms against bark beetle attack and their associated microorganisms, such as phytopathogenic fungi (Franceschi et al., 2005; Raffa et al., 2005). The first mechanism is a constitutive physical defense (i.e., preformed) based on resin ducts which can mechanically seal the entrance holes built by attacking beetles (Ferrenberg et al., 2014; Kane & Kolb, 2010). The second mechanism is an inducible chemical defense (i.e., newly-produced under attack) based on terpenoid and phenolic compounds with inhibitory and toxic effects on attacking beetles and associated fungi (Raffa & Berryman, 1983). This latter mechanism is only activated when the physical defense fails and bark beetles successfully infest the host tissues. Once a tree part is infested, the concentration of defense compounds increases, and the cell structure around the injured tissue changes to form a necrotic area. The necrotic area is impregnated with defense compounds to restrain the infestation and prevent the development of beetle galleries and the growth of associated fungi (Christiansen et al., 1987). Moreover, such inducible mechanisms can also repair damaged tissue and limit opportunistic or subsequent infestations (Franceschi et al., 2005).

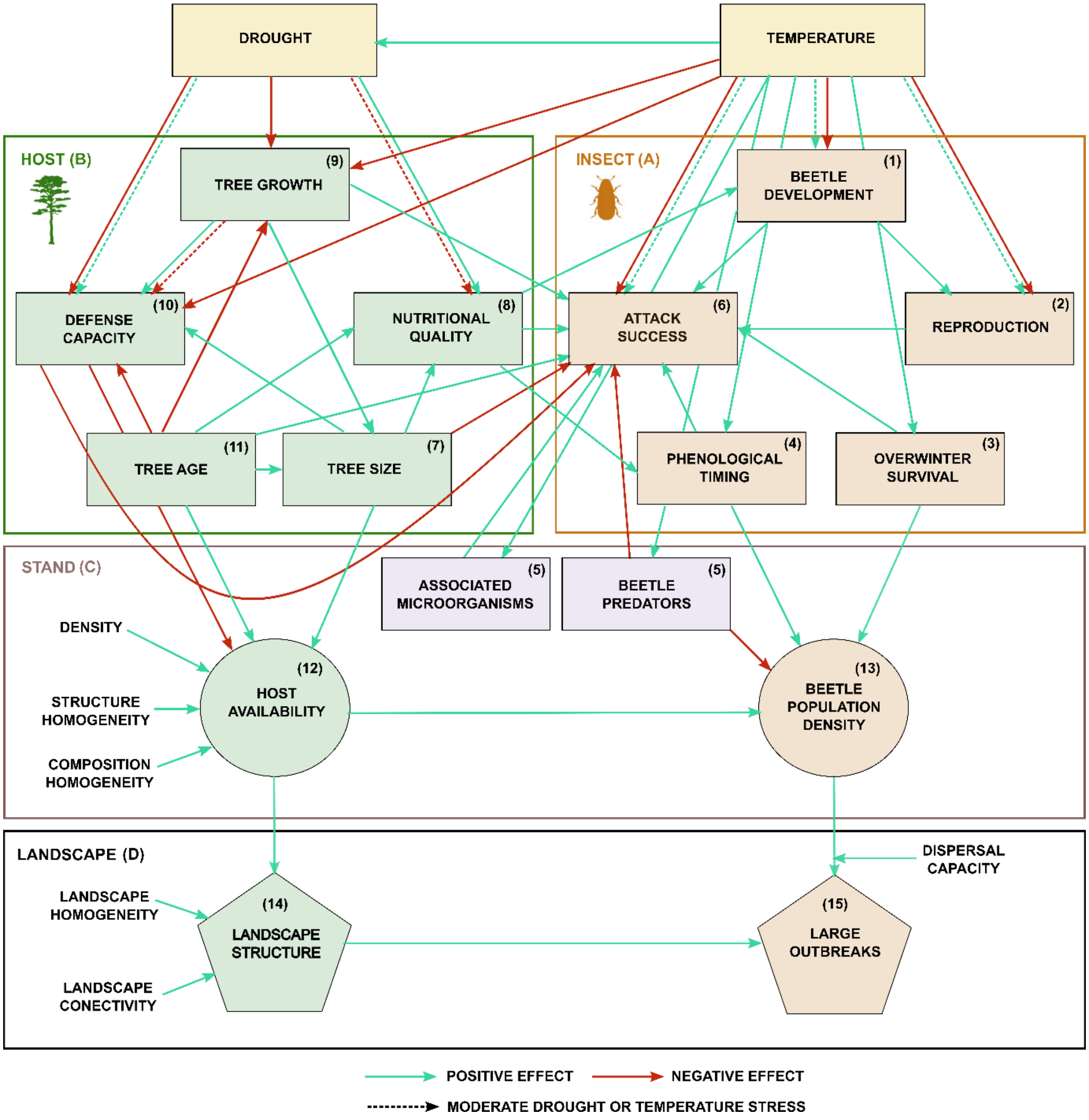

Figure 1.1. Network of relationships among the different processes involved on the insect-host system, operating from the individual, to the stand, and the landscape scale under climate, as indicated by green and red arrows. The effect of the relationships can vary with the intensity of drought and warming, as seen by shifting colors when moderate levels of drought or temperature are attained (discontinuous arrows). Numbers in brackets correspond to superscripts in the main text.

Properties of individual trees, such as size$^{\text{Fig.1.1; B(7)}}$, can determine tree resistance to bark beetle attacks. Generally, small trees are poorly defended compared to large trees, and beetles easily overcome their resistance mechanisms (Raffa et al., 2016). However, despite being better defended, beetles preferentially select large-diameter trees because their thicker and more nutritional phloem$^{\text{Fig.1.1; B(8)}}$ allows the development of larger broods (Boone et al., 2011; Reid & Robb, 1999). Tree phenology also influences tree resistance since trees can be more susceptible to infestation during the growing season (Krokene, 2015; Reeve et al., 1995; Rossi et al., 2006). Defense compounds are costly to produce, so periods of fast growth$^{\text{Fig.1.1; B(9)}}$ could reduce resource allocation to defenses$^{\text{Fig.1.1; B(10)}}$ (Cooper et al., 2018; Herms & Mattson, 1992; Stamp, 2003). Indeed, in some *Pinus* species, higher resistance to bark beetle attack has been documented in those trees that invested more resources in producing resin ducts than in fast-growing (Ferrenberg et al., 2015; Ferrenberg et al., 2014; Hood & Sala, 2015; Kane & Kolb, 2010). In Norway spruce, higher levels of constitutive and inducible defenses have been seen on trees with slow-growing (Baier et al., 2002). However, this is not a general relationship, since in some cases, such as *Pinus taeda*, higher levels of induced defenses were found in fast-growing trees (Lombardero et al., 2000). Also, host resistance declines with age-related senescence$^{\text{Fig.1.1; B(11)}}$. Hence older trees may be more susceptible to a great variety of insects and pathogens (Christiansen et al., 1987; Kulakowski et al., 2016).

Stand-level characteristics such as structure (e.g., basal area, stem density, stand age, and spatial distribution) and species composition can also influence the resistance to bark beetle infestation according to host availability$^{\text{Fig.1.1; C(12)}}$ (Fettig et al., 2007). For instance, in stands with high basal area or density, high levels of among-tree competition and presumably reduced tree vigor are expected (Fettig et al., 2014). Competition for water, nutrients, and sunlight may limit resource allocation to produce defenses against bark beetle attacks (Christiansen et al., 1987; Raffa & Berryman, 1983). In terms of species composition and structure, homogeneous stands with trees distributed on a clustered pattern are more susceptible to infestation (Akkuzu et al., 2017; Aoki et al., 2018), because for bark beetles, olfactory recognition of host trees is easier in monospecific and even-aged aggregations of trees (Byers, 2004; Raffa et al., 2016). Such characteristics of stand structure and composition can increase the availability of host trees to be attacked, resulting in a positive effect on beetle population density$^{\text{Fig.1.1; C(13)}}$.

On the contrary, in mixed forests, the chemical stimuli from non-host trees can produce a "chemical barrier" disrupting host tree recognition by beetles (Zhang & Schlyter, 2004). Specifically, many volatile compounds from non-host trees show a repellent effect in bark beetles (Byers et al., 1998), thus host trees located in mixed stands could go unnoticed by these insects (Jactel & Brockerhoff, 2007). Lastly, at landscape and regional scales, the homogeneity and connectivity of the landscape$^{\text{Fig.1.1; D(14)}}$ can favor beetle dispersal and the development of large outbreaks$^{\text{Fig.1.1; D(15)}}$ (Chapman et al., 2012), modulating the cessation or maintenance of outbreaks across time and space (Seidl et al., 2016).

Resistance and climate change

Heatwaves can accelerate the susceptibility of host trees to bark beetle attacks due to their negative effects on tree defense capacity (Huang et al., 2020). Excessive temperatures disrupt many tree physiological processes, including photosynthesis, transpiration, and the production of volatile organic compounds. This is reflected in a consumption of carbohydrates for the maintenance of tree basal metabolism, decreased growth $^{\text{Fig.1.1; B(9)}}$, and an increment of foliar damage, reducing tree performance and investment in defense $^{\text{Fig.1.1; B(10)}}$ (Teskey et al., 2015). Therefore, high temperatures can lead to weakened trees with less defense capacity to resist bark beetle attacks. Additionally, the increase of temperature in tree phloem favors beetle development (Powell & Bentz, 2009).

Drought stress, in many cases concomitant with high temperatures, also affects the resistance of host trees. Its effects on constitutive and induced tree defenses can be negative, neutral, or even positive depending on the intensity and duration of the dry event and tree recovery time (Ayres & Lombardero, 2000; Gaylord et al., 2013; Kolb et al., 2019). According to the Growth – Differentiation Balance Theory (GDB; Herms & Mattson 1992), moderate water stress would stimulate tree defenses, while severe water stress would decrease tree resistance. Under moderate drought, tree growth [Fig.1.1; B(9)] is more limited than photosynthesis due to the negative effects on turgor-driven cell growth; that leads to an increase of carbon allocation to constitutive defenses [Fig.1.1; B(10)] improving, in turn, tree resistance to bark beetle attack (Koontz et al., 2021; Lombardero et al., 2000). On the contrary, under extreme drought stress, trees close stomata to reduce transpiration, drastically reducing photosynthesis and carbon assimilation. Water and carbon scarcity compromises both growth [Fig.1.1; B(9)] and the production of secondary metabolites [Fig.1.1; B(10)] (Reeve et al., 1995), resulting in slow-growing trees without enough defensive capacity to cope with bark beetle attacks (Rolland & Lempérière, 2004). In addition, under the influence of drought stress, trees decay [Fig.1.1; B(11)] more quickly and release concentrated nutritional compounds [Fig.1.1; B(8)] that enhance beetle population development (White, 2015). Importantly, carbon starvation and hydraulic failure of the host tree both under extreme and long-lasting droughts or under several successive short cycles of water stress can be determinants of tree resistance capacity (Lieutier, 2007; McDowell et al., 2008).

1.4. From endemic to epidemic phase.

Tree-killing bark beetle species are typically found at an endemic phase (i.e., low-density populations) in most of the forests that they may eventually attack massively (Fig. 1.2; A). During the endemic phase, beetles can only overcome the defensive mechanisms of weakened trees by suppression, disease, or mechanical damage, which are scattered over the forest (Carroll et al., 2006; Hroššo et al., 2020). These trees tend to have thin phloem and low nutritional quality, which restricts the brood production and limits the beetle population, maintaining it at low-densities (Bleiker et al., 2014). From these small epicenters of infestation, usually as clumps of infested trees, the insect-host system is at a critical threshold between the transition of beetle populations from an endemic to an epidemic phase (i.e., outbreak; Fig. 1.2; B), in which, for instance, climatic factors such as drought conditions and warm temperatures can promote or avoid this transition (Creeden et al., 2014; Kolb et al., 2016; Marini et al., 2017). Importantly, drought and temperature can disrupt the positive and negative relationships that regulate the dynamics of insect-host systems from their individual components to landscape scale (Fig. 1.1). This includes the alteration of (i) host tree characteristics such as growth, defense capacity, and nutritional quality, (ii) beetle characteristics such as life cycle, development, and dispersal capacity, (iii) presence of associated microorganisms and beetle predators, (iv) stand structure and composition, and (v) landscape structure (Raffa et al., 2005; Seidl et al., 2016; Simard et al., 2012; Wallin & Raffa, 2004).

Once the epidemic phase has started, beetles begin to attack larger and healthier trees that provide more nutritional quality for brood development, although they have a better defense capacity (Boone et al., 2011). At this point, the efficacy of the host defense capacity varies in relation to beetles' population density. Specifically, 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 mortality (Christiansen et al., 1987; Raffa & Berryman, 1983). Therefore, as the beetle population grows, insects can kill more vigorous trees regardless of their defensive of stress level (Stephenson et al., 2019). Another factor to consider is that the new beetle generations developed after infestation can tolerate and overwhelm host tree defense chemicals, even in well defended trees (Franceschi et al., 2005; Wallin & Raffa, 2004). The heritability of such beetles' increased tolerance could explain, in part, why some outbreaks continue several years after cessation of a drought and heat event (Ryan et al., 2015). Finally, the collapse phase (Fig. 1.2; C) occurs when the outbreak massively kills the host trees, and the beetle population declines until densities low enough that insects cannot kill new healthy trees (Biedermann et al., 2019). Unsuitable weather conditions, such as extremely cold temperatures, can also play an important role in the collapse of outbreaks (Sambaraju et al., 2012).

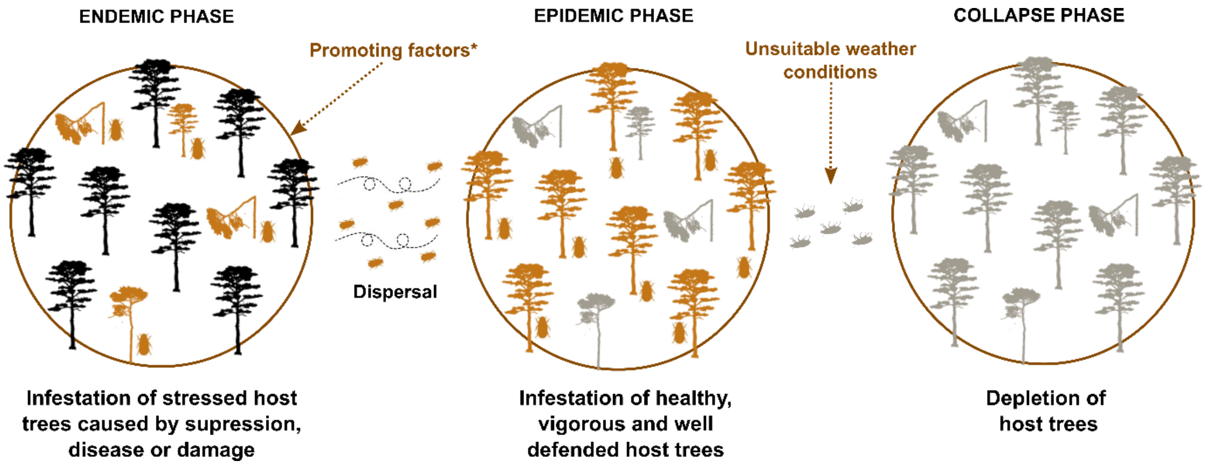

Figure 1.2. Transition from an endemic phase to an epidemic (outbreak) and collapse phase. *The promoting factors include the increasing drought stress and temperatures which influence the components of the insect-host system (Fig. 1.1). Black, orange, and grey trees correspond to healthy, infested, and dead trees, respectively.

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

As explained above, warm temperatures and drought conditions influence the dynamics of the insect-host system and have facilitated, to some extent, past outbreaks (Berg et al., 2006; Hebertson & Jenkins, 2008; Negrón & Huckaby, 2020; Sambaraju et al., 2019). However, particularly in North America and Europe, current patterns of bark beetle outbreaks appear to be different from past observations, suggesting that changes in some key factors such as climate are responsible for these emerging new patterns (Bentz et al., 2010; Raffa et al., 2008). First, the synchronicity between outbreaks has increased. Outbreaks of several bark beetle species are occurring simultaneously at regional scales (Aukema et al., 2006; Økland et al., 2005; Sherriff et al., 2011). Second, outbreaks are more frequent, their duration is longer, and host trees are dying faster (Meddens & Hicke, 2014). 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; Marini et al., 2017; Siitonen, 2014). Third, some bark beetle species are extending their distribution beyond their historical range, spreading geographically (Carroll et al., 2004; Cudmore et al., 2010; Siitonen, 2014; Weed et al., 2013), with the risk of behaving as invasive species. Finally, associated with range expansions, some bark beetle species are infesting new and previously non-recorded coniferous species, suggesting changes in host tree preferences (Cullingham et al., 2011; Logan et al., 2010; Raffa et al., 2013).

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. Only in the western United States, during 2000-2018, more than 36 million forest hectares were affected by outbreaks of tree-killing species belonging to *Dendroctonus*, *Scolytus,* and *Ips* genera (USDA, 2015, 2020). Particularly, the mountain pine beetle (*Dendroctonus ponderosae*) and the spruce beetle (*Dendroctonus rufipennis*) caused much of the tree mortality over major forested areas (Bentz & Klepzig, 2014). For instance, in British Columbia (Canada), mountain pine beetle outbreaks have resulted in mortality of mature lodgepole pine (*Pinus contorta*) over 14 million ha (Woods et al., 2010). 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, warming conditions, and extreme drought events, leading to devastating effects on forests (Bentz et al., 2010; Preisler et al., 2012; Seidl & 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 defenses appear to be a distant, secondary driver of the recorded outbreaks (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 synchronized spruce beetle outbreaks (Berg et al., 2006; Sherriff et al., 2011). In other cases, however, the effects of drought conditions on the host tree appear to be most determinant in driving recent outbreaks, such as in spruce beetle (Hart et al., 2014; Hart et al., 2017) and pinyon beetle (*Ips confusus*) infestation in western North America (Breshears et al., 2005; Kleinman et al., 2012). For other species, such as the mountain pine beetle, both warming and drought conditions greatly influence outbreak severity and expansion (Cooper et al., 2018; Preisler et al., 2012; Sidder et al., 2016). This reveals that climate change effects on beetle outbreaks and the response of host populations vary both regionally and among different insect-host systems, likely due to differences in critical feedbacks that drive beetle population dynamics as well as physiological differences among host tree species (Reed & Hood, 2021).

The response of host tree populations under the interacting effects of drought and bark beetle disturbances have also varied across species' distribution range. For instance, stands of pinyon pine (*Pinus edulis*) with historically suitable conditions for tree populations were more damaged by bark beetle outbreaks concurrent with a severe drought event (Kleinman et al., 2012; Lloret & Kitzberger, 2018). In addition, temperature increases can cause range shifts of bark beetle species by turning climatically unsuitable habitats to these insects into suitable ones, or vice versa (Sambaraju et al., 2019; Ungerer et al., 1999; Williams & Liebhold, 2002). In the case of the mountain pine beetle, its distribution range is expanding to northern areas in Canada, such as British Columbia, 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). The range expansion of the mountain pine beetle has also allowed this species to infest other coniferous species, such as the jack pine (*Pinus banksiana*) at its western range edge in north-central Alberta (Cullingham et al., 2011).

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). The most injurious species is the European spruce beetle (*Ips typographus*), which has attacked a large part of the European spruce forests in the last decades (Seidl et al., 2014). Only in the Czech Republic, more than 23 million m^3 of Norway spruces (*Picea abies*) were killed by European spruce 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 phase 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 and waves of hotter-droughts (Netherer et al., 2019; Neumann et al., 2017; Rouault et al., 2006).

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). Notably, regional summer droughts and prolonged water stress are triggering infestation pulses of the European spruce beetle on spruce populations (Seidl et al., 2016). Severe water-limiting conditions also impair Norway spruce resistance to bark beetle attack due to decreased constitutive defense compounds (Netherer et al., 2015). Similarly, drought events are weakening the resistance of Scots pine (*Pinus sylvestris*) populations to bark beetle attacks (Krams et al., 2012; Rebetez & Dobbertin, 2004). Moreover, warmer temperatures are promoting population increases of the most frequent bark beetle species that attack Scots pines, *Tomicus piniperda*, *Tomicus minor*, *Ips sexdentatus,* and *Ips acuminatus* (Dobbertin et al., 2007; Lieutier et al., 2004; Wermelinger et al., 2008).

Warming temperatures can also shift the voltinism of beetles from one to two or even three generations per year, increasing outbreaks' likelihood (Bentz & Jönsson, 2015). Multivoltinism has been observed in the last decades in populations of *I. typographus* in northern Europe (Jönsson et al., 2009; Jönsson et al., 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 Scots pine trees in southern Finland (Siitonen, 2014).

1.6. Outbreak predictions under climate change scenarios.

The observed changes in historical insect-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 mountain pine beetle outbreaks in higher elevations and northern latitudes (Sambaraju et al., 2012). By contrast, at lower elevations and latitudes, warming could reduce the current climatically suitable habitat for this beetle species (Evangelista et al., 2011; Sidder et al., 2016; Williams & Liebhold, 2002). This result from alterations in its seasonal life cycle, such as the emergence of adults at an appropriate time of the year to overwhelm host defenses (Logan & Powell, 2001). For the spruce beetle, 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 Engelmann spruce trees, which may trigger a shift in forest composition and structure (Temperli et al., 2015). For other species, such as the western pine beetle (*Dendroctonus brevicomis*), climatically suitable habitat will continue to increase over time (Evangelista et al., 2011).

In Europe, outbreaks of the European spruce beetle could be strongly amplified, with projected increases between 59% to 221% in outbreak activity (Kausrud et al., 2012; Sommerfeld et al., 2020), as a result of the development of more beetle generations per year (Jönsson et al., 2011). Outbreaks' increase could reduce the dominance of Norway spruce on the landscape (Sommerfeld et al., 2020). For secondary forest pests, such as the pine bark beetle *I. sexdentatus*, more generations per year also are expected to increase beetle population levels, triggering more frequent outbreaks under future climate scenarios (Pineau et al., 2017).

Despite the accelerated beetle population development and the drought-induced decline in host resistance associated to climate change, the emerging forest composition and landscape structure could be less susceptible to infestation in both North America and Europe. Empirical and simulation studies revealed that past bark beetle outbreaks exerted negative feedbacks on subsequent ones (Hart et al., 2015; Kashian et al., 2011; 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 activity (Honkaniemi et al., 2020; Thom et al., 2017b). However, other studies indicate that such negative feedbacks may not fully compensate for the increased beetle activity (Sommerfeld et al., 2020), evidencing the complexity in predicting the effects of climate change on insect-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). Under warmer and highly fluctuating environments, coniferous species could be locally extinct, 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, 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 Scots pine in Europe and Engelmann spruce in North America (Dyderski et al., 2018; Matías et al., 2017; Rehfeldt et al., 2006), whereas range expansions are predicted towards higher altitudes and latitudes. Changes in host trees' distribution will determine, in turn, range shifts of their attacking bark beetle species.

1.7. Research needs and priorities.

As outlined in the previous sections, multiple factors govern beetle infestation and current and expected patterns. Understanding the response of insect-host systems to climate change requires, therefore, addressing a multiplicity of issues.

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

how the insect-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 the insect-host system to increasing drought and temperature (Fig. 1.1). The analyses should also include the interactions between relevant factors determining such relationships. In addition, climate-induced responses may vary among insect-host systems (Reed & Hood, 2021), making it necessary to analyze the influence of host tree physiology and beetle life cycle dynamics in each system. The integration of this information into modeling 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 is needed. At stand scale, no consistent patterns have been identified to explain why some host tree populations are more susceptible to be affected by an outbreak, while others maintain beetle populations at an endemic phase. 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). However, the translation 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, such as species climatic suitability, 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 & Kitzberger, 2018).

(3) Early detection of bark beetle attack in which trees have yet to show visual signs of infestation stress will be crucial to better understand the promoting factors of 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 a strong potential to develop tools for early detection of beetle activity and parametrize spatiotemporal

models of outbreak dynamics (Meddens & Hicke, 2014; Hart & Veblen, 2015; Abdullah et al., 2019; Rodman et al., 2021).

(4) 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 (Bentz et al., 2010; Raffa et al., 2008; Thom et al., 2017a). 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 host-insect invasiveness into new areas, tree hybridization, 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 (Lantschner et al., 2020; Marini et al., 2011). 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, 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).

1.8. Thesis aims and scope.

Given the complexity of insect-host systems and the important knowledge gaps that continue to exist about their response to climate change, the major aim of my thesis is to elucidate how climatic factors determine the patterns of bark beetle infestation and host tree mortality from local to regional scale. For that, I used niche modeling tools to standardize the climatic conditions experienced by host trees and insects and to assess the dynamics of different insect-host systems across space and time.

1.8.1. The species niche as integrator factor of the insect-host system response to climate change.

The niche concept emerged at the beginning of the 20th century with Grinnell (1917) and Elton (1927) and was formalized by Hutchinson (1957, 1978), who defined the niche as the n-dimensional set of abiotic and biotic suitable conditions within which a species or population can grow, reproduce, and survive, maintaining its persistence. Hutchinson distinguished between the *fundamental niche*, as the full range of the environmental conditions that a species can occupy and use in the absence of limiting factors such as competition, and the *realized niche*, as the subset of the fundamental niche in which species can persist in the presence of limiting factors, such as other species competing for resources. From the niche concept, it is inferred that species distribution ranges are the geographical translation of their environmental requirements in the n-dimensional space, which constitutes the base of species distribution modeling (Colwell & Rangel, 2009; Soberón & Peterson, 2005). Such modeling approaches have been broadly applied in biogeography, ecology, conservation biology, and studies of climate change (Guisan & Thuiller, 2005; Zimmermann et al., 2010).

Species distribution models (SDMs), also known as environmental niche, envelope or habitat models, represent a suit of methods that predicts the distribution of a species across the geographic space and time using environmental data (Franklin, 2010). There are several techniques of SDMs, spanning from correlative to mechanistic models (Dormann et al., 2012). Purely mechanistic models, also called process-based models, predict species distributions using mathematical functions of ecological processes (e.g., physiology, demography, and dispersal) that link the performance of a species with a range of environmental variables, being an approximation to the species *fundamental niche* (Kearney & Porter, 2009). However, these models are not widely used due to their high experimental data requirements, which is especially challenging to obtain across the entire biogeographic species range. Conversely, purely correlative models predict species distributions by describing relationships between geographic species occurrence (or abundance) and the environmental conditions where species occur, without explicit consideration of ecological processes, but implicitly including biotic interactions and dispersal limitations (Sillero, 2011). This approach, therefore, approximates to the species *realized niche* (Colwell & Rangel, 2009; Kearney, 2006). Since correlative models are the most used, an important number of different algorithms have been developed (e.g., Maxent, GLMs, GAMs, Random Forests). In all cases, the algorithms provide quantitative outputs ranged between 0 and 1 that, based on climatic variables, can be interpreted as an index of climatic suitability for populations of a given species in a given place (Franklin, 2010; Sexton 2006). Such suitability indices allow comparisons between populations of the same species or among coexisting species, for instance, to correlate them with the degree of forest decay or tree mortality resulting from extreme weather events, such as droughts (Margalef-Marrase et al., 2020).

Species occurrences and environmental variables can also be used to characterize the species niche directly within the n-dimensional space (Blonder et al., 2014; Broennimann et al., 2012). Contrary to SDMs, such niche characterization allows to obtain parameters other than climatic suitability, such as niche breadth, niche optimum, and niche edge, as well as to quantify niche similarity and overlap between species or populations. Importantly, this method also allows assessing the influence of inter-annual variability in the species climatic niche. Both techniques, SDMs and niche characterization, can be used as standardization tools as they permit comparisons of environmental niches among species. As such, they allow integrating the response of the insect-host system at different spatiotemporal scales to detect patterns of response under extreme episodes of warming and drought stress.

1.8.2. Objectives.

In this thesis, I aim to assess whether the response of the insect-host systems from individual trees to regional scale can be explained from a species niche perspective, assuming the correspondence between population performance and their position within species niche (MacArthur, 1972; Sexton et al., 2009). Additionally, I also aim to assess the influence of other factors that, together with species suitability, may determine the response of the insect-host system, such as tree characteristics and stand attributes. My thesis intends to provide insights to answer two major open questions: "Why some host tree populations are infested and killed by bark beetles while others resist and maintain low beetle populations?" and "How does the interaction between the components of the insect-host system vary across the species´ climatic niche and how it is affected by extreme weather conditions?". To that, I defined specific questions and objectives in different host-insect systems that are specified in the chapters listed below:

- **Chapter 2:** What factors determine host tree mortality and infestation at tree and stand scale?

In this chapter, I explored the likelihood of the host tree mortality by bark beetle attack and the stand susceptibility to be infested. For that, I surveyed Scots pine populations located in the northern Iberian Peninsula, which experienced drought-induced mortality and bark beetle infestation. At the tree-level, I examined the role of tree characteristics and host climatic suitability in the likelihood of being attacked and killed by bark beetles. At the stand-level, I assessed the role of stand attributes and the influence of insect-host climatic suitability in the likelihood of stand infestation.

- **Chapter 3:** What factors drive outbreak dynamics, initiation and spread, at regional scale?

In this chapter, I assessed the role of the host and insect climatic suitability, together with forest attributes, in the dynamics of spruce beetle outbreaks in the Southern Rocky

Mountain Ecoregion during the 2000-2014 period. To do so, I analyzed outbreak dynamics considering different spatiotemporal approaches spanning from the overall cumulative outbreak at the regional scale to the yearly patterns of outbreak initiation and spread across the landscape.

- **Chapter 4:** What factors determine forest resistance to bark beetle disturbance considering different insect and host tree species?

In this chapter, I assessed the resistance of forests dominated by five conifer species across Europe to beetle disturbance caused by five bark beetle species. Specifically, I investigated the role of the host and beetle species niche optimum (obtained by niche characterization), the duration and intensity of previous drought events, and forest characteristics in the overall and species-specific responses of forest resistance to beetle attack and subsequent tree mortality.

Chapter 2

Scots pine (*Pinus sylvestris* L.) mortality is explained by the climatic suitability of both host tree and bark beetle populations

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Abstract

Higher temperatures and extreme drought events are promoting insect-driven tree mortality. However, there is great uncertainty about the impact of extreme climatic variations on the susceptibility to infestation, as this depends on the suitability of climatic conditions to both host trees and insects. For instance, the consequences of infestation could be more intense in tree populations living closer to the limits of tree species' climatic tolerance, where resource allocation to defenses could be compromised by other functions essential to tree survival. In this article, we explored 22 Scots pine populations in the northeast of the Iberian Peninsula that experienced a tree mortality episode involving bark beetle infestation and drought. We hypothesized that the infestation and eventual tree mortality varied according to the climatic suitability of a particular location for the host tree and bark beetles. Climatic suitability values were estimated by using Species Distribution Models. Then, we developed generalized linear mixed-effects models and partial least squares-generalized linear models to study tree mortality and stand bark beetle infestation (proportion of dead trees presenting signs of a successful attack) in relation to host and insect suitability, intensity of bark beetle attack, tree characteristics, and stand structure. At tree-level intensity of bark beetle attack and tree size were the main factors determining the probability of tree mortality. Smaller trees in particular exhibited a higher likelihood of dying at lower intensities of beetle attack. At stand-level, bark beetle infestation was negatively associated with tree density and basal area of Scots pine, and positively with tree species richness. Taken together, the response of Scots pine populations in relation to the tree characteristics and stand structure suggested low-density attack by bark beetles (i.e., not in epidemic phase) which affected weakened smaller trees. Remarkably, our results showed that Scots pine populations established in higher climatic suitability areas were susceptible to infestation, particularly when such locations were also suitable for the bark beetle species. Therefore, previous drought events and differential resource allocation for growth and defenses among central and

peripheral tree populations seem to regulate infestation patterns, as mediated by the climatic suitability for both hosts and insects. Our study demonstrates the importance of assessing species' climatic suitability to better understand and anticipate tree mortality episodes driven by bark beetles, particularly under climate scenarios with increasingly frequent extreme weather events.

2.1. Introduction.

Extreme climatic variability related to climate change has been linked to increased mortality of coniferous tree species around the globe due to acute drought, heat, and associated insect outbreaks (Allen et al., 2010; Das et al., 2013; García de la Serrana et al., 2015; Logan et al., 2003; Raffa et al., 2008). Specifically, the contribution of bark beetles (Curculionidae: Scolytinae) to tree mortality has emerged as a major disturbance under the context of global climate change (Anderegg et al., 2015). Unprecedented outbreaks in North America and Europe, in which some bark beetle species have killed billions of coniferous trees across vast areas (e.g., Rouault et al., 2006; Bentz et al., 2010; Meddens et al., 2012; Seidl et al., 2016) and the expansion of the geographic range of native beetle species into new areas (Økland et al., 2019; Siitonen, 2014; Weed et al., 2013) indicate that disturbance regimes associated with insect-driven tree mortality are changing. Furthermore, extreme weather events such as drought episodes are likely to affect local tree populations differently across their geographic distribution range (Hampe & Petit, 2005). However, there are still many uncertainties about how drought interacts with other co-drivers, particularly bark beetle infestation, in modulating the vulnerability and mortality of host tree populations across climatic gradients (Creeden et al., 2014; Gaylord et al., 2013).

Several studies of insect-driven tree mortality have determined that the emergence of outbreaks of infestation depends on the habitat conditions, such as tree characteristics and forest structure and composition (Bentz et al., 2010; Jenkins et al., 2014; Raffa et al., 2008). More specifically, monospecific stands with high basal area and high density of the host tree are the most susceptible to bark beetle infestation (Chapman et al., 2012; Fettig et al., 2007; Perkins & Roberts, 2003; Shore et al., 2000), as beetles are more likely to find a susceptible tree and achieve a successful attack (Raffa et al., 2016). Furthermore, trees exhibit differences in their defensive ability to regulate bark beetle populations (Raffa & Berryman, 1983) according to their age, size, and the level of insect attack they support (Krokene, 2015). The insect-host system is also highly sensitive to climatic variability, since warming accelerates beetle development (Bentz et al., 2010; Creeden et al., 2014; Temperli et al., 2015), while severe drought stress disrupts host tree defenses increasing trees' overall susceptibility to infestation (Gaylord et al., 2013; Netherer et al., 2015). Thereby, abiotic disturbances such as severe droughts events create opportunities for host colonization that can lead to a massive increase of insect population levels (Rouault et al., 2006; Wermelinger et al., 2008). This is especially relevant in the ongoing warming scenario and the predicted increase in extreme climatic conditions that will affect the habitat suitability of both insects and hosts (Kirschbaum, 2000; Walther et al., 2002). For instance, the insect-host system could be modified at the edges of the geographic range of tree populations when these correspond to the limits of species' climatic tolerance (Thuiller et al., 2008). Additionally, the emergence of climates favoring bark beetle populations would enhance their attack in places where infestations have not previously been recorded (Buotte et al., 2017; Lantschner et al., 2017).

According to the classic niche theory (Hutchinson, 1978; MacArthur, 1972), disturbances in the phenology, abundance, and ecological interactions of species are more evident in localities with less suitable environmental conditions and higher limitations on population performance due to harsher climatic conditions (Lynch et al., 2014; Morin et al., 2007; Raffa et al., 2015), which often correspond to the edges of the geographic range of a species' distribution (Parmesan, 2006). However, some recent studies have suggested that locally adapted tree populations living close to the edges of a species’ climatic range can be more resistant to extreme drought episodes than core populations (Cavin & Jump, 2017; Lloret & Kitzberger, 2018; Rehm et al., 2015), probably due to genetic adaptations and/or higher plastic responses (Aitken et al., 2008; Hampe & Petit, 2005; Jump & Peñuelas, 2005; Savolainen et al., 2007). In contrast, populations living in localities with more suitable environmental conditions could be less tolerant to extreme climatic fluctuations since they have to invest a higher proportion of resources to maintain high growth rates, basal area, or stand density (Anderegg et al., 2015; Gutschick & BassiriRad, 2003; Jump et al., 2017; McDowell et al., 2008). Based on these premises, tree populations probably respond differently to biotic disturbances if such disturbances take place under environmental conditions within the historical range of variability or during extreme drought episodes. In this work, we propose that the climatic suitability of both the host trees and the insects are involved in the response of tree populations to bark beetle attacks. A better understanding of the consequences of climate change on host-insect dynamics across biogeographical gradients will allow improving and adapting specific management and conservation actions on tree populations.

Scots pine (*Pinus sylvestris* L.) is one of the most widespread conifer species in the world and one of the most abundant trees in Europe, representing a keystone species for many ecosystems. This species reaches its southern distribution limit in the Mediterranean Basin, where it is primarily restricted by a combination of high temperatures and summer drought (Carlisle & Brown, 1968). Scots pine populations located in this region may therefore be particularly sensitive to extreme weather events when these are combined with insect attack (Hampe & Petit, 2005; Matías & Jump, 2012). In fact, drought-induced Scots pine dieback has recently been observed in the Iberian Peninsula (Galiano et al., 2010; Hódar et al., 2003; Martínez-Vilalta & Piñol, 2002), along with variable intensity of insect attacks, particularly of bark beetle species belonging to the *Ips* and *Tomicus* genera (Lieutier et al., 2004). Nevertheless, the contribution of bark beetle attacks to the mortality of Scots pine populations exhibiting drought-induced decline has not been fully addressed (Dobbertin et al., 2007; Krams et al., 2012; Wermelinger et al., 2008).

In this study, we considered the climatic suitability of the host and insect species, inferred from of species distribution models (SDMs), in order to evaluate Scots pine tree vulnerability to die due to bark beetle attack concurrent with a drought event, and the stand susceptibility to being infested by bark beetle (proportion of dead trees presenting signs of a successful attack) in populations from the northeast of the Iberian Peninsula. In particular, we assessed tree-level mortality and stand-level bark beetle infestation in relation to the climatic suitability of both the host tree and insect, tree characteristics, and stand attributes. We examined at tree-level whether (i) larger and closer trees with evidence of bark beetle attack have a greater probability of mortality; (ii) trees living in localities with low values of climatic suitability are more susceptible to die. At stand-level, we studied whether (iii) denser and monospecific stands of the host tree are more prone to be infested; (iv) high insect climatic suitability results in a higher probability of stand infestation by bark beetles, and how this is modulated by the interaction of host-insect suitabilities.

2.2. Material and methods.

Description of the study area

The study was carried out on the northeast Iberian Peninsula (Catalonia, Spain), in locations with evidence of recent Scots pine drought-induced mortality and bark beetle infestation. Scots pine reaches the southernmost and driest limit of its wide natural distribution range in the Iberian Peninsula, where the species occupies large areas in the Pyrenees, along with some marginal populations in central and southern mountain regions (Matías & Jump, 2012). In 2005, the Iberian Peninsula experienced an extreme drought episode that was followed by several dry years until 2014 (EEA, 2017). This drought period affected, among other conifer species, Scots pine populations in Catalonia where various symptoms were detected including tree defoliation, mortality (Banqué-Casanovas et al., 2013; Galiano et al., 2010), and bark beetle infestation (Blanco et al., 2009).

Our study focused on the post-drought period that took place during 2005–2013 (Serra-Maluquer et al., 2018; Tejedor et al., 2017).

We selected 22 different Scots pine populations throughout the species distribution range in Catalonia, to compare the tree mortality and infestation processes along a precipitation gradient (mean distance between populations: 52.4 km, SD: ±37.7 km) (Fig. 2.1). The populations' elevation ranged from 600 to 1600m a.s.l. (above sea level), with mean annual temperatures from 6.5 °C to 13 °C and annual precipitation between 700 and 1100 mm/year (WorldClim, version 2.0., Fick & Hijmans 2017). Sites included pure stands of Scots pine (*Pinus sylvestris*) and mixed stands of Scots pine and holm oak (*Quercus ilex*) or mountain pine (*Pinus uncinata*) with an understory dominated by strawberry tree (*Arbutus unedo*), kermes oak (*Quercus coccifera*), boxwood (*Buxus sempervirens*) and common juniper (*Juniperus communis*) (see Appendix A).

Field data collection

During 2013–2014, a circular fixed area plot (of 314 m^2) was established in each of the 22 selected populations. On each plot, we recorded tree characteristics: the size of all adult trees (diameter at breast height, dbh > 2.5 cm for Scots pine, and dbh > 5 cm for other tree species), identified all trees to species, and registered their status (living or dead). We also recorded the distance from all Scots pine trees to their nearest conspecific neighbor (living or dead) to evaluate their role in tree mortality. A total of 962 Scots pines were sampled.

Within the study region, Scots pine trees were naturally attacked by four bark beetle species: *Ips acuminatus*, *Ips sexdentatus*, *Tomicus minor*, and *Tomicus piniperda*. The relative frequency of insect occurrence in dead infested trees was 58%, 19%, 7%, and 40%, respectively, considering that some trees presented more than one bark beetle species. The identification of each beetle species was principally based on galleries and/or bark beetle imagoes. The distribution in the tree of these four bark beetle species is related to bark thickness. *Tomicus* species concentrates their attack near to the bole base, where the bark is thicker. On the contrary, *Ips* species prefer attack thinner bark, such as that presented by the upper part of the bole, the branches, and smaller trees (Sauvard, 2004). Despite the high relative frequency of *I. acuminatus*, its presence was almost always associated (within stand) with the presence of *T. piniperda* or *I. sexdentatus*, which are considered two of the most damaging pests in Europe and cause significant forest loss every year (Sauvard, 2004).

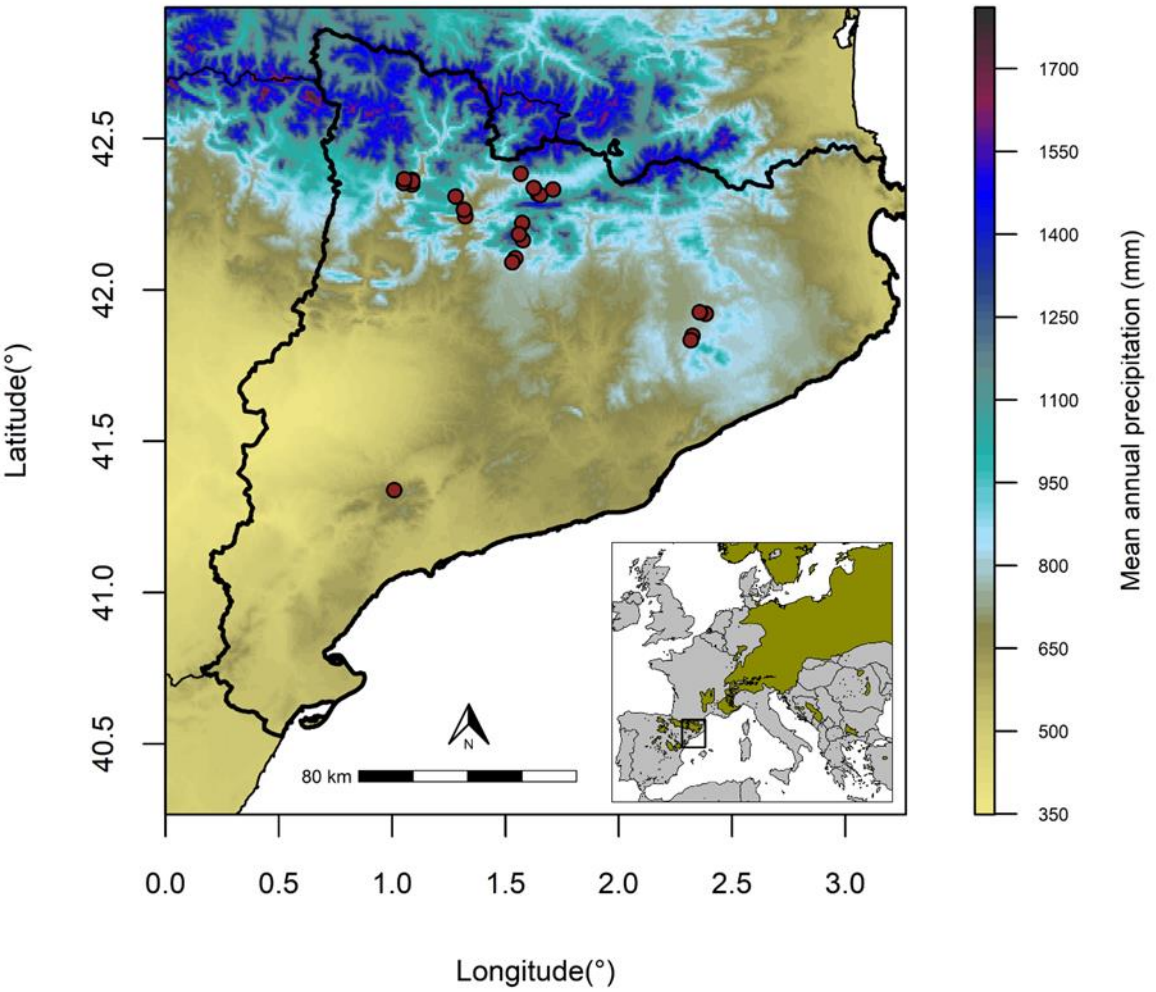

Figure 2.1. Map of the study area in the northeast of the Iberian Peninsula and location of the 22 sampled Scots pine populations (red dots) across the precipitation gradient (mean annual precipitation (mm). The inset map depicts in green the natural distribution range of Scots pine across Europe (source Euforgen; http://www.euforgen.org/).

For all Scots pine individuals, we measured the intensity of attack in a bark sample area of 20 × 30 cm at 130 cm height by counting the number of bore holes. Entrance holes are a common estimate of attack intensity (e.g., Lieutier et al., 1995; Borkowski & Skrzecz, 2016). However, exit holes are often difficult to differentiate from entrance holes, so we considered both exit and entrance holes as a measure of the intensity of attack per m^2. By using this approach, we may have overestimated the attack intensity, since exit holes may be more abundant than entrance ones in successful population; on the other hand, underestimation may occur when multiple individuals use the same entrance hole. In our case, the differentiation of the entrance and exit holes was unreliable, and we thus opted to assume the uncertainty of this measure which overall provides a measure of attack intensity after accounting for overestimation and underestimation effects. Moreover, we visually assessed the presence of bark beetle species outside of the bark sample area using binoculars. Signs of galleries in the branches and the upper part of the stem were considered as a successful beetle attack.

For each plot, we calculated the following attributes to characterize the stand structure and composition: Scots pine density (trees ha^{-1}), Scots pine basal area (m^2 ha^{-1}), tree species richness, and an aggregation index (R) based on the distances to the nearest neighbor recorded for all Scots pine trees (following Clark & Evans, 1954; R package spatstat; Baddeley & Turner, 2006). We used the aggregation index to describe the spatial distribution pattern of the Scots pine trees in each plot. The index is calculated as the ratio between the observed mean distance to the nearest neighbor in the population and the mean expected distance if the trees were randomly distributed. High values of this index ($R > 1$) suggest a regular distribution of trees, low values ($R < 1$) suggest a clustered pattern, and values equal or close to 1 indicate a random distribution. We expected that a clustered host tree pattern was more susceptible to beetle infestation. Finally, bark beetle infestation in each plot was considered as the proportion of dead trees presenting signs of a successful attack (i.e., bore holes and maternal galleries along the tree).

Climatic suitability modeling

We used species distribution models (SDMs) built at the European scale to obtain estimates of the probability of species' occurrences or climatic suitability both for Scots pine and bark beetles, under the averaged climatic conditions that characterize our study sites (1970–2000 period). The assumption behind SDMs is that species occurrences in the geographical space represent the environmental conditions suitable for a given species to reproduce and survive (Soberón & Peterson, 2005). Model outputs can thus be interpreted as a species-specific index of the climatic suitability historically experienced by populations living in a given site (Franklin, 2010) and can be used to evaluate intra- and inter-specific responses (e.g., mortality, decline, and insect infestation) to short-term climatic events (Lloret & Kitzberger, 2018; Pérez Navarro et al., 2019; Sapes et al., 2017). The estimates obtained were subsequently used to assess the contribution of the climatic suitability of the host tree and beetle species in the Scots pine mortality and infestation processes.

Occurrence data

To delineate the distribution of Scots pine, we obtained occurrence records from the 249,410 plots of the European Forest data (Mauri et al., 2017), including a total of 9,368 occurrences. For bark beetle species, sufficient records could only be obtained for two of the four beetle species present in our study stands: 73 occurrences for *T. piniperda* (including the 1998–2014 period) and 100 occurrences for *I. sexdentatus* (including the 1970–2017 period). So, we only used the climatic suitability of these two species in the stand-level analyses of the infestation. For each of these two species, we collated beetle occurrences from different sources, due to the scarcity of records; these sources included the Global Biodiversity Information Facility (GBIF 2018, http://www.gbif.org/), the ICP Forests Level I (Eichhorn et al., 2016), and previously published studies carried out in Europe and the Mediterranean Basin (Gallego & Galián, 2001; Kerdelhué et al., 2002; Kohlmayr et al., 2002; Ritzerow et al., 2004; Vasconcelos et al., 2006; Rossi et al., 2009; Horn et al., 2009; Jankowiak, 2012; Moraza et al., 2013; Olsovsky et al., 2013; Borkowski & Skrzecz, 2016; Pineau et al., 2017). Despite the absence of records of *I. acuminatus* and *T. minor* to obtain their climatic suitability, our analyses were not seriously compromised since a large part of the Scots pine infestation was attributed to *I. sexdentatus* and *T. piniperda*. Besides, both *Tomicus* species and *Ips* species present intra-genera similarities in their life cycle and phenology. *Tomicus* species are monovoltine, with brood development and maturation in the same season, and the necessity of low temperatures to complete their cycle. On the contrary, *Ips* species can be multivoltine if the climatic conditions are favorable, and prefer warmer temperatures to survive during the overwinter (Lieutier et al., 2004). Therefore, based on these similarities and the higher damage potential of *I. sexdentatus* and *T. piniperda*, we considered these two species suitabilities good representatives for analyzing the total stand infestation process that occurred in our study.

Both host tree and beetle occurrence data were filtered for collection year (since 1970) and location to remove taxonomic and geographic inconsistencies. We also filtered occurrences by a minimum distance of 15 km, which corresponds to the coarsest resolution of species' records in our database, in order to deal with aggregated records that may introduce model biases or overfitting in the SDMs (Veloz, 2009). Moreover, we used a land cover layer (Corine Land Cover 2000, version 18.5) to compile appropriate areas of possible hosts for bark beetles (Lantschner et al., 2017), and we thus created a mask, which was then used to select the distribution of each bark beetle generated from SDMs. The mask included the following land cover classes: agro-forestry areas, different types of forest, and semi-natural areas of transitional woodland-shrub with herbaceous vegetation.

Environmental data

SDM climatic predictor variables were selected from the 19 bioclimatic variables available in WorldClim database version 2.0 (Fick & Hijmans, 2017) at a resolution of 30 s (~1 km^2).

The selection was specific to the tree host and bark beetle species based on known climatic factors that influence their biology. In the case of the Scots pine, precipitation and temperature mainly influence seed production, recruitment, and growth of this species (Carlisle & Brown, 1968). Particularly, drier conditions reduce seedling recruitment and survival (Matías & Jump, 2012) and can compromise tree defensive capabilities to the attack of bark beetles (Raffa et al., 2008). For bark beetles, temperature largely controls their life cycles, especially the number of generations per year. High summer and winter temperatures may accelerate beetle development and increase overwinter survival (Sauvard, 2004), and marked differences between the cold and the warm seasons may allow completing beetle cycle (Rossi et al., 2009). Aside from biological aspects, and to prevent multicollinearity among climatic variables, they were also filtered by means of a Variance Inflation Factor (VIF) < 10 as a critical threshold (Quinn & Keough, 2002) and a cluster dissimilarity < 0.8.

Finally, we retained six climatic variables as predictors of the distribution of the two bark beetles species: isothermality (mean diurnal temperature range/temperature annual range), temperature seasonality, mean temperature of the driest quarter, mean temperature of the coldest quarter, precipitation seasonality, and precipitation of the driest quarter. For Scots pine, we used isothermality, temperature annual range, mean temperature of the warmest quarter, annual precipitation, precipitation seasonality, and precipitation of the warmest quarter.

Model algorithm and settings

Given the nature of the data, especially the low number of bark beetle occurrences and the lack of absence data, the algorithm selected to fit the SDMs was MaxEnt software (version 3.4.1, Phillips et al., 2006). This algorithm implements the maximum entropy for modeling species distributions with presence-only data and with a good performance for small number of occurrences (Pearson et al., 2007). Particularly, we standardized the modeling criteria using the same algorithm for the Scots pine and the two bark beetle species.

We experimentally calibrated the three MaxEnt models by tuning the feature classes and regularization multiplier (R package ENMeval, Muscarella et al., 2014). The final settings selected to run each model are described in Table 2.1. To test the models, we used a 5-fold cross-validation for the two bark beetle species models and a 10-fold cross-validation for the Scots pine model (Fielding & Bell, 1997). Then, climatic suitability was obtained by projecting the models over the selected climatic layers. Outputs of the models were averaged across 500 model replicates and a log raw transformation was applied to obtain a climatic suitability value between 0 and 1, as the relative likelihood of species' occurrence in each cell. The models' predictive accuracy was evaluated using the area under the receiver-operating characteristic curve (AUC; Fielding & Bell, 1997), and we also applied jackknife test to measure percent contribution of each variable to the final model.

Tree mortality and stand infestation modeling

Statistical analyses were conducted to evaluate the response of tree-level mortality and stand-level bark beetle infestation. To improve the stability and the accuracy of parameter estimates, we standardized the values of all explanatory variables into dimensionless variables by subtracting the mean value of each variable and dividing them by two standard deviations (Gelman, 2008).

At the tree-level, we used generalized linear mixed effects models (GLMM, R package lme4, Bates et al., 2015) to analyze the vulnerability of Scots pine (mortality) as a function of tree size, distance to the nearest neighbor, intensity of bark beetle attack (regardless of involved species), and climatic suitability of Scots pine. The binary response of tree mortality (living or dead tree) was modeled with a logit-link function and a binomial distribution error structure (Bolker et al., 2008). Starting from the null model, we created a fully crossed set of models, including the saturated model with all the second-order interactions between predictors. All the GLMMs were fitted by Laplace approximation and included "stand" as a random effect. The models were ranked from lowest to highest AICc (second-order AIC; Akaike, 1973) and considered best models (lowest AICc) within 2 AICc units. The final model was selected considering the highest value of marginal and conditional R^2 (R package MuMln, Nakagawa & Schielzeth 2013). The R^2 marginal can be considered as the proportion of variance explained only by fixed effects, whereas R^2 conditional represents the variance explained by both fixed and random effects. To avoid inflated measures of explained variance, we inspected model assumptions and possible model overdispersion in the selected best models (R package blmeco, Harrison, 2014).

At the stand-level, we used the Partial Least Squares (PLS) approach to analyze the susceptibility to stand-level bark beetle infestation, defined as the proportion of dead infested trees in relation to total dead trees. Infestation was modeled as a function of tree density, basal area, richness of tree species, the aggregation index R, Scots pine suitability, and the suitability of two bark beetle species (*I. sexdentatus* and *T. piniperda*). We chose the PLS technique because it is particularly useful for analyzing correlated predictor variables with a small sample compared with the number of predictors (Carrascal et al., 2009); note that we found non-independence between Scots pine and *I. sexdentatus* suitabilities. PLS generalizes and combines principal component analysis and multiple regression features to model relationships between the response and explanatory variables (Bastien et al., 2005). This method deals with collinearity of predictors by constructing "latent" variables, i.e., unobserved variables which underlie the observed collinear variables. The latent variables are calculated to maximize the covariance between the scores of an independent block (X) and the scores of a dependent block (Y). Both X and Y blocks (datasets) are modeled to find out the variables in an X matrix that will best describe the Y matrix (Abdi, 2003). Therefore, this method addresses variability and collinearity at the same time. Interpretation of the relationship between X data and Y data is then simplified, as this relationship is concentrated on the smallest possible number of components. Scores and loading are calculated by successive projections of the data matrix, as described for PCA. However, in the PLS method, the loadings vectors are optimized to capture the covariance between the independent and dependent blocks (Carrascal et al., 2009).

The response variable infestation was assessed as a binomial variable formulated as a two-column matrix holding the number of successes and failures, with an infested dead tree a success and a non-infested dead tree a failure. Therefore, since our response variable followed a binomial error distribution rather than a normal distribution, we used a PLS-GLM with a logit-link function (R package plsRglm, Bastien et al., 2005) to model the infestation process. To build the model, we focused on the independent effect of each predictor and the possible 2- and 3-way interactions between Scots pine and bark beetle species suitability. The meaning of PLS components was derived from the scores and loadings of the original predictors on each component. Predictors' scores explain the signal of their effect and its square value (loadings) the magnitude and importance of the effect on the component. The significance level for predictors in the analysis was established at $P < 0.05$ and the coefficient of non-significant predictors was set at 0. Once the PLS components were obtained, we checked their significance by building a binomial response GLM with them. We selected the best candidate model, considering the smallest AIC and checked model fit and performance by inspecting model assumptions and possible model overdispersion.

2.3. Results.

Climatic suitability modeling

The two bark beetle species SDMs showed good performance accuracy, with mean AUC values higher than 0.75 and a standard deviation lower than ±0.04 (Table 2.1). According to the relative contribution and jackknife test of variables importance, the mean temperature of the coldest quarter had the highest contribution in both the *I. sexdentatus* and *T. piniperda* models, followed by mean temperature of the driest quarter, temperature seasonality, and isothermality. The Scots pine model showed poorer performance than the bark beetle models, with a mean AUC value of 0.67 and a standard deviation of ±0.005 (Table 2.1). According to the relative contribution and jackknife test, the mean temperature of the warmest quarter had the highest contribution, followed by precipitation of the warmest quarter, annual temperature range, and isothermality. Despite the suboptimal statistical accuracy of the Scots pine model, the results obtained yielded a distribution range of the host tree consistent with the ecological requirements of the studied species (Matías & Jump, 2012).

Table 2.1. Description and evaluation of the climatic suitability models built for Scots pine and the two bark beetle species, *T. piniperda* and *I. sexdentatus*. In each case, the model description includes: number of occurrences (N occur.), number of background points (N backg.), feature classes (Feat.) for model fitting (L: Linear, Q: Quadratic, H: Hinge), regularization multiplier (RG), number of K-fold cross-validation, number of climatic variables used (N var.), and the top climate variables listed by their highest contribution in the model. Model evaluation includes the mean area under the receiver-operating characteristic curve (Mean AUC) ± standard errors.

Model description								Model evaluation
Specie	N occur.	N backg.	Feat.	RG	Cross-validation	N var.	Top variables	Mean AUC
Tomicus piniperda	73	10,000	LQH	3.0	5-fold	6	Mean temperature of coldest quarter; Mean temperature of driest quarter; Temperature seasonality; Isothermality	0.81 (±0.03)
Ips sexdentatus	100	10,000	LQH	2.5	5-fold	6	Mean temperature of coldest quarter; Mean temperature of driest quarter; Temperature seasonality; Isothermality	0.79 (±0.04)
Pinus sylvestris	9,368	20,000	LQH	0.5	10-fold	6	Mean temperature of warmest quarter; Precipitation of warmest quarter; Temperature annual range; Isothermality	0.67 (±0.01)

Within the surveyed stands, the SDM-derived climatic suitability values ranged from 0.37 to 0.73 for *I. sexdentatus*, from 0.33 to 0.68 for *T. piniperda*, and from 0.34 to 0.64 for Scots pine, thus indicating great variability between the sites (Fig. 2.2). In general, values of *T. piniperda* climatic suitability were expected to be greater at higher altitude areas with colder temperatures than for *I. sexdentatus*, where warmer areas were more suitable for its survival and development. Scots pine did not present high suitability values in our study sites, probably because this tree species reaches its southern limit of distribution in the Iberian Peninsula.

Determinants of tree mortality and stand infestation

A total of 56.2% (N=541) of the sampled Scots pine trees corresponded to dead trees, of which 78% (N=425) showed signs of bark beetle infestation (Table 2.2). In contrast, only 13% (N=56) of the living trees showed evidence of bark beetle attack. Stands showed different severities of mortality and infestation, ranging from 14% to 82% when considering dead trees in relation to total trees, and from 0% to 100% when considering dead infested trees in relation to total dead trees.

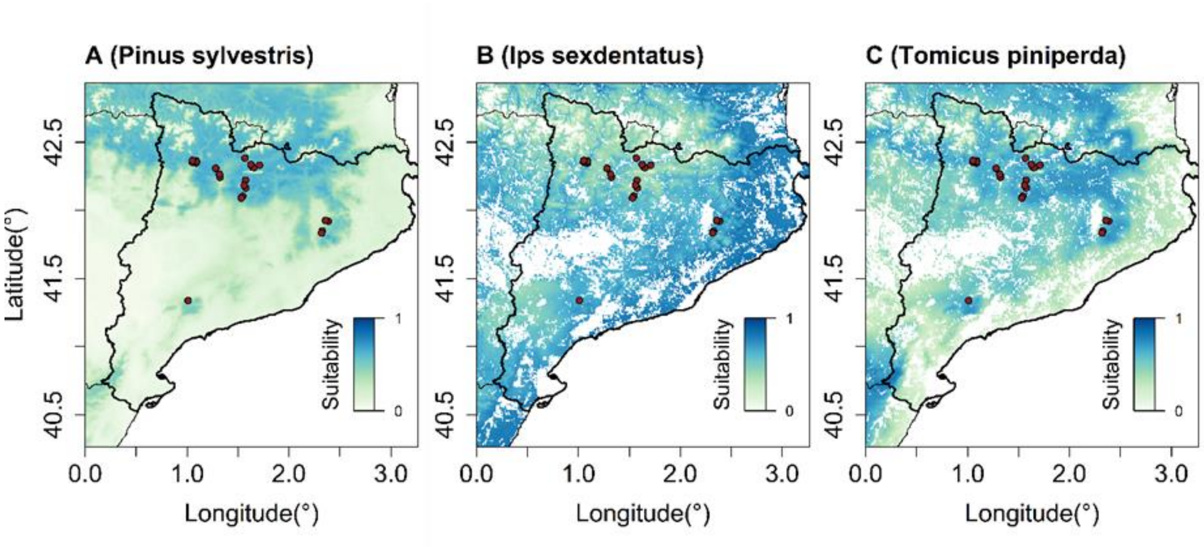

Figure 2.2. Climatic suitability maps obtained in MaxEnt models for *P. sylvestris* (A), *I. sexdentatus* (B), and *T. piniperda* (C). Red dots correspond to the 22 study stands. Note that in (B) and (C) a land cover mask (white areas) was applied to exclude those habitat types not suitable to bark beetles occurrence.

Table 2.2. Description of the tree characteristics and stand attributes (mean ± standard deviation) within the study populations. Abbreviations are: dbh (diameter at breast height), dnn (distance to the nearest neighbor), iat (intensity of attack).

	Living trees	Living infested trees	Dead trees	Dead infested trees	Total stands
Number of trees	421	56	541	425	962
Mean dbh (cm)	14.6 (±9.9)	19.4 (±11.9)	15.2 (±8.3)	15.4 (±7.9)	14.9 (±9.1)
Mean dnn (cm)	1.4 (±1.0)	1.4 (±1.1)	1.2 (±1.0)	1.2 (±1.0)	1.3 (±1.0)
Mean iat (n holes/m^2)	75 (±72)	105 (±168)	207 (±211)	238 (±210)	123 (±191)
Mean stand basal area (m^2/ha)	14.9 (±9.9)	3.1 (±3.3)	18.5 (±10)	14.44 (±8.4)	33.4 (±14.4)
Mean stand density (n/ha)	609.1 (±469)	81.0 (±92)	782.8 (±577)	614.9 (±482)	1429.5 (±909.9)
Mean stand richness	--	--	--	--	2.9 (±1.5)
Mean stand aggregation index	--	--	--	--	0.8 (±0.2)

At tree-level, the final GLMM selected to describe Scots pine mortality had the lowest AICc, and the highest deviance explained (marginal nearest neighbor, intensity of attack, Scots pine suitability, and the 2- way interactions between the predictors (Table 2.3). Tree mortality was mostly explained by the intensity of bark beetle attack and tree size. Higher levels of tree mortality were associated with a greater intensity of attack and lower tree size (Fig. 2.3; A and B). The interaction between the intensity of attack and tree size revealed that small trees were particularly prone to die with increasing intensity of attack, even with a low number of attacks (Fig. 2.3; C). Although Scots pines at sites with higher suitability were more resistant to low intensity attacks than pines at less climatically suitable sites, their mortality increased more markedly as the beetle attack intensified (Fig. 2.3; D). The interactions between distance to the nearest neighbor and intensity of attack, and between distance to the nearest neighbor and tree size, were not significant (Table 2.3).

At stand-level, the PLS-GLM model built to describe Scots pine infestation (i.e., the proportion of dead infested trees) provided two significant components that together explained 77% of the original variance (Table 2.4), revealing that insect and host climatic suitability are significantly related to the infestation success. The first component (explaining 42% of the variance) positively related infestation to Scots pine suitability, *T.*

piniperda suitability, and the positive interaction between Scots pine and *I. sexdentatus* suitabilities. In contrast, *I. sexdentatus* suitability was negatively related to infestation. Scots pine suitability and its interaction with *I. sexdentatus* suitability had the highest contribution in the first component (35% and 29%, respectively), followed by *I. sexdentatus* suitability (14%), and *T. piniperda* suitability (11%). These four predictors retained 89% of the information within the Component 1. In the second PLS-GLM component (explaining 35% of the variance), the infestation was negatively associated with stand density and basal area, and positively with richness of tree species, *I. sexdentatus* suitability, and the three-way interaction between Scots pine, *I. sexdentatus*, and *T. piniperda* suitabilities. This component was best explained by the three-way interaction, which alone retained nearly half of the information content (43%), whereas *I. sexdentatus* suitability, tree species richness, basal area, and stand density retained 16%, 15%, 11%, and 9%, respectively. All these variables together explained 85% of Component 2.

Table 2.3. Results of the GLMM describing the process of mortality at tree-level. The model was carried out with mortality as a binary response variable (dead and living trees), eight fixed predictor variables (including two 2-way interactions), and stand as a random factor. In bold, significant fixed effects (p<0.01).

Fixed effects	Coefficient	z value	Pr(>|Z|)
Intercept	**2.17 (± 0.32)**	**6.81**	**<0.001**
Tree size (dbh)	**-1.88 (± 0.34)**	**-5.51**	**<0.001**
Distance nearest neighbor (dnn)	-0.01 (± 0.32)	-0.32	0.97
Intensity of attack (iat)	**9.18 (± 0.93)**	**9.85**	**<0.001**
Scots pine suitability (sps)	0.11 (± 0.35)	0.32	0.75
iat x dbh	**-6.74 (± 0.96)**	**-6.99**	**<0.001**
iat x dnn	0.97 (± 0.99)	0.98	0.33
dbh x dnn	-0.56 (± 0.35)	-1.59	0.11
iat x sps	**2.03 (± 0.76)**	**2.67**	**<0.01**

Only the final model is shown. AIC = 835; R^2 marginal = 0.83; R^2 conditional = 0.85; Dispersion statistic = 0.90; N = 962. Standard errors are in brackets

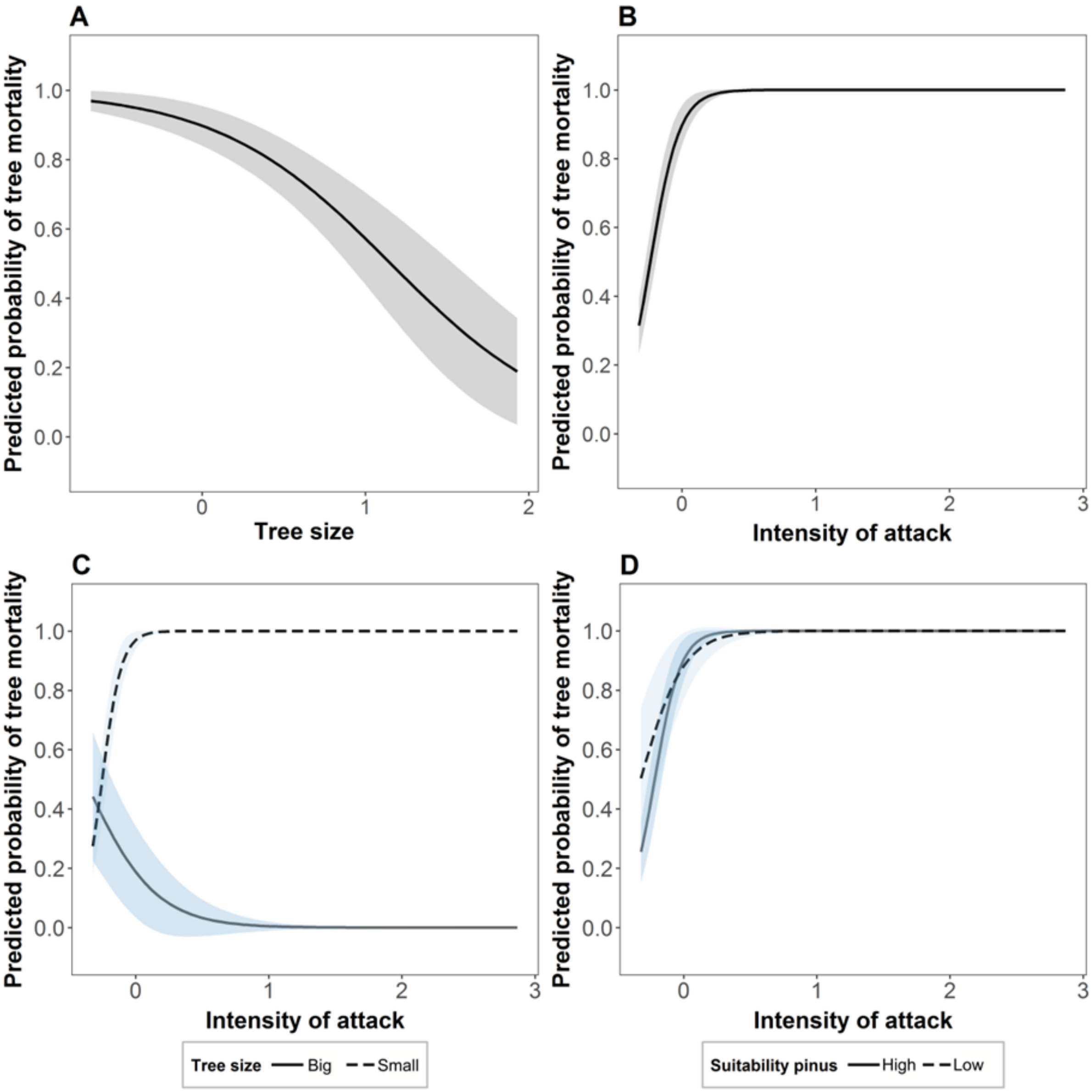

Figure 2.3. Plots depicting the significant relationships obtained within the tree-level mortality model. A: Correlation between tree size (dbh scaled) and predicted probability of tree mortality; B: Correlation between intensity of attack (number of holes scaled) and predicted probability of tree mortality. Black lines represent prediction of the model and gray shaded areas show the 95% confidence interval. C: Effect of the two-way interaction between intensity of attack (number of holes scaled) and tree size (maximum and minimum of dbh scaled; 1.93 and -0.68 respectively) on predicted tree mortality; D: Effect of the two-way interaction between intensity of attack (number of holes scaled) and Scots pine suitability (maximum and minimum of suitability scaled; 0.54 and -1.48 respectively) on predicted tree mortality. Black and dashed lines represent predictions of the model and blue shaded areas show the 95% confidence interval. See methods for details on variable standardization.

Table 2.4. Scores and loadings of the PLS-GLM estimates of stand-level variables to explain the proportion of dead infested trees. Predictors' scores explain the signal of their effect and its square value (loadings) the magnitude and importance of the effect on the component. In bold, significant predictors ($p<0.05$). R^2: proportion of the variance in the response variable accounted in the model by each component; p value: signification of each component obtained in GLM analysis. The coefficient of non-significant predictors was set to 0.

Variables	Component 1	Component 2
Density (den)	-0.00 (0.00)	**-0.30 (0.09)**
Basal area (ba)	**-0.28 (0.08)**	**-0.34 (0.11)**
Richness of tree species (r)	0.00 (0.00)	**+0.38 (0.15)**
Aggregation index (ai)	0.00 (0.00)	0.00 (0.00)
Scots pine suitability (sps)	**+0.59 (0.35)**	0.00 (0.00)
Ips suitability (ips)	**-0.37 (0.14)**	**+0.40 (0.16)**
Tomicus suitability (tos)	**+0.33 (0.11)**	0.00 (0.00)
sps x ips	**+0.54 (0.29)**	0.00 (0.00)
sps x tos	**-0.19 (0.03)**	0.00 (0.00)
ips x tos	0.00 (0.00)	**-0.24 (0.06)**
sps x ips x tos	0.00 (0.00)	**+0.66 (0.43)**
R^2	0.42	0.35
p_value	<0.001 ***	<0.001 ***

Only the final model is shown. AIC = 98.96; Dispersion statistic = 1.98; N = 22.
Square value of predictor's (loadings) in brackets

2.4. Discussion.

The climatic suitability of both the host tree and bark beetles species, in combination with tree characteristics and stand structure, explained a large portion of the Scots pine mortality and bark beetle infestation patterns across our study area. However, we unexpectedly identified patterns of tree mortality driven by bark beetles that are inconsistent with host tree populations close to reach a beetle epidemic phase (i.e., outbreak). Previously reported promoting factors for insect outbreak are related to the opportunities for host colonization after abiotic disturbances, according to the quantity (e.g., high abundance of host individuals and high basal area) and the quality (e.g., high level of nutrients) of suitable material breeding (Gilbert et al., 2005; Negron & Wilson, 2003; Rouault et al., 2006; Shore et al., 2000). It is also well known that not all populations of susceptible host trees are infested with the same severity, suggesting that causes other than those related to the defensive ability of individual trees (Raffa et al., 2016; Raffa & Berryman, 1983) modulate the beginning of bark beetle outbreaks. Interestingly, our study shows that the climatic suitability of the host tree may also have a relevant role in tree mortality and insect infestation patterns at regional scales. We also find that host climatic suitability interacts with the bark beetles suitability to explain these infestation patterns.

Regarding tree characteristics, Scots pine mortality was related to tree size and intensity of beetle attack in our study, but contrary to our expectations, smaller trees experienced a higher probability of dying at lower values of intensity of attack. This was evidenced by the significant and negative interaction between tree size and intensity of attack. Also, the contribution of beetle attack in larger trees did not appear as a significant factor to explain tree death. This conforms to the reported effects under low beetle densities, where the attack pattern on small trees or trees with reduced vigor could be related to endemic bark beetle population levels (Boone et al., 2011). During endemic phase, density of beetle populations is low and can only exploit weakened trees (Ryan et al., 2015), such as small and suppressed individuals with competitive disadvantages for light interception and belowground water uptake (Dawson, 1996; Lloret et al., 2004; Bravo-Oviedo et al., 2006). Furthermore, the defenses in small trees are less substantial than those of larger and more vigorous trees, and lower levels of attack intensity are thus required to overcome their resistance mechanisms (Raffa et al., 2016). The absence of any significant effect exerted by the distance to the nearest conspecific neighbor in the study populations further supports this interpretation. The scattered pattern of pine mortality described in our sites is not characteristic of beetle epidemic phases.

At stand-level, infestation patterns and their relationship to stand structure also suggest that bark beetle populations remained close to an endemic phase and did not achieve an epidemic phase (i.e., outbreak). The probability of dead Scots pines to be infested was negatively associated with Scots pine density and basal area, and positively related to the tree richness. Several studies have reported that dense and monospecific stands are more susceptible to bark beetle infestation (Chapman et al., 2012; Fettig et al., 2007; Perkins & Roberts, 2003), although this occurs when beetle populations reach eruptive dynamics (Raffa et al., 2008). In other words, once the beetle population surpasses a threshold of critical population level, they can increase their intensity of attack and select larger and more vigorous trees, despite having better defenses (Krokene, 2015). However, if the beetle populations levels are incipient, they preferentially attack and kill trees that are more susceptible (Bone et al., 2013), as we found at tree-level, where small trees exhibited a higher vulnerability. Besides, the absence of a significant relationship between the aggregation index and infestation likely reflects the lack of the typical clustered pattern of an epidemic phase of bark beetle attack. Although the size of the sampled stands may not have been large enough to include complete clumps of infestation, embedded within the forest matrix (Carrer et al., 2018). On the other hand, the mechanisms underlying the positive relationship between richness and bark beetle infestation appear to be complex. Baier and others (2002) found that Norway spruce from mixed stands presented lower resin defenses against beetle attack. Also, some studies have suggested that mixed stands reduced the probability of host trees being colonized by bark beetles because other tree species produce an olfactory mask (Zhang & Schlyter, 2004).

It should be noted that a relevant number of dead trees (21%, N=116) did not show any signs of bark beetle attack. Although there may be an underestimation of attacks due to the limitations of our visual survey, this value suggests that causes other than insects contributed to tree mortality in the study sites. Recent drought periods have been the major driver of Scots pine die-off and mortality in the region (Barba et al., 2018; Galiano et al., 2010; Martínez-Vilalta et al., 2012; Vilà-Cabrera et al., 2011). Tree mortality is recognized to be a multifactorial process with positive feedbacks between insect attack and tree weakness due to environmental stress, such as drought (Anderegg et al., 2015; Hartmann et al., 2018). In this context, species climatic suitability in sites where hosts and insects interact acquires special relevance.

In opposition to the notion that tree populations are more susceptible to disturbances when living closer to the species' climatic tolerance limits, our results indicate that Scots pine populations living in more climatically suitable areas were also susceptible to bark beetle infestation. These remarkable results could be explained by trade-offs between tree growth and resource allocation to resin defenses (Ferrenberg et al., 2015; Lorio, 1986; Stamp, 2003). Some studies have reported that Scots pine populations living in wetter, more suitable sites in the Iberian Peninsula exhibit fast-growing trends and higher vulnerability to intense drought (Martínez-Vilalta & Piñol, 2002), whereas resistance to drought appears to be associated with low growth rates in populations of Scots pine living in the south of this region, due to genetic adaptations (Alía et al., 2001). Therefore, a higher pre-drought investment of resources in growth in areas more suitable to the hosts might reduce a subsequent investment in resin defenses against bark beetles, while slow-growing patterns in less suitable localities could allow trees to allocate more resources to defense, with respect to growth rates. This hypothesis concurs with Rigling and others (2003) results, who reported that the radial growth of Scots pine is positively associated with wetter and cooler climatic conditions, while the production of resin ducts is stimulated by hot summer temperatures. Moreover, other studies have found that greater tree growth results in fewer resin ducts for defense and more susceptibility to bark beetles (Ferrenberg et al., 2014).

Stand-level infestation in our Scots pine populations was more intense on sites where the climatic suitability for *I. sexdentatus* and *T. piniperda* was higher. Therefore, maximum infestation levels were only attained when high suitability values coincided in both the bark beetles and the host tree. Even though the two studied bark beetle species have different climatic requirements, these results suggest a synergistic interaction between both beetle species when the climatic suitability of the host is high. This line of reasoning concurs with the findings of Amezaga and Rodríguez (1998), who found niche overlaps between *T. piniperda* and *I. sexdentatus* on sites where resources were less limited. Moreover, in many cases, the interspecific competition between beetle species can be minimized by using different parts of a common resource (Paine et al., 1981), allowing them to coexist in the same host population. *I. sexdentatus* typically infests the branches and upper parts of large trees, and it can potentially kill small trees. In contrast, *T. piniperda* concentrates its attack and brooding near the bole base, where the bark is thicker (Sauvard, 2004). These two species would probably compete for food resources and habitat in an epidemic phase, reducing coexistence within the same stand (Light et al., 1983; Rankin & Borden, 1991). However, given the likely low densities of the beetle population in our stands, the two species' niche differentiation within the tree may enable them to cohabit in the same host or trees of a different size, contributing to overcome tree defenses and promoting higher infestation levels.

2.5. Conclusions.

This study reveals that the climatic suitability of both host trees and bark beetle species explain regional patterns of tree mortality and the success of beetle infestation. Species distribution models have proved useful for this purpose by providing indexes of climatic suitability that can be combined to explain population-level processes such as bark beetle infestation. Interestingly, our results evidence a higher vulnerability to bark beetle-driven mortality after drought episodes in tree populations established in climatically suitable sites, particularly when these sites are also suitable for such insects. Furthermore, the relationships recorded between tree characteristics and stand structure with tree mortality and stand infestation suggested attacks by low-density populations of bark beetles in which smaller trees were more susceptible to the attack. Though not directly addressed by this study, our findings point that the phase of the infestation process would also be relevant to interpreting the relationship between the success of an attack and the climatic suitability of both the host tree and the bark beetle.

Models of insect-driven mortality that incorporate relationships between the radial growth of Scots pine, the production of resin ducts (Ferrenberg et al., 2014; Rigling et al., 2003), and the density of beetle populations (Colombari et al., 2012; Wermelinger et al., 2008) might be particularly useful for predicting more precisely whether trade-offs of resource allocation are modulating the vulnerability of tree populations to infestation along their range of climatic suitability. Furthermore, the local insect-driven mortality patterns observed in this work suggest, in line with recent studies (Cavin & Jump, 2017; Lloret & Kitzberger, 2018), that tree populations located closer to the species’ central climatic ranges could also be at risk under future climate scenarios. Additional studies should confirm whether mortality patterns in the climatically central versus peripheral tree populations are maintained in areas where a massive attack has occurred, such as recent outbreaks in North America (Meddens et al., 2012; Weed et al., 2013). Overall, our study demonstrates the uncertainty around tree mortality and bark beetle infestation processes in a context of climate change in which drought and warming temperatures are expected to increase in many regions, potentially altering insect-host dynamics. Therefore, further studies examining the climatic niche of both the insect and host species are needed to better anticipate the potential effects of these interactions on future forest dynamics.

Chapter 3

Species climatic suitability explains insect-host dynamics in the Southern Rocky Mountains, USA

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Abstract

Recent extreme events of drought and heat have been associated with insect-driven tree mortality. However, there is substantial uncertainty about the impact of climate variability and extreme climatic episodes on insect-host dynamics, especially over species biogeographical ranges. Here, we use climatic suitability indices derived from Species Distribution Models to analyze the spruce beetle (*Dendroctonus rufipennis*) outbreak dynamics in spruce-fir forests across the Southern Rocky Mountains (USA) during a warm and dry episode (2000-2013). We estimated the historical climatic suitability of the host tree (1969-1998), its interannual variability, and the climatic suitability during the 2000-2013 episode for both beetle and host tree. Overall, outbreak was more like to occur in host tree populations inhabiting areas with historically suitable climatic conditions that were also characterized by loss of suitability during the episode. Specifically, the outbreak initiation was located in areas with suitable climatic conditions for the beetle and high historical suitability for the host. However, the year-to-year analysis revealed that low-moderate amounts of outbreak initiation and spread were also determined by high host historical climatic suitability, with high historical interannual variability, and a modest reduction of suitability during the episode. Years with high amounts of outbreak initiation and spread mostly occurred in dense forests with large trees, and were promoted by suitable climate conditions for the beetle. This study highlights the importance of considering the climatic suitability of the insect-host system to understand and anticipate outbreak dynamics at different temporal scales.

3.1. Introduction.

Extreme episodes of dry and warm conditions have led to increased forest mortality from fire, extreme drought, and insect disturbances worldwide (Seidl et al., 2017; Sommerfeld et al., 2018). In particular, bark beetles have emerged as an important biotic disturbance in recent decades (Anderegg et al., 2015; Raffa et al., 2008). Unprecedented outbreaks and the expansion of beetle species distribution into new areas are altering insect-host interactions (Bentz et al., 2010; Sommerfeld et al., 2020). Furthermore, tree populations are responding differently to abiotic and biotic disturbances throughout their distributional ranges (Camarero et al., 2015; Cavin & Jump, 2017). This underscores many uncertainties about the effects of climate on insect and host tree populations, especially in the context of climate change, which may bring more frequent and intense episodes of climatic extremes (Kolb et al., 2016; Mezei et al., 2017; Biedermann et al., 2019).

The bark beetle-host system is sensitive to climatic variability because warming may accelerate insect development, while drought stress may reduce host tree defenses (Bentz et al., 2010; Raffa et al., 2016). Habitat conditions such as tree characteristics, stand structure, and landscape-level patterns of tree populations are also known to influence insect populations' capacity to grow and spread (Aoki et al., 2018; Bakaj et al., 2016). Variable responses of tree populations to drought and insect disturbances may also be explained by the climatic suitability experienced across species' geographic ranges (Cavin & Jump, 2017; Jaime et al., 2019; Lloret & Kitzberger, 2018; Margalef-Marrase et al., 2020). On the one hand, the occurrence and severity of disturbances may be more evident near the edge of a species' distribution due to higher limitations on population performance (Abeli et al., 2014). Alternatively, locally adapted populations living under less suitable environmental conditions may be more resistant to drought due to plastic responses or directional selection (Vilà-Cabrera et al., 2019). Likewise, tree populations inhabiting areas with historically suitable environmental conditions may show greater sensitivity and lower resistance to extreme drought events (Lloret & Kitzberger, 2018; Margalef-

Marrase et al., 2020), likely due to acclimation to favorable conditions, and higher susceptibility to biotic disturbances, especially when these sites are also suitable for insects (Jaime et al., 2019).

Species Distribution Models (SDMs) are commonly used to obtain estimates of climatic suitability for assessing ecological processes - such as mortality, decline, establishment, and insect outbreaks - related to short-term climatic events (Evans & Lyons, 2013; Lloret & Kitzberger, 2018; Pérez Navarro et al., 2019). Unlike process-based models that incorporate mechanistic relationships, SDMs are correlative statistical approaches that are used to characterize a species' environmental niche (Franklin, 2010). Concerning climate, SDMs quantify the probability of species occurrence under a set of climate conditions that characterize a given location. Such probabilities can be interpreted as a species-specific index of climatic suitability experienced by a population living at a given site (Soberón & Peterson, 2005). Generally, SDMs are parameterized with current species distribution and historical climatic conditions to predict past or future distribution changes in relation to altered climates (Elith & Graham, 2009). SDMs can also be used to quantify a populations' climatic suitability during an adverse climatic episode, as a measure of the episode's magnitude, and to consider the inter-annual variability in historical climatic conditions, as a measure of site environmental stability. Such stability is a key element to ecosystem vulnerability to extreme climatic events (Gutschick & BassiriRad, 2003), for instance, because structural overshoot during favorable periods can lead to a mismatch between water demand and availability during drought (Jump et al., 2017).

Across the Southern Rocky Mountain Ecoregion, USA (SRME; U.S. EPA, 2011), populations of Engelmann spruce (*Picea engelmannii*) have recently experienced widespread and severe spruce beetle (*Dendroctonus rufipennis*) outbreaks concurrent with warm and dry conditions. Specifically, the initiation of recent (i.e., post-2000) spruce beetle outbreaks in the SRME has been driven by summer, winter, and multi-year drought, whereas the proximity and the extent of the nearest affected forest drove the spread (Hart et al., 2017). The presence of vast areas of susceptible habitat (e.g., stands with a high basal area and high density of spruce; (Jenkins et al., 2014; Schmid & Hinds, 1974) and suitable climatic conditions for the beetle may also be responsible for the recent broad-scale outbreaks (DeRose et al., 2013; DeRose & Long, 2012; Pettit et al., 2020). Despite the evidence that the dynamics of spruce beetle outbreaks are functionally associated with climate, it remains unknown how site-specific host-beetle climatic suitability influences outbreak patterns.

Using annual time series of climatic data, we developed SDMs for both the host tree (i.e., Engelmann spruce) and spruce beetle to analyze outbreak dynamics in the SRME during the warm-dry 2000-2013 episode. To better understand how both host and beetle climatic suitability influence outbreaks, we defined the following suitability indices: 1) the average historical, or long-term, climatic suitability for the host (HCS_{host}; period 1969-1998); 2) the standard deviation of the historical climatic suitability for the host ($HCS\text{-}SD_{host}$), as a measure of the inter-annual variability; and 3) the average and yearly episode climatic suitability of the host and beetle for the 2000-2013 period (ECS_{host} and ECS_{beetle}). A negative or positive effect of HCS_{host} on beetle outbreak would indicate a higher infestation in host populations living close to their climatic limit of tolerance or their climatic optimum, respectively. Whereas a positive effect of $HCS\text{-}SD_{host}$ on beetle outbreak would indicate increased amounts of infestation in environments with greater variability in historical climate conditions. Finally, a negative or positive effect of ECS_{host} on beetle outbreak would suggest that infestation is lower or higher, respectively, under less suitable climatic conditions for the host during the episode. Similarly, a positive effect of ECS_{beetle} on outbreak would indicate that high climatic suitability for the beetle is associated with greater infestation amounts. To understand the roles of climatic suitability, together with forest attributes, in driving spruce beetle outbreaks, we analyzed their effects in the response of outbreak dynamics at three spatiotemporal approaches: 1) cumulative outbreak occurrence during the 2000-2013 episode, 2) Locations of outbreak initiation and spread, 3) Year-to-year patterns of outbreak initiation and spread.

3.2. Material and methods.

Study area

Our study area was constrained to spruce-fir forests in the SRME, extending from southern Wyoming to northern New Mexico, USA (Fig. 3.1). Within this region, spruce-fir forests range from 2,500 to 3,700 m in elevation. From December to March, average temperatures were –8.6 ± 1.5 °C and total precipitation was 138.4 ± 50.7 mm; from June to August, mean temperatures were 10.3 ± 2.1 °C and mean total precipitation was 138.1 ± 37.8 mm (1969-1999, CHELSA, Karger et al., 2017). During the study period (2000-2013), the climate in SRME became increasingly warm and dry, with an increase of mean temperatures of 1 ± 0.2 °C from June to August and of 0.1 ± 0.3 °C from December to March. Likewise, a decrease of mean total precipitation of 29.5 ± 9.7 mm from June to August and 30.1 ± 20.2 mm from December to March (2000-2013, CHELSA, Karger et al., 2017). Specifically, two severe drought events occurred in 2000-2003 and 2012-2013 across the region (Lukas et al., 2014). The dominant tree species in spruce-fir forests of the SRME are Engelmann spruce and subalpine fir (*Abies lasiocarpa*), with some lodgepole pine (*Pinus contorta*), limber pine (*Pinus flexilis*), and trembling aspen (*Populus tremuloides*).

Maps of spruce beetle outbreaks

To analyze the spatiotemporal dynamics of spruce beetle outbreaks in the SRME, we used annual maps describing the Engelmann spruce mortality attributed to spruce beetles at 30 × 30 m resolution (Hart & Veblen, 2015; Hart et al., 2017). These maps were developed using Landsat imagery from 2000-2014, in which gray-stage outbreak was identified within spruce-fir forests using multi-temporal trends in vegetation indices sensitive to tree mortality (Hart & Veblen, 2015). Because beetle infestation precedes tree mortality's spectral signal (Meddens & Hicke, 2014), we subtracted one year from the Landsat-derived detection year to identify the timing of the outbreaks (i.e., from 2000-2014 to 1999-2013). The 1999 map, which included prior spruce beetle-caused tree mortality, was used as a reference point for identifying newly outbreak pixels in subsequent years. From the spruce beetle outbreak maps, we removed burned, harvested, and blowndown areas that occurred 0-10 years before the outbreak period (Appendix B, Table B1).

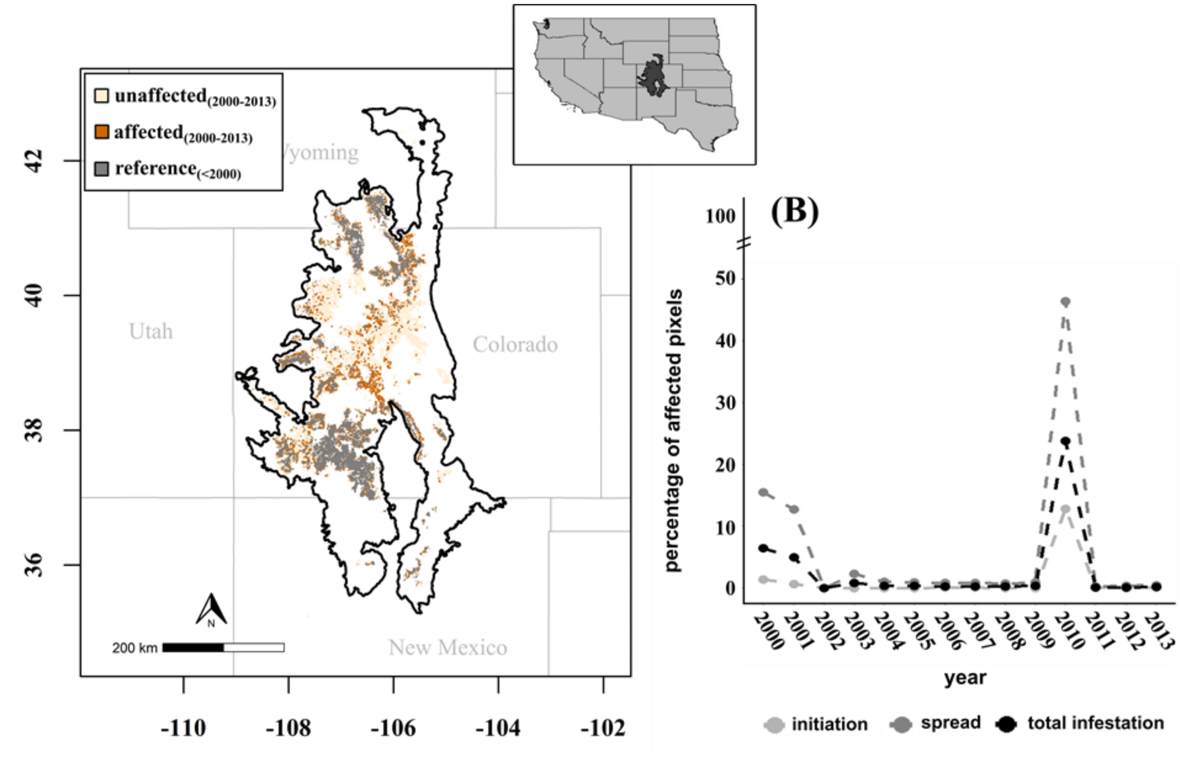

Figure 3.1. (A) Map of the Southern Rocky Mountain Ecoregion (SRME) displaying the total affected (N = 6,712) and unaffected pixels (N =13,414) of spruce-fir forest by spruce beetle outbreak during the 2000-2013 episode. Data were obtained from Landsat annual maps describing the Engelmann spruce mortality attributed to spruce beetles. The reference area encompassed the forest affected in previous years and was considered the baseline to account for new outbreak points over the 2000-2013 period. (B) Percentage of affected pixels from the available ones susceptible to be affected each year, thus reflecting the evolution of the total infestation, outbreak initiation, and outbreak spread during the 2000-2013 episode.

Because tree mortality identified using remotely-sensed vegetation indices may also be due to other factors besides spruce beetle, we overlaid the Landsat-based maps of beetle outbreak with a map of the cumulative spruce beetle damage from 1997-2014 period, derived from Aerial Detection Survey (ADS) data (McConnell et al., 2000). Only areas included in both datasets were identified as affected by spruce beetle outbreak. Finally, we aggregated the 30 × 30 m grids of outbreak occurrence to 1 × 1 km pixels to match the scale of the available climatic predictors, while still retaining a spatial resolution fine enough to differentiate the initiation and spread processes of spruce beetle outbreaks. This pixel size selection is supported by mark and recapture studies showing that most spruce beetle dispersal occurs within 90-1600 m (Lindemann & Baker, 2001; Schmid, 1970; Werner & Holsten, 1997).

Forest attributes

Given that the susceptibility of spruce-fir stands to beetle outbreak increases with average tree size and stand density (Jenkins et al., 2014; Schmid & Frye, 1977; Schmid & Hinds, 1974), we obtained spatially-extensive proxies for each of these variables. To estimate stand density, we obtained Landsat-based maps of percent tree cover in 2000 (Sexton et al., 2013) and calculated the percentage of tree cover within each 1 × 1 km pixel over the study region. To characterize dominant tree size, we used maps of stand structure (USFS, 2003) to calculate the proportion of each 1 × 1 km pixel dominated by large trees (diameter at breast height >22 cm) (Appendix B, Table B1). Though the relative proportion of host tree *vs.* non-host tree may also influence stand–scale infestation (Schmid & Frye, 1977), we did not have this geospatial information for spruce-fir forests, and therefore, this could not be included in our analysis.

Host–Beetle historical and episode climatic suitability

We used SDMs to estimate climatic suitability indices for the host tree and the bark beetle species. To build SDMs, we obtained 2,965 occurrence locations of Engelmann spruce from the ForeCASTS Project Tree Atlas V5 (2014) spanning the species' distribution in western North America (Appendix B, Table B1). For the spruce beetle, we extracted the infestation occurrence from the ADS of the US Forest Service (McConnell et al., 2000) and the Aerial Overview Survey (AOS) of the Canadian Forest Service (Koot, 1997) (Appendix B, Table B1). These datasets contain polygons derived from aerial surveys that delineate spruce beetle infestation and other forest disturbances at an annual time-step. In particular, we obtained polygons affected by spruce beetle from 2001-2014 collected in the

Conterminous United States, Alaska, British Columbia, and Yukon territory. Within these polygons, we generated point locations using a stratified random sample to obtain annual infestation occurrence records of spruce beetle. Because infestation precedes visible effects of tree mortality, we assigned the year of spruce beetle infestation to the year before the recorded year in aerial surveys (i.e., from 2001-2014 to 2000-2013). To build SDMs, we also generated 10,000 pseudoabsences for the Engelmann spruce and 30,000 for the spruce beetle, based on the number of occurrences. To limit the influence of spatial autocorrelation (Veloz, 2009) and match the resolution with the climate data, we filtered all the records by a minimum distance of 1 × 1 km.

Climate data were obtained from the CHELSA climate database v.1.2 and CHELSAcruts (Karger et al., 2017) with 1 × 1 km resolution from 1969 to 2013. Over this period, we calculated 19 standard bioclimatic variables from monthly rainfall and maximum and minimum temperatures data, representing annual trends, seasonality, and extreme or limiting environmental factors, using the dismo package in R (Hijmans et al., 2012). To limit multicollinearity, we filtered bioclimatic variables using a Variance Inflation Factor (VIF) <10 as a critical threshold (Quinn & Keough, 2002) and a cluster dissimilarity value <0.8. From this filtered subset, we selected six variables with the lowest correlation among them. These final variables, describing temperature and precipitation regimes, helped characterize environmental limitations for the host tree and beetle (see variables in Appendix B, Table B1).

We used four different algorithms – GLM (generalized linear models), GAM (generalized additive models), Random Forest, and MaxEnt (maximum entropy) – to obtain robust estimates of climatic suitability for Engelmann spruce and spruce beetle. We evaluated each model's predictive accuracy by comparing model predictions with test sets in cross-validation using the area under the receiver operating characteristic curve (AUC) (mean AUC values range from 0.85 ± 0.001 to 0.96 ± 0.001; Appendix B, Table B2). Then, we combined individual model predictions into an ensemble prediction using a weighted mean value, with individual weights proportional to AUC scores (Araújo &

New, 2007). We used the biomod2 package in R (Thuiller et al., 2019) to build all SDMs and develop predictions.

To develop SDMs for Engelmann spruce, we used 30-year historical climate data (1969-1998) of the six selected climatic variables. For spruce beetle SDMs, we used annual climate variables from the year of infestation (t) and two years before infestation (t-2) in the warm-dry 2000-2013 episode to account for temporal lags in the response of infestation occurrence associated with climate variability, as well as the time (1 to 3 yr) required for beetle reproduction (Schmid & Frye, 1977). Finally, we projected both host tree and beetle SDMs to obtain the following suitability indices throughout the SRME: 1) the averaged historical climatic suitability for the host tree (HCS_{host}) from 1969 to 1998, 2) the inter-annual variability in historical climatic suitability for the host tree ($HCS\text{-}SD_{host}$), corresponding to the standard deviation of annual suitability values from 1969 to 1998, and 3) the averaged episode climatic suitability for both the host tree and the beetle ($aECS_{host}$ and $aECS_{beetle}$) and the year-specific ($yECS_{host}$ and $yECS_{beetle}$) values during the 2000 to 2013 episode.

Outbreak initiation and spread

To explore the factors that determine the emergence and maintenance of outbreaks, we classified spruce beetle-occurrence pixels in the annual Landsat-derived maps as "outbreak initiation"/"non-initiation" and "outbreak spread"/"non-spread". Most spruce beetle dispersal occurs at distances of 90 m to 1.6 km (Lindemann & Baker, 2001; Schmid, 1970; Werner & Holsten, 1997). Thus, a pixel was classified as "outbreak spread" for a given year if it was within a radius of 1.5 km of any pixels affected by outbreak in the previous year. Alternatively, the "non-spread" category was assigned to unaffected pixels within 1.5 km of any previously affected pixel. We defined "outbreak initiation" as affected pixels further than 1.5 km from any pixels considered affected by outbreak in the previous year. Finally, the "non-initiation" category during a given year was assigned to all unaffected pixels further than 1.5 km from any outbreak initiation or outbreak spread pixels in the previous year.

Modeling the development of spruce beetle outbreak

To assess how the climatic suitability of both host and beetle, as well as forest attributes, influenced the spatiotemporal dynamics of spruce beetle outbreak from 2000 to 2013, we used three modeling approaches to analyze 1) the likelihood of any outbreak occurrence based on the cumulative infestation during the 2000-2013 episode, 2) the locations of outbreak initiation and spread as individual responses during the episode, and 3) the annual patterns of outbreak initiation and spread related to year-to-year climatic variability. Because spruce beetle outbreaks result in clustered patterns of affected pixels, typical of contagious processes, we addressed spatial autocorrelation in each analysis approach using different methods depending on the database size and the available computational capacity. The use of replicates with subsets of randomly selected pixels without incorporating spatial dependence terms allowed the inclusion of bivariate interactions in the models. In contrast, autoregressive methods allowed more accurate control of spatial dependence but prevented such interactions because of high computational demand.

First, we used GLMs with a logit-link function and binomial error structure to model the occurrence/absence of cumulative (2000-2013) spruce beetle outbreak as a function of HCS_{host} (1969-1998), $HCS\text{-}SD_{host}$, $aECS_{host}$ (average 2000-2013), $aECS_{beetle}$ (average 2000-2013), proportion of large trees, and tree cover. While the estimation of regression coefficients may be sensitive to multicollinearity, none of our predictor variables were strongly correlated (correlation coefficient ($|r|$) < 0.7; Appendix B, Table B3) supporting their inclusion into the models (Dormann et al., 2013). We also included bivariate interactions between predictors of climatic suitability. Because spatial autocorrelation was present in residuals when using a GLM with the full dataset, we ran

100 replicates of the final model with subsets of randomly selected pixels with a minimum spacing of 10 km.

Second, we used Generalized Linear Mixed-effects Models with a logit-link function and binomial error structure (GLMMs; R package lme4, Bates et al., 2015) to model outbreak initiation and spread locations as a function of HCS_{host} (1969-1998), $HCS\text{-}SD_{host}$, $yECS_{host}$ (year-specific values 2000-2013), $yECS_{beetle}$ (year-specific values 2000-2013), and forest attributes. Bivariate interactions between predictors were also included. We considered the "outbreak initiation" *vs.* "non-initiation" and the "outbreak spread" *vs.* "non-spread"pixel categories from 2000 to 2013 as response variables in two separate analyses. We fit GLMMs by Laplace approximation and included "year" as a random intercept term to account for individual variation among years related to the locations of outbreak initiation and spread. Given the extreme imbalance in the number of observations per year, we only used years with more than ten outbreak pixels. Thus, for the outbreak initiation model, we included data from 2000, 2001, and 2011; for the outbreak spread model, we included all years except 2002. We ran 100 replicates for each final model with subsets of randomly selected pixels with a minimum spacing of 2 km, accommodating the beetle's dispersal distance to limit spatial autocorrelation effects.

Third, we developed conditional autoregressive models (CARs) using the R-INLA package (Rue et al., 2009) to evaluate the annual responses of outbreak initiation and spread from 2000 to 2013 as a function of HCS_{host} (average 1969-1998), $HCS\text{-}SD_{host}$, $yECS_{host}$ (year-specific values 2000-2013), $yECS_{beetle}$ (year-specific values 2000-2013), and forest attributes. In CARs, spatial dependence is incorporated using a matrix of spatial neighborhood weights (Fletcher & Fortin, 2018). We considered the "outbreak initiation" *vs.* "non-initiation" and the "outbreak spread" *vs.* "non-spread" as response variables in separate analyses for each year. CAR annual models added information at finer spatiotemporal scale to our GLM and GLMM-based analysis.

To improve model stability and permit a direct comparison of effect sizes, we rescaled explanatory variables in each statistical model using the series-wide means and standard deviations (i.e., z-score transformation). For GLM and GLMM, we selected the most parsimonious models by minimizing the Akaike Information Criterion (AIC) from an initial full model, including the individual effects of forest attributes and the individual and interaction between climatic suitability indices for the host tree and the beetle. We tested for spatial correlation in all model residuals using correlograms (Appendix B, Fig. B1.1-1.4).

3.3. Results.

Across the SRME, approximately 33% of the total area of spruce-fir forests was affected by spruce beetle outbreaks from 2000 to 2013 (Fig. 3.1). Specifically, 78% of the spruce-fir affected forest was located in areas with suitable historical climatic conditions for the host tree (HCS_{host} values > 0.7, Fig. 3.2; A). However, during the 2000-2013 episode, the host's climatic suitability declined by 44.8% (± 13.3 SD), and 66% out of the total affected area experienced unsuitable climatic conditions ($aECS_{host}$ values < 0.5, Fig. 3.2; B). For comparison, almost 95% of the affected area of spruce-fir forests was found in areas with highly favorable climatic conditions for the spruce beetle during the 2000-2013 episode ($aECS_{beetle}$ values > 0.7, Fig. 3.2; C).

The GLM of outbreak likelihood (i.e., cumulative infestation) from 2000 to 2013 (Table 3.1) indicated that outbreak occurrence was promoted by suitable climatic conditions for the spruce beetle, a high proportion of large trees, and the interaction between $aECS_{host}$ and HCS_{host}, where the likelihood of an outbreak tended to increase under the combination of high values of both HCS_{host} (average 1969-1998) and $aECS_{host}$ (average 2000-2013). This HCS_{host}-$aECS_{host}$ interaction was driven by sites with high historical suitability that experienced a lower average reduction of climatic suitability over the 2000-2013 episode (Appendix B, Fig. B2).

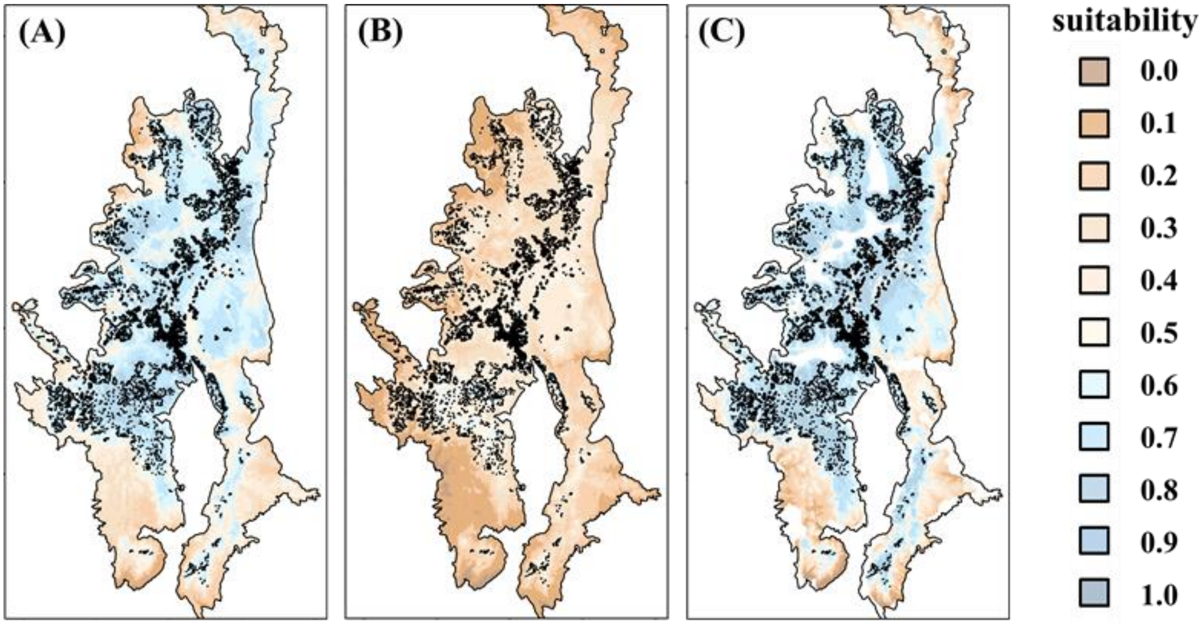

Figure 3.2. (A) Historical (1969-1998) climatic suitability (HCS_{host}) for the host tree in the SRME (67 px < 0.5; 1407 px ~ 0.5-0.7; 5238 px > 0.7 suitability values); (B) Episode (average 2000-2013) climatic suitability ($aECS_{host}$) for the host tree in the SRME (4449 px < 0.5; 2263 px ~ 0.5-0.7; 0 px > 0.7 suitability values); (C) Episode (average 2000-2013) climatic suitability ($aECS_{beetle}$) for the bark beetle in the SRME (7 px < 0.5; 336 px ~ 0.5-0.7; 6369 px > 0.7 suitability values). Black dots show pixels affected by spruce beetle infestation during the 2000-2013 episode. Brown to dark blue colors indicate low to high values of climatic suitability, respectively.

Table 3.1. Generalized linear model (GLM) results of the occurrence of cumulative spruce beetle outbreak in relation to insect-host climatic suitability and forest attributes during the 2000-2013 episode. Coefficient and p-value estimates are the mean values from 100 replicates of 600 pixels (300 affected and 300 unaffected), corresponding to randomly selected pixels within each 10 × 10 km cell over the study region. The models were carried out with outbreak occurrence/absence as binary response variable and seven predictor variables (including one 2-way interaction).

Random pixels – 100 km^2				
Term	Coefficient	*SD**	*SE*	p value
Intercept	–0.114	0.035	0.097	0.272
HCS_{host}	0.337	0.165	0.260	0.266
$HCS–SD_{host}$	0.208	0.143	0.206	0.379
$aECS_{host}$	0.275	0.157	0.257	0.335
$aECS_{beetle}$	**0.700**	**0.181**	**0.246**	**0.018**
$aECS_{host} \times HCS_{host}$	**0.727**	**0.209**	**0.302**	**0.044**
Large trees	**0.559**	**0.185**	**0.186**	**0.029**
Tree cover	0.254	0.137	0.196	0.255
R^2	0.10 ± 0.02			

Abbreviations: HCS_{host}, historical climatic suitability for the host; $HCS\text{-}SD_{host}$, inter-annual variability in historical climatic suitability for the host; $aECS_{host}$, averaged episode climatic suitability for the host; $aECS_{beetle}$, averaged episode climatic suitability for the beetle. Standard deviation (SD*) from the 100 replicates and standard error (SE) of model estimates. *Notes*: In bold, significant effects ($p < 0.05$).

Table 3.2. Generalized linear mixed models (GLMM) results of the outbreak initiation and spread locations in relation to insect-host climatic suitability and forest attributes during the 2000-2013 episode. Coefficient and p-value estimates are the mean values from 100 replicates of 600 pixels (300 of initiation/spread and 300 non-initiation/non-spread), corresponding to randomly selected pixels within each 2 × 2 km cell over the study region. The models were carried out with initiation and spread as binary response variables (outbreak initiation/non-initiation, outbreak spread/non-spread), seven fixed predictor variables (including one 2-way interaction), and year as random effect.

	Initiation				Spread			
Term	Coefficient	SD *	SE	p value	Coefficient	SD *	SE	p value
Intercept	-0.590	0.061	0.690	0.393	–1.296	0.498	0.054	0.133
$\mathrm{HCS}_{\mathrm{host}}$	**0.860**	**0.239**	**0.263**	**0.011**	0.347	0.319	0.019	0.359
$\mathrm{HCS–SD}_{\mathrm{host}}$	0.371	0.188	0.224	0.185	0.128	0.268	0.012	0.483
$\mathrm{yECS}_{\mathrm{host}}$	0.024	0.196	0.219	0.534	0.144	0.277	0.010	0.446
$\mathrm{yECS}_{\mathrm{beetle}}$	0.383	0.255	0.245	0.252	0.328	0.372	0.025	0.400
$\mathrm{yECS}_{\mathrm{beetle}} \times \mathrm{HCS}_{\mathrm{host}}$	**0.850**	**0.300**	**0.326**	**0.049**	-0.035	0.435	0.073	0.510
Large trees	0.360	0.213	0.209	0.205	-0.530	0.538	0.032	0.404
Tree cover	–0.061	0.176	0.205	0.554	-0.354	0.813	0.034	0.490
R marginal	0.05 ± 0.02				0.02 ± 0.01			
R conditional	0.29 ± 0.03				0.48 ± 0.05			

Abbreviations: $\mathrm{HCS}_{\mathrm{host}}$, historical climatic suitability for the host; $\mathrm{HCS\text{-}SD}_{\mathrm{host}}$, inter-annual variability in historical climatic suitability for the host; $\mathrm{yECS}_{\mathrm{host}}$, yearly episode climatic suitability for the host; $\mathrm{yECS}_{\mathrm{beetle}}$, yearly episode climatic suitability for the beetle. Standard deviation (SD*) from the 100 replicates and standard error (SE) of model estimates. *Notes*: In bold, significant fixed effects ($p < 0.05$).

Individual GLMMs of the locations of (1) outbreak initiation and (2) spread over the study period (2000-2013) revealed that outbreak initiation typically occurred where year-specific suitable climatic conditions for the spruce beetle aligned with a high historical climatic suitability for the host tree, as reflected by a significant positive interaction between $\mathrm{yECS}_{\mathrm{beetle}}$ and $\mathrm{HCS}_{\mathrm{host}}$ (Table 3.2). In contrast, none of the considered predictors explained patterns of outbreak spread. There was substantial variability in both initiation and spread models' temporal components, reflected by the variance explained per year as a random effect (R conditional).

Annual maps showed that the initiation and spread of spruce beetle outbreaks primarily occurred in 2000, 2001, and 2010 at the square kilometer scale (Fig. 3.3); 33% of the cumulative outbreak area experienced initiation and spread in 2000-2001 and 60% in 2010. Host climatic suitability ($\mathrm{yECS}_{\mathrm{host}}$) was low throughout the study area during these years. A very small percentage of spruce-fir forest was affected by outbreak initiation or

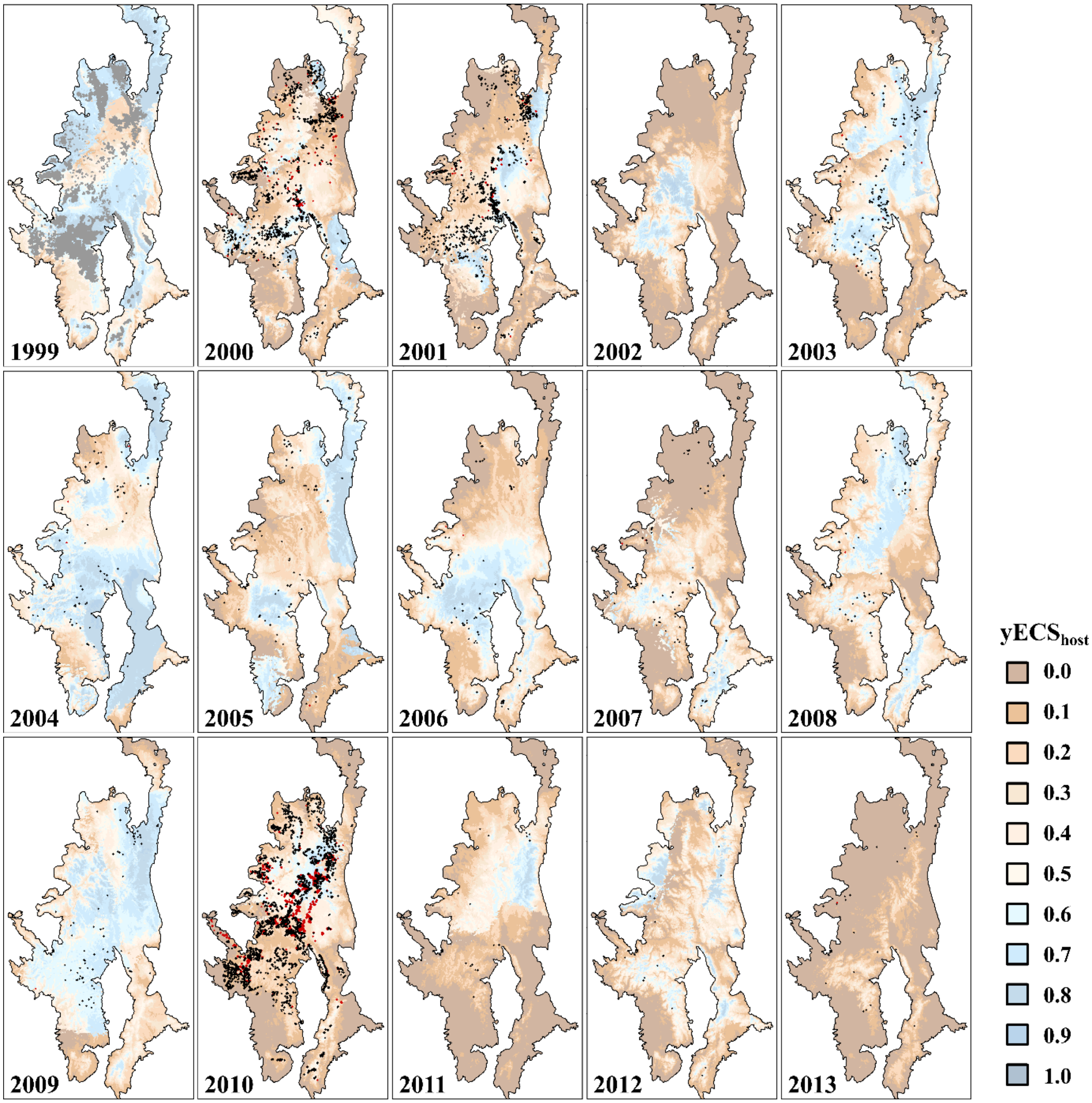

Figure 3.3. Newly-affected pixels per year in relation to the climatic suitability of the host tree during the 2000-2013 episode. The year 1999 was taken as reference to the previously affected area (grey dots) to create a baseline for the newly affected pixels in the following years. Black dots indicate outbreak spread pixels and red dots the outbreak initiation pixels. Brown to dark blue colors show low to high climatic suitability values. Number of new pixels per year (initiation/spread): 2000 (170/1115); 2001 (73/863); 2002 (0/0); 2003 (0/134); 2004 (1/57); 2005 (1/49); 2006 (2/43); 2007 (2/41); 2008 (1/38); 2009 (1/50); 2010 (1465/2565); 2011 (1/12); 2012 (0/9); 2013 (2/13).

spread in the rest of the years (~7%), even though host climatic suitability was low in several years, such as 2007, 2011, 2012, and climate conditions were suitable for the spruce beetle (yECS$_{\text{beetle}}$) from 2000 to 2013. (Appendix B, Fig. B3). CAR models provided additional insight into annual responses of outbreak initiation and spread (Fig. 3.4). These models demonstrated that in years with low amounts of newly-affected forest (2003-2009 and 2011-2013), small proportion of large trees, high suitable historical climatic conditions (HCS$_{\text{host}}$), and a decline in year-specific host suitability (yECS$_{\text{host}}$) were positively associated with outbreak spread. In 2010, the year with the highest amount of newly-affected forest, both initiation and spread emerged in areas with a high proportion of large spruce-fir trees and high tree cover. Additionally, in 2010, sites affected by spread showed favorable year-specific climatic conditions for the spruce beetle (yECS$_{\text{beetle}}$) and had higher variability in host tree climatic suitability in the historical period (HCS-SD$_{\text{host}}$). In years with moderate amounts of initiation and spread (2000 and 2001), newly-affected areas were found in sites with favorable historical conditions for the host tree (HCS$_{\text{host}}$), which in 2001 was combined with high inter-annual historical variability (HCS-SD$_{\text{host}}$), and a higher year-specific suitability for the host tree (yECS$_{\text{host}}$).

3.4. Discussion.

Climatic suitability of both the host tree and the beetle, as well as forest cover and tree size, strongly influenced outbreak patterns during the warm and dry 2000-2013 episode in the SRME. The integration of Landsat-based data of Engelmann spruce mortality driven by spruce beetle with indices of climatic suitability obtained by Species Distribution Models improves our understanding of complex outbreak dynamics at a regional scale. In addition, the combination of three approaches to analyze the outbreak, from the general response for the whole episode to the yearly pattern of outbreak initiation and spread, revealed the importance of processes operating at different temporal scales.

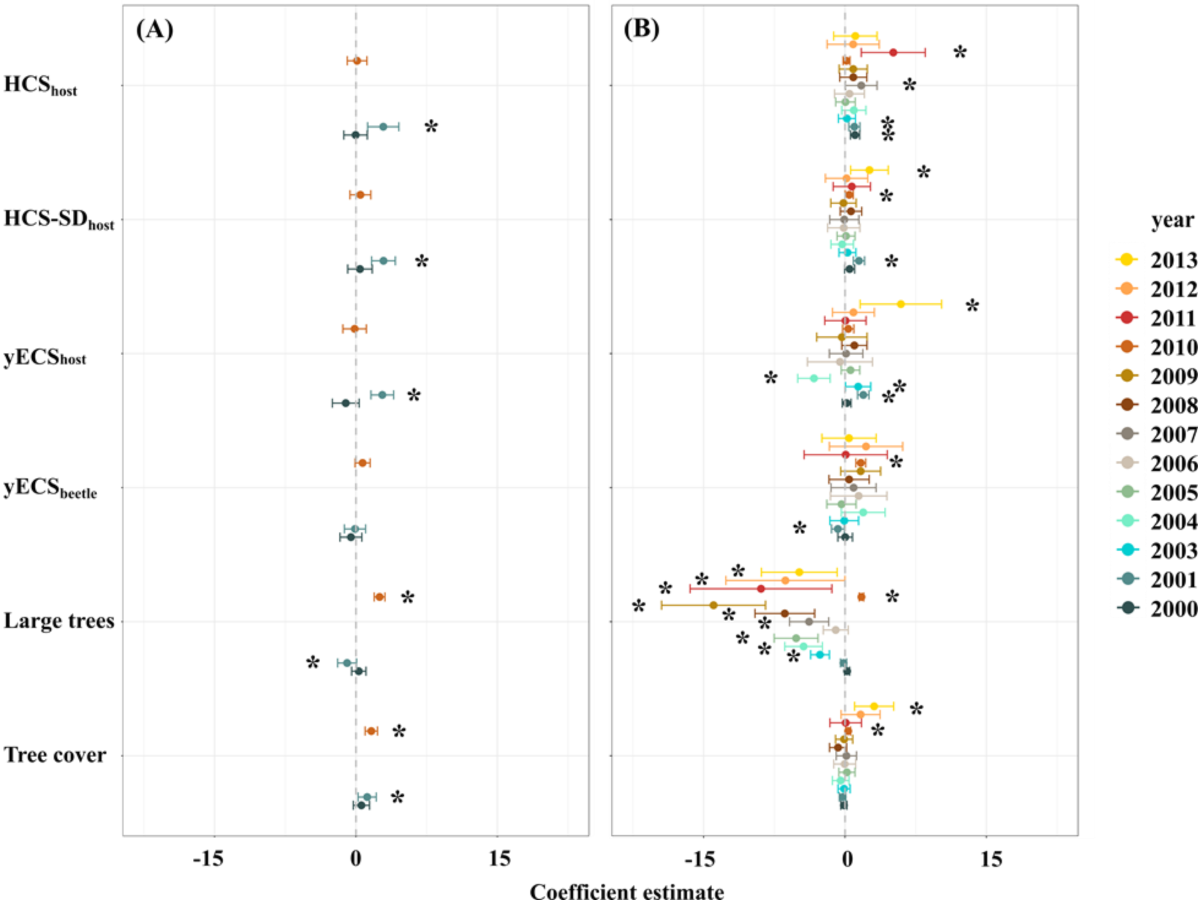

Figure 3.4. Summary of coefficient estimates obtained in the conditional autoregressive models (CAR) performed for each year, describing: (A) outbreak initiation *vs.* non-initiation and (B) outbreak spread *vs.* non-spread of spruce beetle in relation to climatic suitability and forest attributes in each year of the 2000-2013 episode. Abbreviations: HCS_{host}, historical climatic suitability for the host; $HCS\text{-}SD_{host}$, inter-annual variability in historical climatic suitability for the host; $yECS_{host}$, yearly episode climatic suitability for the host; $yECS_{beetle}$, yearly episode climatic suitability for the beetle. Only years with more than ten affected pixels were included: 2000, 2001, and 2010 for initiation; and all years except 2002 for spread. * indicates significance ($p < 0.05$).

Outbreak likelihood

The positive association of high historic and episodic climatic suitability for the host with the spruce beetle outbreak occurrence over the 2000-2013 period agrees with studies in other regions that observed a greater susceptibility of tree populations living near their climatic optimum to drought episodes (Cavin & Jump, 2017; Margalef-Marrase et al., 2020), bark beetle infestation (Jaime et al., 2019), or the combination of both (Lloret &

Kitzberger, 2018). Notably, our results showed that an extreme loss of host climatic suitability during a warm and dry episode was not strictly necessary to increase the likelihood of outbreak occurrence. The direct effects of drought and heat on host trees may be less important than climate impact on bark beetle life cycle and outbreak likelihood (Pettit et al., 2020). Historically favorable growing conditions for the host may result in dense stands with high tree competition, especially during episodes of reduced water availability (Jump et al., 2017), leading to successful beetle colonization due to greater availability of stressed hosts (Schmid & Frye, 1977; Schmid & Hinds, 1974). In addition, in areas with climatic conditions historically suitable for host trees, favorable conditions for beetles during the episode could promote insect population development rates and thus the infestation of larger and more vigorous trees, despite their stronger defenses (Krokene, 2015).

Location of outbreak initiation and spread

Outbreaks were most likely to initiate in regions historically suitable for host trees when the year-specific climatic conditions were also suitable for the beetles. This aligns with the idea that favorable climatic conditions for beetle development may be more determinant than decreased host climatic suitability for the initiation of spruce beetle outbreaks (Hart et al., 2017; Pettit et al., 2020). In contrast, the lack of association between the overall pattern of outbreak spread with host and beetle climatic suitability may reflect an amplifying mechanism in which, once the outbreak is initiated, large beetle populations can colonize nearby healthy trees and, consequently, the size of the beetle population governs subsequent propagation of the outbreak (Raffa et al., 2016). As such, when climatic conditions do not adversely affect insect survival, beetle pressure and the proximity to previously affected sites may be stronger predictors of outbreak spread (Hart et al., 2017; Preisler et al., 2012) than the climatic suitability of individual components of the host-beetle system.

Annual patterns of spruce beetle outbreak initiation and spread

Year-to-year climatic variability determines the patterns of outbreak initiation and spread. Low to moderate amounts of outbreak activity were observed in years with moderately warm and dry conditions, as indicated by year-specific host climatic suitability. During these years, initiation was scarce and spread mostly occurred in sites with historically favorable conditions and high inter-annual variability for the host. High climatic variability involving multiple past dry and heat episodes can have cumulative effects on tree vigor (Lloret et al., 2004) and enhance the likelihood of outbreak due to the presence of more stressed trees (Hart et al., 2014). Repeated, unfavorable year-specific climatic conditions leading to drought stress may affect tree vigor by compromising essential physiological processes, like photosynthesis, gas flux, resin production, and absorption of water and ions (Anderegg et al., 2015). However, during years with moderate water stress, the increase of tree resistance may also contribute to maintaining low and moderate amounts of initiation and spread if tree growth is more constrained than the production of defense compounds (Kolb et al., 2016).

A high amount of outbreak initiation and spread, and therefore years in which vast areas of forests were newly-affected, was associated with highly favorable conditions for the beetle but not with extreme conditions for the host (i.e., severe reduction of year-specific climatic suitability). This further supports the idea that outbreak dynamics are linked with unfavorable climatic conditions for the host that develop over multiple years (e.g., warming trends, frequent extreme events; Bigler et al., 2007; Hebertson & Jenkins, 2008; Hart et al., 2014). Indeed, the two years in which outbreak initiation and spread were most common (2000 and 2010) were preceded by a year with favorable climatic conditions for the host after several years of unfavorable conditions (Huberty & Denno, 2004). In turn, the substantial initiation and spread of new outbreaks in 2010 were preceded by three years of highly suitable conditions for the beetle. Importantly, these suitable climatic conditions captured mild winter and warm summer temperatures, which might have increased the survival rates of overwintering beetles (Miller & Werner, 1987; Schmid & Frye, 1977) and accelerated beetle population growth (Hansen & Bentz, 2003), facilitating a mass attack or spread to neighboring areas (Raffa et al., 2016).

Forest attributes mediated the influence of host and beetle climatic suitability on outbreak patterns. In years with low to moderate amounts of new infestation, initiation and spread mainly occurred in areas of high tree density dominated by small trees. On the contrary, in the year with the highest amount of new infestation, the outbreaks emerged and propagated in areas dominated by large trees. Small tree size can play an important role in constraining spruce beetle activity when previous outbreaks mostly kill large trees (Bakaj et al., 2016; Hart et al., 2015) and also in areas affected by stand-replacing fires, in which the regenerating small tree-sized forests are buffered from regional-scale outbreaks (Bebi et al., 2003; Kulakowski et al., 2016). However, our results suggest that in areas dominated by small trees, infested hosts could operate as reservoirs of beetles (Logan et al., 2010), helping to maintain outbreak activity in years when conditions are not optimal for the beetle. Eventually, the occurrence of highly suitable climatic conditions for the beetle may promote expansion into areas dominated by large trees, which along with the growth of endemic populations, may allow for the emergence of widespread and severe outbreaks in areas of old spruce-fir forests (DeRose & Long, 2012).

3.5. Conclusions.

This study improves our knowledge of how insect-host climatic suitability, together with forest attributes, modulates the outbreak pattern during episodes of warm and dry conditions. Particularly, it highlights the need to integrate the different components of the insect-host system to understand the processes driving the outbreak dynamics at different temporal scales. Overall, the observed regional insect-host dynamics suggest that tree populations located closer to the species' climatic optimum can be affected by outbreaks under future warmer and drier conditions (Jaime et al., 2019; Lloret & Kitzberger, 2018). By contrast, in populations closer to the species’ climatic edge, drought stress itself may play a limited role in determining the outbreak dynamics (Pettit et al., 2020). Specifically, the combination of suitable drought-stressed trees, that experienced suitable historical conditions, with favorable climate for the insect may predispose forests to a rapid emergence of outbreaks with widespread tree mortality. This may lead to shifts in forest structure, carbon pools, and other forest ecosystem functions at broad spatial scales (Biedermann et al., 2019; Hart et al., 2015). Understanding the spatiotemporal variability of this changing disturbance regime provides opportunities to apply site-specific management actions. For instance, this variability can contribute to understand the limited role of thinning and shelterwood on bark beetle control, while being effective to enhance resilience following outbreaks (Temperli et al., 2014). Also, this approach can be used to elaborate risk maps summarizing regional host-insect suitability under future climate scenarios, in order to maintain spruce-fir forests in the Southern Rocky Mountains while climate becomes more favorable to spruce beetle outbreaks.

Chapter 4

Climatic and stand drivers of forest resistance to recent bark beetle disturbance in European coniferous forests

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Abstract

Bark-beetle infestation is a major driver of tree mortality that may be critical for forest persistence under climate change, and the forecasted increased of extreme heat and drought episodes. Under this context, the environmental position of host tree populations within the species' climatic niche (e.g., central *vs.* marginal populations) is expected to be determinant in the dynamics of insect-host systems. Here, we analyzed recent patterns of bark beetle disturbance and consequent forest resistance across European coniferous forests during the 2010-2018 period. We obtained bark beetle attack and subsequent mortality data from successive forest damage surveys on 130 plots including five host trees (*Picea abies, Pinus sylvestris, Pinus nigra, Pinus pinaster*, and *Pinus uncinata*) and five bark beetle species (*Ips typographus, Ips sexdentatus, Ips acuminatus, Tomicus piniperda,* and *Tomicus minor*) and characterized the climatic niche of each species within a common environmental space. Then, we analyzed the overall forest resistance and the species-specific response, in terms of bark beetle attack and mortality, in relation to the distance to the niche optimum of both host tree and beetle species, the characteristics of previous drought events (duration, intensity, and time since extreme drought), and plot features. The results evidenced that overall forest resistance in terms of bark beetle attack was lower in monospecific plots located close to both host and beetle climatic optimums and that experienced long duration droughts. However, forest resistance to beetle attack varied among insect-host systems likely reflecting critical feedbacks driving the dynamics of the different bark beetle species. By contrast, forest resistance in terms of mortality did not appear related to the position of forests within species' climatic niche and it was mainly determined by the duration and intensity of droughts. Overall, our findings highlight the importance of disturbance interactions and suggest that the joint influence of drought events and bark beetle disturbance will threaten the persistence of current European coniferous, even in those tree populations close to their species climatic optimum.

4.1. Introduction.

Climate warming and increasing recurrence of extreme drought events are inducing widespread forest mortality around the globe (Allen et al., 2015; Senf et al., 2018). Such widespread mortality has impacts on forest structure and composition (Batllori et al., 2020), carbon balance (Seidl et al., 2014; Sippel et al., 2018), and hydrological cycles (Anderegg et al., 2013), as well as changes on the resilience capacity of forests to subsequent disturbances (Johnstone et al., 2016). In addition, increased drought and heat may change the regimes of other abiotic and biotic disturbances that contribute to forest mortality, such as wildfire, windthrows, and epidemics of forest insects (Jakoby et al., 2019; McDowell et al., 2020; Seidl et al., 2017). Forests are typically well adapted to a particular historical disturbance regime, however modifications of these regimes under global change could alter forests' response and reduce their resilience to other concurrent disturbances (Buma, 2015; Johnstone et al., 2016; Seidl & Rammer, 2017). For instance, the interaction between climatic conditions (e.g., drought) and biotic disturbances has led to unprecedented levels of bark beetle outbreaks in recent years, both in North American (Bentz et al., 2010) and European countries (Sommerfeld et al., 2020). Therefore, under the ongoing global climatic trends and the expected increase of beetle outbreaks (Bale et al., 2002), it is crucial to understand the mechanisms that determine when, where, and how changing disturbance regimes may surpass forest resilience and cause irreversible changes in forest persistence (Bentz et al., 2010; Thom et al., 2017b).

Bark beetles typically exhibit low population levels within forests (i.e., endemic phase), causing limited tree mortality, since specialized physical and chemical host tree defenses hinder infestation success (Raffa et al., 2016). Occasionally, favorable climatic conditions for insects combined with other triggering factors, such as suitable forest structure and composition, can allow beetle populations to reach outbreak levels (i.e., epidemic phase), overcoming host defenses and killing trees across large areas (Raffa et al., 2008). In this sense, the severity of bark beetle outbreaks has been related to the positive effect of increasing temperatures on the development of beetle populations and the negative effect of drought on individual host tree resistance (Bentz & Jönsson, 2015; Ryan et al., 2015). The overall resistance of forests to beetle infestation could be approximated in terms of likelihood of bark beetle attack and induced tree mortality (Hood et al., 2016). Thus, a resistant forest could withstand bark beetle attack and persist without pervasive host tree mortality. In contrast, a forest would not be resistant if bark beetle attack provokes widespread tree mortality, potentially pushing the system into a different state by changes in species dominance and composition (Sommerfeld et al., 2020).

The response of a particular forest to bark beetle disturbance could also be influenced by its environmental position within the climatic niche of the species involved (Jaime et al., 2019, 2021; Lloret & Kitzberger, 2018). According to the niche theory, species performance declines from the niche optimum or center to the edge or periphery of the species' climatic niche (Carscadden et al., 2020; Hirzel & Le Lay, 2008; Hutchinson, 1957). Under this assumption, it could be hypothesized that forest resistance to bark beetle disturbance is determined by the position of both host tree and beetle populations in the respective species’ climatic niche. Forest resistance in a given site would be high if such location is close to the niche optimum of the host tree, due to a better species performance (Abeli et al., 2014; Martínez-Meyer et al., 2013; Sexton et al., 2009). This enhanced resistance would be the result of a greater host tree defense capacity. However, in the same site, forest resistance would diminish if such location is also close to the beetle niche optimum, as the conditions suitable for insect development may allow overcoming host tree defenses. Importantly, episodes of extreme weather (e.g., drought) could modify the relationships between the climatic niches of the host tree and insect, affecting tree performance and its defense capacity, and beetle development. Under extreme weather episodes forest locations close to the host tree niche optimum could thus become susceptible to bark beetle disturbance (Kleinman et al., 2012).

The combination of warm and drought extreme events, also called "hotter droughts" (Allen et al., 2015), might have more severe impacts on forests and insect populations than droughts with normal temperatures (Pettit et al., 2020). Particularly, in European coniferous forests, recent hotter droughts (Brun et al., 2020; Hanel et al., 2018; Schuldt et al., 2020) have regionally increased the mortality rates associated with bark beetle infestation (Krams et al., 2012; Marini et al., 2012; Rouault et al., 2006; Seidl et al., 2016; Wermelinger et al., 2008). In addition, some bark beetle species, such as *Ips acuminatus*, are infesting with unexpected aggressiveness and outside of their historical distribution range (Siitonen, 2014). These facts highlight that the resistance of European coniferous forests to a wide variety of bark beetle species is declining, and this trend will likely continue under more frequent extreme events of drought and heat in the coming decades (Buras & Menzel, 2019).

Here, we analyzed forest resistance by assessing bark beetle attack and mortality episodes, with the combined effect of drought, in European coniferous forests during the 2010-2018 period. We use plot-level data of beetle attack and mortality caused by five different species of bark beetles (*Ips typographus*, *Ips sexdentatus*, *Ips acuminatus*, *Tomicus piniperda*, and *Tomicus minor*) on five different host tree species (*Picea abies*, *Pinus sylvestris*, *Pinus nigra*, *Pinus uncinata*, and *Pinus pinaster*). First, we explored the spatiotemporal patterns of the recent bark beetle disturbance across Europe for each species. Then, we analyzed (1) how driving factors including host tree and beetle climatic niches (distance to the niche optimum), duration, intensity, and time since previous extreme drought events, and plot characteristics (host tree proportion and species tree richness) determined the overall forest resistance in terms of bark beetle attack and mortality; (2) whether driving factors of bark beetle attack and mortality episodes were common among insect-host systems. We expected a decrease in forest resistance in locations close to the host tree optimum that recently experienced extreme drought events and which are close to beetle niche optimum (Jaime et al., 2019; Kleinman et al., 2012; Lloret & Kitzberger, 2018). Moreover, we expected a reduction of forest resistance in locations with lower species richness and a high abundance of host trees due to the positive influence of host availability on beetle populations (Raffa et al., 2008). Additionally, we expected that differences in forest resistance among insect-host systems feedbacks modulate the influence of the driving factors assessed here.

4.2. Material and methods.

Host tree attack and mortality data

We used data from the ICP Forests Level I tree condition survey, conducted annually on ca. 6000 plots distributed in a 16 × 16 km grid (nominal density) across Europe since 1987 (Lorenz & Fischer, 2013). At this level of assessment, ICP Forests data provide annual information on the spatial and temporal variation of the vitality of individual co-dominant trees, by recording defoliation status and the occurrence of symptoms attributable to biotic and abiotic damaging agents in each plot. Normally, at least 20 trees with a height > 60 cm were surveyed annually per plot (see Eichhorn et al., 2016 for survey methods). For our purposes, we collected data from plots assessed from 2010 to 2018 and in which visual symptoms of damage by any of the five bark beetle species, *I. typographus*, *I. sexdentatus*, *I. acuminatus*, *T. piniperda,* and *T. minor* were identified. All these species are considered capable of killing host trees across large areas when conditions are favorable (Lieutier et al., 2004). The main host tree species attacked by the beetle species considered here were *P. abies*, *P. sylvestris*, *P. nigra*, *P. pinaster*, and *P. uncinata*. The annual resolution of the ICP Forests data allowed us analyzing the progress from the first time in which a host tree was attacked by bark beetles to its eventual mortality.

The final plot selection was made by setting a minimum abundance threshold of > 10% of trees belonging to a host tree species at the beginning of the study period. Our selection derived in a total of 130 infested plots (Appendix C, Table C1), 47 of which exhibited tree mortality caused by beetle attack over the study period. It is important to note that not all selected plots have data for each year of the study period. Although *Tomicus* and *Ips* species can coexist on the same host tree or population when host trees are abundant (Amezaga & Rodríguez, 1998), only one of the selected plots showed more than one attacking bark beetle species. In this case, we considered the attack caused by the dominant bark beetle species in the plot.

In each plot and host tree species, we considered the following tree status: (1) infested, living tree with symptoms of bark beetle attack; (2) non infested, living tree without symptoms of bark beetle attack; (3) dead infested, with 100% defoliation and symptoms of bark beetle attack; (4) dead non infested, with 100% defoliation and without symptoms of bark beetle attack. Dead trees (infested or not) were no longer included in the survey of the following year. The yearly state of the host tree attack and mortality allowed the computation of rates of annual bark beetle attack and mortality per plot. Additionally, we calculated the plot-level annual proportion of each host tree (number of trees in a given year relative to the total trees in that year) and the tree species richness (number of tree species in a given year).

Drought characterization

To characterize the drought conditions experienced in each plot, we used the Standardized Precipitation-Evapotranspiration Index (SPEI; Vicente-Serrano et al., 2010). SPEI is a multi-scalar index based on the difference between precipitation and potential evapotranspiration (PET), which calculates climatic drought deviations in relation to a temporal reference span considering different time-scales. In our case, we took the 1960-2018 period as temporal span and a 12 months SPEI scale. We chose a 12-month scale because it should identify prolonged droughts with negative effects on tree defense capacity. To compute annual SPEI values, we used climate data at 4 km^2 resolution obtained from TerraClimate world database v.1.2 (Abatzoglou et al., 2018) and the SPEI package in R (Beguería & Vicente-Serrano, 2017). This spatial scale reflects the climatic differences between selected plots, which were separated by at least 16 km. We considered SPEI values under -1.5 as indicators of severe drought conditions and values under -2.0 as extreme drought conditions (Paulo et al., 2012). From this, the following

SPEI-derived variables were calculated: (1) drought duration, as the number of months with SPEI < -1.5; (2) maximum drought intensity, as the minimum SPEI value; and (3) time since maximum drought, as the number of months from the minimum SPEI value. All these explanatory variables were considered within the ten-years prior to the beginning of bark beetle infestation or mortality period in each plot.

Niche characterization and distance to the species' climatic niche optimum

To characterize the climatic niche of each host tree and bark beetle species listed above, we collected occurrence data for the five host tree species from the European Forest Data (Mauri et al., 2017) and for the five bark beetle species from the Global Biodiversity Information Facility (GBIF, 2020). To reduce possible sampling bias in occurrence records, we filtered them by a minimum distance of 4 km^2 between observations, conforming to the spatial resolution of the climatic dataset (see below). Only occurrence data from 1960 to 2000 were retained. The resulting dataset had a total of 58,436 occurrences (Appendix C, Table C2).

We obtained monthly precipitation, maximum, and minimum temperatures from TerraClimate world database v.1.2 (Abatzoglou et al., 2018) at 4 km^2 resolution for each year of the 1960-2000 period, as historical climatic conditions. These variables were used to calculate 19 yearly standard bioclimatic variables using the dismo R package (Hijmans et al., 2012). These bioclimatic variables included: annual mean temperature, mean diurnal range, isothermality, temperature seasonality, max temperature of warmest month, min temperature of coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, precipitation of coldest quarter.

We used the annual occurrence records of the five host tree and the five bark beetle species from the European Forest Data and GBIF datasets, respectively, to extract for each occurrence the annual values of the 19 bioclimatic variables in the 1960-2000 period. Then, we used Principal Component Analysis (PCA) to reduce the common, host tree and beetle species environmental space (i.e., all climatic records) of this inter-annual dataset into a two-dimensional space defined by the first and second principal components, accounting for 66.1% of the variability within the original variables (Appendix C, Fig. C1) (Broennimann et al., 2012). To characterize each species climatic niche, we used the first and second PCA scores to project the climatic values of their occurrences into the two-dimensional environmental space. Subsequently, we applied kernel density functions (Broennimann et al., 2012; R package ks, Duong, 2018) to determine the density values of each species' occurrences within the two-dimensional environmental space. Specifically, we applied Gaussian kernel functions selecting the optimal bandwidth by cross-validation (Duong & Hazelton, 2005) and removing values under the 0.05 lowest percentile. Finally, to define the species' climatic niche optimum, we used the 5% density kernel within each species' climatic niche (Appendix C, Fig. C2).

To obtain annual distances to the climatic niche optimum of each host tree and bark beetle species within the 130 study plots, we translated the annual climatic conditions of each plot during the 2010-2018 period into the common two-dimensional environmental space. To this, based on plots' coordinates, we extracted the climatic conditions for each plot during the study period from TerraClimate (Abatzoglou et al., 2018) and calculated the same 19 bioclimatic variables used in niche characterization to compute plot-level PCA scores. Subsequently, within the common two-dimensional environmental space, we estimated the Euclidean distances between the respective plot position and the species niche optimum for each year of the 2010-2018 period in which bark beetle infestation or mortality was recorded (Appendix C, Fig. C3). In addition, we obtained the position of each plot under historical climatic conditions (1960-2000 period) and calculated the baseline distances to the niche optimum of the host trees species. This information was used to verify the assumption that the relative position of each plot into the common environmental space was maintained between the historical and the years of infestation (Appendix C, Fig. C4).

Patterns of recent bark beetle disturbance

To explore what forest regions were more affected by the recent bark beetle disturbance across Europe, we calculated the percentage of cumulative bark beetle attack and mortality (avoiding tree repetitions among years) in each plot, as the total number of infested or dead infested host trees, respectively, in relation to the total host trees for the entire 2010-2018 period. Then, to explore the spatiotemporal patterns of bark beetle disturbance, we examined the time-series of host tree attack and mortality to analyze the variation of these two processes (attack and mortality) among species. To that, we computed annual rates of newly infested or newly dead infested trees for each year of the 2010-2018 study period at the plot level. We calculated them as the percentage of newly infested or dead infested host trees in a particular year in relation to the total host trees in a particular year.

Forest resistance analysis

To assess forest resistance in the surveyed plots during the study period, we focused on the overall response and the species specific-response of (1) the likelihood of bark beetle attack as the proportion of infested host trees in relation to the total host trees and (2) the likelihood of mortality caused by beetle attack as the proportion of dead infested trees in relation to total host trees. In plots with more than one year of attack or mortality, we pooled together the data of the different implicated years. Then, the bark beetle attack and mortality were examined in relation to the following plot-level explanatory variables: (1) distance at a given time (see below) to the host tree climatic niche optimum, (2) distance at a given time (see below) to the bark beetle climatic niche optimum; (3) drought duration, maximum drought intensity, and time since maximum drought (SPEI-derived indices), and (4) host tree proportion and tree species richness (plot characteristics). For each plot, we computed the distance of the plot's host tree and beetle species to the respective climatic niche optimum during the year of infestation or mortality. In cases where infestation or mortality lasted for several years (5.4% of the plots), we considered the distance to beetle and host niche optimums in the year of maximum distance for the host tree in such period, in order to capture the most stressful conditions experienced by the host. All explanatory variables were centered and rescaled to improve the subsequent model stability and permit a direct comparison of effect sizes.

To analyze overall bark beetle attack and mortality responses, we built a set of candidate Generalized Linear Mixed Models (GLMMs) with binomial error distribution (log-link function), including different combinations of the explanatory variables and two-way interactions between the distances of the host tree and the bark beetle to their respective climatic niche optimum. We added as random effects the main host tree and bark beetle species present in each plot (see Table 4.1). The best GLMM for each response variable was selected based on the Akaike Information Criteria (AIC) and considering the highest value of marginal and conditional R^2 (R package MuMIn; Nakagawa & Schielzeth 2013). The R^2 marginal represents the proportion of variance explained only by fixed effects and R^2 conditional the variance explained by both fixed and random effects. For two-way interactions, we calculated Johnson-Neyman intervals to estimate the range of values of the moderator variable in which the slope of the predictor is significant (R package interactions, Long, 2019).

To analyze species-specific bark beetle attack and mortality patterns, we built a set of Generalized Linear Models (GLMs) with binomial error distribution (log-link function), including different combinations of the explanatory variables and two-way interactions between the distances of the host tree and the bark beetle to their respective climatic niche optimum. We built models for each bark beetles species, since beetle species explained most of the model variance within the previous GLMMs. The best GLMs for each beetle species was selected based on the Akaike Information Criteria (AIC) and considering the highest of R^2. In the GLMs, we analyzed together *I. sexdentatus* with *I.*

acuminatus, and *T. piniperda* with *T. minor* to have enough plots with mortality caused by beetle attack. This grouping considered the similarity among the species biology and the main host tree attacked.

Finally, we checked model fit and performance by inspecting model assumptions and overdispersion (R package blmeco; Korner-Nievergelt et al., 2015).

4.3. Results.

Patterns of recent bark beetle disturbance in Europe

In total, we analyzed 2805 host trees distributed across 130 plots in 16 countries of Europe. Among them, 1522 trees were non-infested, 825 infested, 288 dead non-infested, and 170 dead infested during the entire 2010-2018 period. During this period, the percentage of cumulative bark beetle attack and mortality at plot-level showed geographical variations, with beetle attack hotspots in central, south-eastern, and northern Europe (Fig. 4.1; A), and mortality hotspots in south-eastern and northern Europe (Fig. 4.1; B). Considering all the species, time-series patterns of average bark beetle attack (black lines in Fig. 4.1; C-4.1; D) revealed that 2010 had the highest percentage of newly infested trees, ~10%. Then, average beetle attack decreased to 1% for 2014-2017 to rise to 6% in 2018. However, the temporal patterns of beetle attack varied substantially among insect-host systems according to the different host tree and bark beetle species with values below and over the average beetle attack (color lines, Fig. 4.1; C-4.1; D). For the host tree species, the maximum value of newly infested trees (over 20%) was found in 2015 for plots of *P. pinaster*. For bark beetles, maximum values were founded in 2010 for plots with *T. minor* as attacking beetle with more than 25% of newly infested trees; and in 2016 and 2018 for plots with *I. acuminatus* with more than 20% of infested trees.

Regarding the average annual rates of bark beetle attack and mortality (Table 4.1), plots with *P. sylvestris* as the main host tree showed the highest beetle attack rate, followed by *P. uncinata* and *P. pinaster*, and lastly by *P. abies* and *P. nigra*. However, the highest mortality rates occurred in *P. abies* plots, followed by *P. sylvestris*, *P. pinaster*, and *P. nigra*.

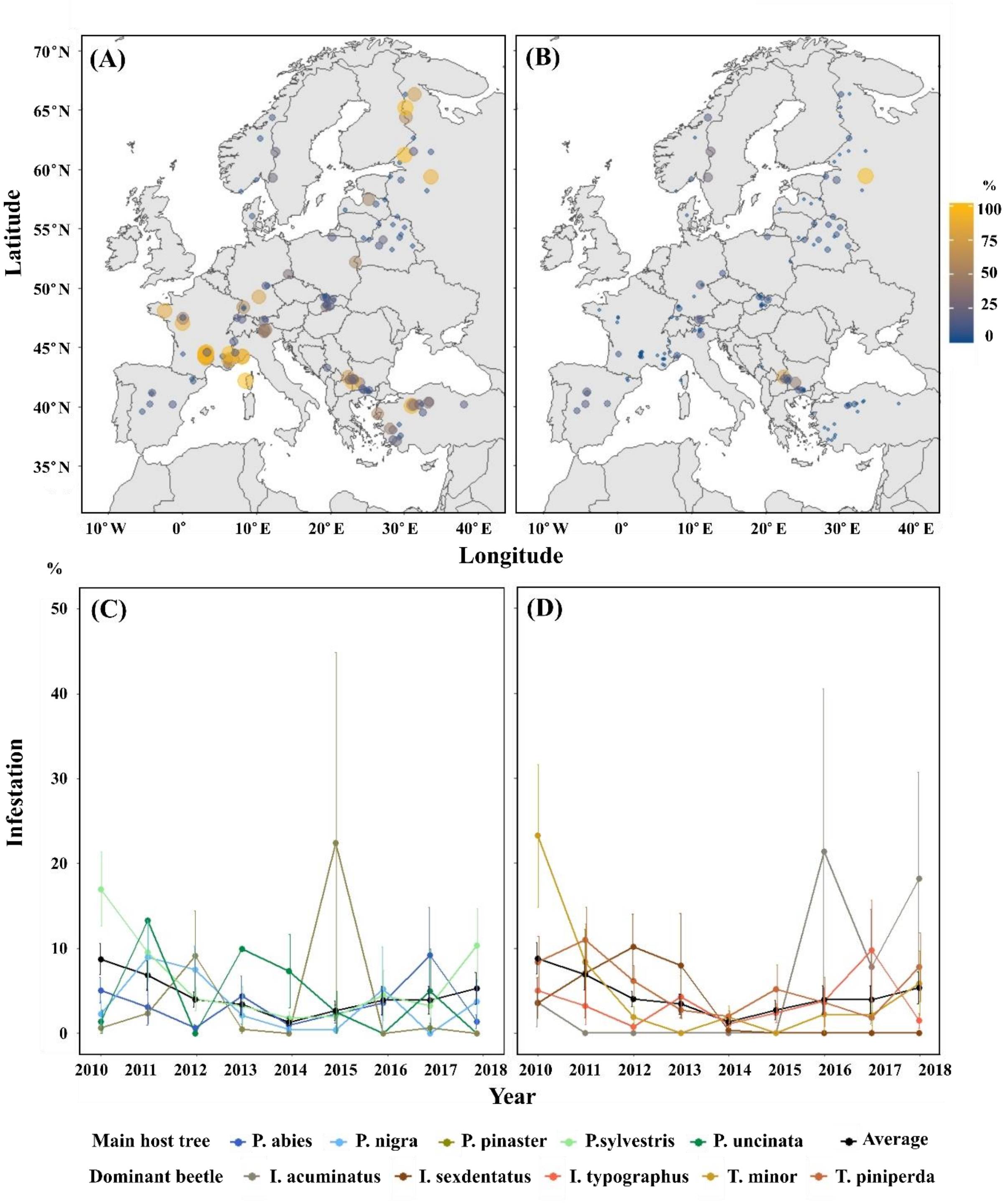


Figure 4.1. Geographic patterns of (A) the cumulative bark beetle attack and (B) the cumulative mortality driven by bark beetle attack in Europe during 2010-2018. For A and B panels, the legend shows the percentage of the cumulative beetle attack or mortality in the 130 ICP Forest monitored plots. (C) Time-series patterns of annual beetle attack rates in the main host tree species: yearly percentage of new infestations in plots dominated by each tree species (means ± SD); black line represents average values considering all species.

Figure 4.1 (continuation). (D) Time-series patterns of annual beetle attack rates for each bark beetle species: yearly percentage of new infestations in plots affected by each beetle species (means ± SD); black line represents average values considering all species. For C and D panels, the legend shows the line-colors representing each main host tree and bark beetle species. Total surveyed plots per year: 124 (2010); 126 (2011); 98 (2012); 103 (2013); 91 (2014); 95 (2015); 85 (2016); 83 (2017); 81 (2018).

Table 4.1. Average annual beetle attack and mortality rates for the 2010-2018 period by the main host tree and bark beetle species. Annual rates of new infested or dead infested trees were first averaged for each species and then within the years of the entire study period. N plots: correspond to the number of plots in which each species of host tree was the main infested, or in which each species of bark beetle was the attacking one.

Role	Species	N plots	Beetle attack (% yr^{-1})	Mortality (% yr^{-1})
Main host tree	*Picea abies*	47	3.42	1.12
	Pinus sylvestris	52	6.23	0.95
	Pinus nigra	20	3.42	0.06
	Pinus uncinata	3	4.40	0.00
	Pinus pinaster	8	3.98	0.64
Bark beetle	*Ips typographus*	46	3.50	1.16
	Ips sexdentatus	16	3.22	0.57
	Ips acuminatus	6	5.66	5.21
	Tomicus piniperda	40	5.37	0.11
	Tomicus minor	22	5.06	0.06

In the case of bark beetle species, *I. acuminatus* showed the highest annual beetle attack rates, followed by *T. piniperda* and *T. minor*, and by *I. typographus* and *Ips sexdentatus*. In relation to mortality rate, plots with *I. acuminatus* exhibited the highest rates, followed by *I. typographus*, *I. sexdentatus*, *T. piniperda*, and *T. minor*.

Forest resistance: bark beetle attack and mortality responses

The likelihood of overall bark beetle attack was significantly determined by the host abundance (host tree proportion) and tree species richness in the plots, the distance to the climatic niche optimum of the host and the beetle, and by drought conditions (Table 4.2). Higher values of beetle attack occurred in locations with lower abundance of host trees, lower richness, and drought events with less intensity but with longer duration during the ten-years previous to the attack (minimum SPEI and number of months with SPEI values <-1.5, respectively). Regarding the distance to the host and the beetle climatic niche optimums, the distance to the host tree optimum was negatively related to beetle attack, while the distance to the beetle optimum was positively related to beetle attack. Additionally, the positive interaction between these two variables reflected that plots' environmental distance to beetle niche optimum modulated the effect of the distance to host niche optimum on forest resistance in terms of beetle attack. Particularly, the likelihood of beetle attack increased in plots close to the optimum for both the host and the beetle, as revealed by Johnson-Neyman intervals (Appendix C, Fig. C5).

Table 4.2. GLMMs results of the overall forest resistance in terms of bark beetle attack and derived tree mortality as response variables and distance to the host and beetle climatic niche optimums, plot characteristics, and drought conditions as explanatory variables. Main host tree and bark beetle species were included as random effects. Minimum SPEI: lower values describe higher drought intensity. N plots = 130.

	Bark beetle attack			Mortality		
Fixed effects	Estimate (SE)	z value	Pr (>|z|)	Estimate (SE)	z value	Pr (>|z|)
Intercept	-1.039 (0.216)	-4.82	<0.001	-4.55 (0.582)	-7.82	<0.001
Host proportion	**-0.525 (0.091)**	**-5.75**	**<0.001**	----------------	-----	-------
Richness	**-0.581 (0.091)**	**-6.38**	**<0.001**	----------------	-----	-------
Distance$_{host}$	**-0.321 (0.063)**	**-5.06**	**<0.001**	----------------	-----	-------
Distance$_{beetle}$	**0.203 (0.050)**	**4.08**	**<0.001**	----------------	-----	-------
D$_{host}$ * d$_{beetle}$	**0.319 (0.048)**	**6.63**	**<0.001**	----------------	-----	-------
Minimum SPEI	**0.288 (0.062)**	**4.66**	**<0.001**	**-1.019 (0.251)**	**-4.07**	**<0.001**
Time since drought	----------------	-----	-------	----------------	-----	-------
N months SPEI <-1.5	**0.355 (0.057)**	**6.18**	**<0.001**	**0.740 (0.147)**	**5.04**	**<0.001**
Random effects	Variance	SD		Variance	SD	
Main host tree	0.12	0.34		0.00	0.00	
Bark beetle	0.09	0.29		1.22	1.10	
Rmarginal	0.09			0.40		
Rconditional	0.15			0.56		
AIC	1477			326		

In contrast to bark beetle attack, the likelihood of mortality was only significantly explained by the maximum drought intensity and the duration of severe drought (i.e., the minimum SPEI value and the number of months with SPEI values <-1.5, respectively; Table 4.2). Forest resistance, in terms of mortality caused by beetle attack, decreased with the intensity and the duration of drought events. In addition, the variance explained in the mortality model, without considering the random effects, was higher (R^2 marginal =

0.40) than for the bark beetle attack model, which was quite low (R^2 marginal = 0.09). Particularly, the random effects explained an important part of the models' variance (R^2 conditional = 0.15 in the beetle attack model and R^2 conditional = 0.56 in the mortality model), mostly due to bark beetle species.

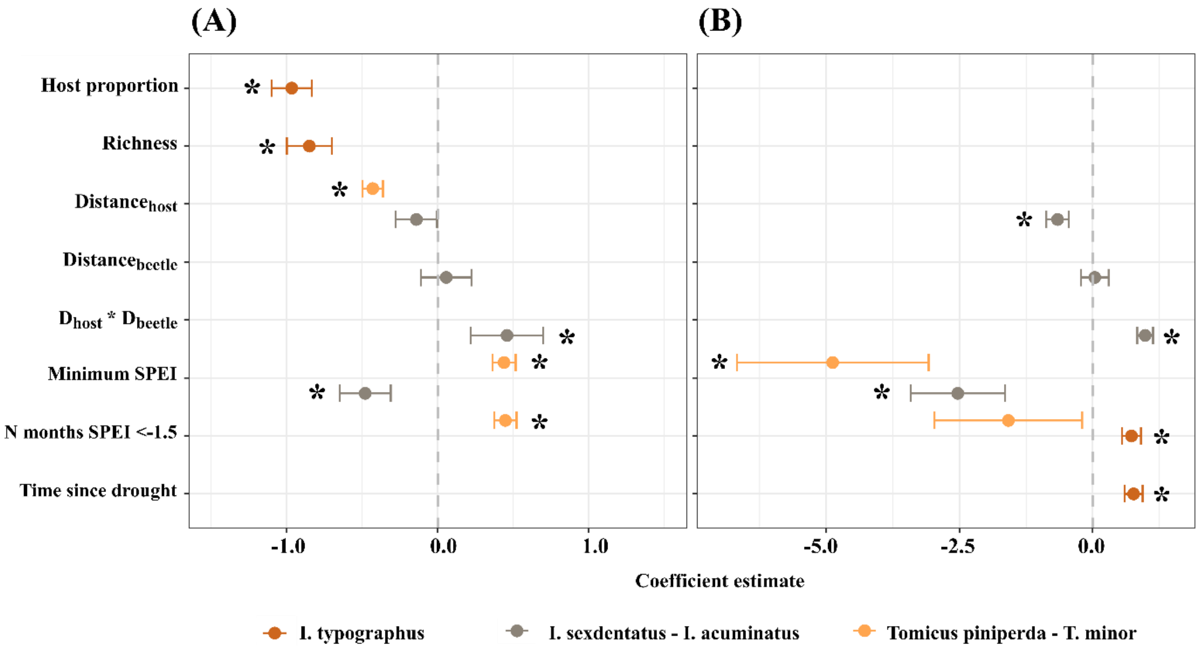


Figure 4.2. Summary of coefficient estimates obtained in GLMs describing the results of the species-specific likelihood of (A) bark beetle attack and (B) tree mortality for each beetle species. Explanatory variables include the distance to the niche optimum of both host tree and beetle species, drought conditions, and plot characteristics. Minimum SPEI: lower values describe higher drought intensity. R^2 for infestation models: *I. typographus* (0.26); *I. sexdentatus - I. acuminatus* (0.29); *T. piniperda - T. minor* (0.10). R^2 for mortality models: *I. typographus* (0.48); *I. sexdentatus - I. acuminatus* (0.91); *T. piniperda - T. minor* (0.96). * indicates significance ($p < 0.05$). N plots: *I. typographus* = 46; *I. sexdentatus* and *I. acuminatus* = 22; *T. piniperda* and *T. minor* = 62.

Patterns of bark beetle attack varied among species (Fig. 4.2; A) For *I. typographus*, the likelihood of beetle attack was negatively determined by plot characteristics (host tree proportion and tree species richness). For the joint activity of *I. acuminatus* and *I. sexdentatus*, the likelihood of beetle attack was determined by the positive interaction between host and beetle distances to species niche optimum and by maximum drought intensity. In the case of the joint activity of *T. piniperda* and *T. minor,* beetle attack increased close to the host climatic niche optimum, and was positively related to droughts events of less intensity and more duration. Tree mortality patterns also varied among bark beetle species (Fig. 4.2; B), but in all cases, it was determined by drought conditions. Particularly, for *I. typographus*, the likelihood of tree mortality increased with the drought duration and the time since the maximum drought, and both for the joint activity of *T. piniperda* and *T. minor* and the joint activity of *I. acuminatus* and *I. sexdentatus*, tree mortality increased with the intensity of drought events (lower values of minimum SPEI, higher mortality). In addition, for the joint activity of *I. acuminatus* and *I. sexdentatus*, mortality was also determined by the proximity to the host and beetle species niche optimums.

4.4. Discussion.

Bark beetle attack and eventual tree mortality were determined by the combination of several drivers, including plot features as well as climate conditions and their interaction with species' environmental preferences. Drought conditions, both duration and intensity, had a critical role on recent bark beetle infestation and mortality patterns, substantially reducing the resistance of European forests to insect attack during the 2010-2018 period. These results are consistent with studies that have linked the ongoing decline of host tree resistance and the intensifying severity of bark beetle outbreaks under increased climatic variability and episodes of hotter-droughts (Netherer et al., 2019; Neumann et al., 2017; Rouault et al., 2006). Our analysis revealed that the influence of drought on forest resistance to bark beetle attack was mediated by the environmental position of the affected forest within the host tree and beetle species climatic niche. Particularly, forest resistance was modulated by the joint influence of the proximity to the respective optimum of both the host tree and beetle species. This highlights the potential of integrating host and beetle niche characterization into a common environmental space to better understand forest resistance to bark beetle disturbance at regional scales under changing climates.

Patterns of bark beetle disturbance

Spatial patterns of recent beetle disturbance showed that host tree populations from north, central, and eastern Europe exhibited high levels of bark beetle attack, while the beetle-induced mortality was more marked in north and eastern populations. At high latitudes of Europe, warmer winters are enhancing bark beetle overwinter survival and increasing the number of generations per year in multivoltine species, such as *I. typographus* and *I. acuminatus* (Jönsson et al., 2009; Siitonen, 2014). This, in combination with years of marked water deficit, such as 2015 and 2018 (Hanel et al., 2018; Schuldt et al., 2020), could trigger the decline of forest resistance due to a reduced host tree defense capacity (Bentz & Jönsson, 2015; Ryan et al., 2015), resulting in increased beetle attack and associated tree mortality rates. Such fact has been observed in *I. acuminatus*, which mainly attacks *P. sylvestris*. This beetle species is not particularly aggressive, but it has benefited from the recent warming and drought stress (Colombari et al., 2012; Siitonen, 2014) which has weakened the resistance of *P. sylvestris* (Jaime et al., 2019; Krams et al., 2012; Rebetez & Dobbertin, 2004). Similarly, in central European forests, regional summer drought and prolonged water stress are promoting infestation pulses of *I. typographus* on *P. abies* forests (Rouault et al., 2006; Seidl et al., 2016) that, may result in high mortality rates in the near future. However, the observed geographic pattern of beetle-induced mortality does not exactly reproduce the geographic pattern of beetle attack, indicating differences in the drivers that determine bark beetle attack and mortality processes.

Forest resistance

Overall, forest resistance in terms of bark beetle attack was determined by the confluence of diverse factors that predispose trees to be attacked by bark beetles, such as forest environmental position in relation to the host and beetle climatic niche optimums, drought conditions, and plot characteristics. At the time of bark beetle attack, plots climatically located closer to the niche optimum of the main host tree and bark beetle species were less resistant to infestation. That is, for a given distance in relation to the beetle climatic optimum, beetle attack increased in tree populations closer to their respective climatic optimum. However, the likelihood of beetle attack also tended to increase with far distances from the beetle optimum. This could be explained by a displacement of beetles optimum during the study period to more suitable conditions for their development (Appendix C, Fig. C6).

Although in host tree populations located close to their climatic optimum, a higher tree defense capacity may be expected due to a better species performance (Abeli and others 2014; Martínez-Meyer and others 2013; Sexton and others 2009), several studies have reported that tree populations established in climatically suitable locations are more likely to be infested when such locations are also suitable for bark beetles (e.g., Jaime et al. 2019), particularly under the influence of drought events (Jaime et al., 2021; Kleinman et al., 2012; Lloret & Kitzberger, 2018). This is reflected in our analyses, as the most attacked forest plots were the ones that experienced long-lasting, moderate droughts during the ten-years before the first time of beetle attack, which could have strongly depleted hosts' resistance (Huang et al., 2020). Under moderate drought stress, tree growth can be more limited than photosynthesis, thus increasing carbon allocation for defense compounds (Koontz et al., 2021). But, long-lasting drought stress can exhaust defense mechanisms due to prolonged compromise of essential physiological processes (Anderegg et al., 2015). On the other hand, host trees located under suitable climatic conditions may invest more resources for fast-growing, limiting the production of defenses (Ferrenberg et al., 2014). As a result, under recurrent drought, vigorous trees established in locations environmentally close to the species climatic niche optimum would become less resistant to beetle attack which, together with increased suitability for beetles and the high nutritional quality of such trees, would increase brood beetle development, facilitating a massive forest attack.

Concerning plot characteristics, locations with low richness of tree species were more likely to be attacked. For bark beetles, olfactory recognition across the landscape is easier in monospecific stands of host trees (Raffa et al., 2016), while in mixed stands, chemical stimuli from non-host trees can produce a "repellent barrier" that disrupts host recognition (Zhang & Schlyter, 2004). However, our results also showed that stands with a lower abundance of host trees were also highly attacked. In our assessment, the likelihood of beetle attack was calculated as the proportion of host trees in plots with symptoms of beetle attack. The observed pattern shows, counterintuitively, that the proportion of infested trees was lower in those plots with a higher number of host trees. However, this reflects that more trees escaped from beetle attack in those plots with a higher abundance of host trees, indicating that other factors also dictate forest resistance to beetle attack, such as stand age structure, density, or basal area (Netherer et al., 2019). Such stand information could not be readily obtained for the analyzed plots and it was not incorporated in our analyses. In addition, the host tree abundance calculated from the plot-level ICP Forests data may have been underestimated in some cases. Surveyed trees were selected according to possible different plot designs, but in general, starting from the center of circular plots / satellites of cross-cluster plots and concentrating the survey effort on dominant and co-dominant trees. Therefore, the degree at which tree selection can reflect the actual tree composition is uncertain and may vary in time and space, particularly in rich stands.

Overall, forest resistance in terms of mortality was exclusively driven by the drought duration and intensity of drought events the years before beetle-induced mortality. Independently of plot characteristics and their environmental location within the host and beetle climatic niche at the time of mortality, trees in plots that previously experienced long-duration droughts and acute drought stress were more likely to die after being attacked. At the tree-level, extreme and prolonged droughts constrict stomata and limits transpiration, reducing photosynthesis and carbon assimilation (McDowell et al., 2011; McDowell et al., 2008). This situation of water and carbon scarcity decreases resin flow, compromises the production of defense compounds to cope with bark beetle attacks, and can accelerate ongoing infestations (Kolb et al., 2019; Raffa et al., 2016). It is worth noting that ICP Forests mortality data could also reflect management activities, as it is common to remove freshly killed and infested trees to avoid bark beetle outbreaks (Hlásny et al., 2019). This fact could have resulted in underestimating the actual number of dead infested trees, thus skewing the observed beetle-induced mortality patterns. Therefore, the reported mortality rates and drivers of tree mortality should be taken with caution because other factors could also be operating in addition to drought conditions. Regardless, the observed mortality patterns highlight the importance of the magnitude and duration of drought episodes prior to beetle attack, which has strong implications in the context of ongoing climate change and the expected increase on extreme climatic events.

Species-specific patterns evidenced differences associated with the attacking bark beetle species. The likelihood of beetle attack by *I. typographus*, which infests *P. abies* populations, was exclusively driven by plot characteristics, despite the relevance of drought stress in the transition of *I. typographus* to a massive attack (Netherer et al., 2021). Particularly, forest resistance to this beetle attack diminished in monospecific plots. In such plots, pioneer beetles may easily find a suitable tree to attack and, then, rapidly spread to host neighbors (Raffa et al., 2016; Schebeck et al., 2017). Thus, for *I. typographus* host availability could be more determinant than host physiological stress caused by drought to select stands to attack (Stephenson et al., 2019). On the contrary, the likelihood of beetle attack by *I. sexdentatus* and *I. acuminatus*, which infest pine populations, increased in plots close to both host tree and beetle populations climatic optimum that experienced extreme drought conditions. The existence of climatic factors that, in turn, predispose the reduction of forest resistance and promote beetle population development could be essential for increasing the capacity of attack of these two less aggressive species (Colombari et al., 2012; Pineau et al., 2017). Finally, in the case of *T. piniperda* and *T. minor*, were necessary the occurrence of moderate and prolonged droughts in pine populations close to its climatic optimum to reduce the forest resistance to beetle attack. Unlike the considered *Ips* species, *Tomicus* species have only one generation per year (Lieutier et al., 2004), hence the increase of attacks could be more determined by the availability of stressed host trees rather than favorable conditions for beetle development. Overall, regardless of the attacking beetle species, infested trees that experienced long-lasting and intense drought conditions prior to the attack subsequently died. This suggests that beetle-induced mortality patterns may be more determined by the negative effects of drought on host tree resistance than by species-specific bark beetle dynamics.

4.5. Conclusions.

This study reveals that the forest resistance of European conifer forests to bark beetle disturbance could be jeopardized under the expected increase in the frequency of extreme drought events in the coming decades, particularly under the threat of multivoltine bark beetle species activity. Our findings emphasize that models that aim to predict forest resistance to bark beetle disturbance under future climate scenarios will need to explicitly account for beetle-drought interactions. We suggest that an approach incorporating the magnitude and duration of drought events, integrated within the framework of insect-host species climatic niche, together with stand characteristics (i.e., structure and composition) would allow more accurate predictions of the rates and patterns of forest resistance to bark beetle attack and derived mortality into the future

Chapter 5

General discussion and conclusions

5.1. General discussion.

The responses of the insect-host systems at different spatiotemporal scales combined with the effects of increasing drought stress and temperatures are complex (see Introduction), and the pathways that such responses could take are not fully understood. Moreover, tree vulnerability to bark beetle disturbance in the context of climate change is expected to increase in many regions, potentially altering insect-host systems' response. Throughout this Thesis, I tried to elucidate the effects of the climatic conditions on the response of different insect-host systems from the tree-level to regional scales, based on the species' climatic niche, considering both host trees and bark beetles. One of the general questions posed at the beginning of this thesis was "Why some host tree populations are infested and killed by bark beetles while others resist and maintain low beetle populations?". Throughout the different studies constituting this Thesis, the environmental position of the tree populations within the species' climatic niche has appeared particularly relevant to answer this question. Host tree populations located close to the most suitable conditions for the species, that is, close to the species climatic niche optimum, were more susceptible to bark beetle infestation. This pattern emerged consistently across the different insect-host systems and study scales considered here. The ultimate reason underlying such pattern is tightly related to the following question "How does the interaction between the components of the insect-host system vary across the species' climatic niche and how it is affected by extreme weather conditions?". Indeed, recent extreme weather events have had a higher impact on the dynamics of insect-host systems in areas environmentally close to the climatic niche optimum of both host tree and beetle species. The proximity to host tree niche optimum (i.e., more vigorous trees) would allow bark beetle development and population density, when episodic climatic conditions (i.e., drought) reduce host tree performance and its resistance to bark beetle attack. These findings lead to the assertion that including the species climatic niche as an input in tree infestation and mortality models provides new insights to better understand why some host tree populations are being more susceptible to bark beetle disturbance. Therefore, the scientific framework used in this Thesis represents a step forward in relation to previous bark beetle disturbance studies, in which no clear patterns were often found.

5.1.1. Factors that determine host tree mortality and infestation at tree- and stand-scale.

In Chapter 2, I explored whether the climatic suitability of both the host tree and bark beetle species, together with tree and stand attributes, explained Scots pine mortality and infestation patterns in NE of the Iberian Peninsula during the 2013-2014 period. I used observational fieldwork data and indices of climatic suitability inferred from Species Distribution Models (SDMs) to reveal that, independently of the study level - tree and stand -, the response of tree populations to bark beetle disturbance was determined by the historical climatic suitability of the host tree and bark beetle populations.

Notably, locations with historically suitable climatic conditions for both the host tree and bark beetle species were more susceptible to experience alterations of the insect-host system after drought episodes. In terms of bark beetle attack, higher climatic suitability for the beetle would promote beetle populations and the likelihood of stand infestation (Bentz et al., 2010). Likewise, in areas historically suitable for the host tree, episodic drought conditions would reduce host tree defense capacity, increasing the attack success and, therefore, the likelihood of tree mortality (Krokene, 2015). Such results challenge the notion that tree populations are more susceptible to disturbances when living closer to the limits of species' climatic tolerance (MacArthur, 1972; Parmesan, 2006). Indeed, other recent studies also reported that tree populations located closer to the species’ climatic optimum could experience low tolerance to extreme weather events (Cavin & Jump, 2017; Lloret & Kitzberger, 2018; Margalef-Marrase et al., 2020), altering their response to biotic disturbances (Kleinman et al., 2012).

However, the relationships found between tree characteristics and tree mortality, and between stand structure and stand infestation, suggested that the studied populations were attacked by a low-density population of bark beetles (i.e., endemic phase), in which smaller trees were more susceptible to succumb to the attack. Based on these results, it could be presumed that the previous drought episode which took place in the area during 2005-2013 (Maluquer et al., 2018; Tejedor et al., 2017) did not weaken enough the defense capacity of large trees and these trees were able to cope with bark beetle attack, limiting the increase of beetle population to epidemic levels (i.e., outbreak phase).

The incorporation of other tree attributes, such as growth rate and the production of defense compounds, and their relation to the density of the attacking beetle populations would have been useful for better understanding whether trade-offs of resource allocation (Ferrenberg et al., 2015; Herms & Mattson, 1992; Kichas et al., 2021; Stamp, 2003) modulated the vulnerability of tree populations to bark beetle attack across the assessed range of tree climatic suitability. Similarly, the assessment of Scots pine mortality and infestation patterns may have also been benefit from the inclusion of detailed measures of the magnitude of extreme weather conditions (i.e., drought) in each site, although this magnitude was indirectly addressed in the analysis. In addition, the temporal variability around the mean historical climatic suitability could be relevant to measure environmental stability and to consider the cumulative effects of past deleterious periods in host tree populations (Anderegg et al., 2015; Lloret et al., 2004).

Overall, the application of SDMs provided indices of climatic suitability to successfully integrate and explain host tree and bark beetle population-level processes, such as bark beetle infestation and tree mortality. Nevertheless, additional research is needed to examine whether infestation and mortality patterns in tree populations close to the climatic optimum *vs.* climatic edge are maintained in areas where the transition of beetle population from an endemic phase to an outbreak one has occurred. Moreover, as outlined above, to further our understanding of the infestation process and the response of host tree populations, it would be necessary to explicitly incorporate measures about the climatic conditions experienced during the infestation and mortality episode in order to capture deviations from the historical climatic conditions across sites.

5.1.2. Factors driving outbreak dynamics at regional scale.

In Chapter 3, I incorporated to the analysis of the dynamics of insect-host systems not only the historical climatic suitability across the study range, but also its variability and the climatic suitability during the outbreak episode. In this study, I assessed the role of tree and beetle climatic suitability and forest attributes in the outbreak dynamics of spruce beetle on Engelmann spruce populations in the Southern Rocky Mountains (USA) during a warm-dry episode of 14 years (2000-2013). For that, I combined the use of Landsat maps of outbreaks and the estimation of different indices of climatic suitability derived from SDMs. Overall, the integration of Landsat-based data informing of the bark beetle impact on forests with indices of climatic suitability obtained by SDMs improved our understanding of the outbreak dynamics across the Southern Rocky Mountains. In addition, the inclusion of three different spatiotemporal approaches to assess the dynamics of the outbreak, from the cumulative outbreak response over the entire episode to the yearly pattern of outbreak initiation and spread, revealed that the response of this insect-host system was determined by the climatic conditions experienced by the host tree and bark beetle populations at different spatiotemporal scales.

Particularly, I found that host tree populations living in historically climatic suitable areas were also more susceptible to experience an outbreak (i.e., epidemic phase). Based on these results and those obtained in Chapter 2, it seems that tree infestation and mortality, under both endemic and epidemic phases of bark beetle populations, are more likely to occur in areas where the historical climatic conditions have been suitable for the host tree. Such remarkable result could be explained by the effects of drought on the trade-offs between tree growth and resource allocation to defenses (Herms & Mattson, 1992; Lorio, 1986; Stamp, 2003). Host tree populations located in areas historically suitable would have a high pre-drought investment of resources in growth that, in turn, reduce tree investment in defenses against bark beetle attack. In addition, during drought episodes, water and carbon scarcity could compromise growth and defense capacity (Reeve et al., 1995) and accelerate host trees' decay, causing them to release concentrated nutritional compounds, which enhances beetle population (White, 2015). Likewise, historically favorable growing conditions for tree populations may result in greater availability of stressed host trees due to competition or to episodic unfavorable climatic conditions, which increase the likelihood of finding susceptible host trees and reaching successful beetle colonization (Raffa et al., 2008). On the other hand, host tree populations close to the species climatic limit could be acclimated to marginal conditions, being more resistant to water deficit (Cavin & Jump, 2017; Lloret & Kitzberger, 2018; Rehm et al., 2015). In these populations, moderate water stress could stimulate the production of tree defenses (Herms & Mattson, 1992) limiting the success of bark beetle attack.

The analyses of Chapter 3 also revealed that during the outbreak episode, particularly in the outbreak initiation, the occurrence of suitable conditions for bark beetle populations was more important to successful attack than a severe loss of climatic suitability of the affected host tree populations. Thus, the direct effects of drought and heat on host trees during the outbreak episode may be less determinant than their impact on the bark beetle life cycle to disrupt the insect-host system and increase the outbreak likelihood (Hart et al., 2017; Pettit et al., 2020). This fact was reflected in the annual outbreak patterns, in which low amounts of outbreak initiation and spread were determined by host climatic suitability, while massive amounts of outbreak initiation and spread by beetle climatic suitability. Moreover, these patterns highlight the importance of processes operating at different temporal scales when considering species, such as host trees and bark beetles, with contrasted life cycles. Therefore, analyses at different temporal resolutions, including the combination of the host tree and bark beetle climatic niche, are necessary to assess the dynamics of such insect-host systems at a regional scale.

Despite not having proxies of forest composition over the study area (e.g., richness and proportion of host trees), which can be determinant to the transition from an endemic to an epidemic beetle phase (Schmid & Frye, 1977), the relationships found between the considered forest attributes (dominant tree size and tree cover) and the levels of outbreak initiation and spread were coincident with epidemic levels (Jenkins et al., 2014). Dense forests with large trees were more affected by bark beetles because they allow the development of larger broods (Boone et al., 2011). The inclusion of yearly proxies of forest attributes, that is, information on forest management, windthrows, and other biotic disturbances that could have altered forest structure and composition during the study period, would have offered a more comprehensive understanding of the spruce beetle outbreak dynamics at small-spatial scales.

In conclusion, this chapter reveals the importance of including different temporal scales (i.e., from the cumulative to the year-to-year patterns) to unravel the major drivers underpinning the dynamics of insect-host systems. Likewise, these analyses emphasize the need to incorporate databases of successive forest assessments to appropriately analyze the infestation process according to the structure and composition of the affected forests.

5.1.3. Factors that determine forest resistance to bark beetle disturbance considering different insect and host tree species.

In Chapter 4, I focused on the forest resistance to bark beetle disturbance in terms of beetle attack and derived tree mortality by considering different insect-host systems in European forests during the 2010-2018 period. In this case, I used monitored plots from the ICP Forests dataset, which allowed me to analyze the progress of the infestation process from the first time in which bark beetles attacked a host tree to its eventual mortality, and the influence of different predisposing and promoting factors. In addition, I computed species' climatic niches by building a common environmental space, allowing me to calculate the environmental distance of each considered plot, at the moment of beetle attack or tree mortality, to the climatic optimum of the dominant host tree and attacking beetle species in the plot. Consistent with the previous chapters, the explanatory variables used to explain beetle disturbance in different insect-host systems were the distance to the species' climatic niche optimum, drought conditions, and forest attributes.

The results revealed that a confluence of predisposing and promoting factors, such as the environmental distance to the host and beetle climatic niches, drought conditions, and forests attributes, determined overall forest resistance to bark beetle attack. Particularly, I found that monospecific forests close to both the host tree and beetle climatic niche optimums were less resistant to beetle attack, especially when such forests experienced long-lasting and moderate droughts. These results reinforce the evidence found in Chapters 2 and 3, which indicated that host tree populations living in areas that historically have been climatically suitable for the host tree were more susceptible to bark beetle disturbance. As seen in the previous Chapters, this was likely due to a combination of recent unfavorable climatic conditions for the host trees, that modify their trade-offs between growth and defense, and favorable climatic conditions for beetles’ development that enhance their attacks, resulting in alterations of the insect-host systems (transition to epidemic phases).

Chapter 4 results also showed that forest resistance to subsequent mortality was exclusively determined by the intensity and duration of drought conditions. Previous intense and long-lasting droughts would have drastically reduced the production of secondary compounds by host trees, including both constitutive and inducible defenses (McDowell et al., 2011; McDowell et al., 2008; Reeve et al., 1995), accelerating ongoing infestations and increasing tree vulnerability to die following bark beetle attacks (Raffa et al., 2016). From the beetles’ point of view, such weakened trees would be an easy choice to surpass their resistance mechanisms and achieve a successful attack (Kolb et al., 2019). Overall, recent beetle-induced mortality patterns across Europe highlight the importance of the magnitude and duration of drought episodes prior to beetle disturbance, emphasizing the relevance of disturbances interactions and pointing to reduced forest resistance under increased drought frequency with changing climates.

Importantly, the predisposing factors of forest resistance to bark beetle attack varied among species, likely due to critical feedbacks driving the dynamics of the particular attacking bark beetle species involved. Specifically, differences among bark beetle species based on the effect of warming conditions on the duration and the timing of their life cycle could have determined their distinct response to the considered predisposing factors (Lieutier et al., 2004; Reed & Hood, 2021). Nevertheless, the analysis of the particularities of species-specific responses was constrained by the limited number of plots with symptoms of bark beetle attack during the study period. In contrast, successive forest monitoring provided a more accurate estimation of the structure and composition of the affected forests at the moment of beetle attack. This information is relevant due to its relationship with management activities and other disturbances which can modify host availability (Hlásny et al., 2019).

5.1.4. The use of standardized indices to integrate the insect-host response.

This Thesis is pioneer in analyzing the role of the climatic niche of both host tree and bark beetle species to disentangle the effects of climatic conditions and their variability in the dynamics of insect-host systems. Particularly, given their current relevance and expected alterations under climate change, the response of these systems to drought periods has been the focus of the three different studies conforming to this Thesis. Across Chapters 2, 3, and 4, I have explored different metrics describing the relationships between climatic variables and species performance estimated from its geographic distribution. These metrics include indices inferred from Species Distribution Models (SDMs) and measures obtained from the characterization of species' climatic niches.

SDMs are widely employed in ecological studies (Araújo et al., 2019; Guisan et al., 2013; Guisan & Zimmermann, 2000) due to the increasing necessity to assess and predict the effects of climate change on the response of populations. However, SDMs have some theoretical and methodological shortcomings in estimating indices of species climatic suitability accurately. One of the limitations is that their reliability depends on the quality of species occurrence data, climatic predictors, and the selected algorithm to calibrate their relationship (Araújo & Guisan, 2006). In addition, SDMs are usually built with climatic predictors at coarse spatial resolution (commonly 1 km^2), ignoring local climatic conditions or without explicit consideration of the ecological processes determining species occurrence (Franklin, 2010; Soberón & Peterson, 2005). Nevertheless, SDMs have proved a powerful tool for analyzing the responses of populations on a biogeographic scale (Guisan & Thuiller, 2005), particularly related to short-term climatic events (Evans & Lyons, 2013; Lloret & Kitzberger, 2018; Margalef-Marrase et al., 2020; Pérez Navarro et al., 2019).

Moreover, SDMs are generally calibrated with current species distribution and historical climatic datasets with averages of 30 or 50 years (Abatzoglou et al., 2018; Fick & Hijmans, 2017; Karger et al., 2017) to predict past or future changes in relation to altered climates (Elith & Graham, 2009). This allowed in Chapter 2 to estimate the historical climatic suitability (HCS) for the host tree and bark beetle species and explore its relevance on recent tree mortality and stand infestation on Scots pine populations. Nevertheless, particularly for short-lived species such as bark beetles, fine temporal resolution data would be required to define more accurately their climatic niche (Hereford et al., 2017). For instance, not considering inter-annual climate variability could lead to misleading species climatic suitability (Perez-Navarro et al., 2020) due to the weak relationship between the geographic distribution of short-living species, such as beetles, and their climatic requirements. For that reason, in Chapter 3, I built SDMs based on annual climatic values for each beetle occurrence in the specific year of recording against pseudoabsences sampled across all years. Moreover, the availability of yearly climatic conditions allowed estimating other SDM-derived indices in addition to the historical climatic suitability (HCS). Particularly, it was quantified the inter-annual variability in historical climatic suitability (HCS-SD), as a measure of site environmental stability and, importantly, the climatic suitability experienced by populations during the years of the adverse climatic episode (ECS), which was used as a measure of the magnitude of the episode of drought and heat conditions.

Despite the utility of climatic suitability indices derived from SDMs to obtain a simple, integrated measure of the species climatic requirements, recent studies have suggested that the use of these indices instead of other direct measures obtained in the n-environmental space (Blonder et al., 2014; Broennimann et al., 2012) can contribute to decoupling the relationship between niche characteristics and species occurrence or abundance (Martínez-Meyer et al., 2013; Osorio-Olvera, Soberón, & Falconi, 2019). Therefore, in Chapter 4, I assessed the predictive capacity of euclidean distances obtained in the environmental space defining the climatic niche of the host and beetle species to explain the response of different insect-host systems. Notably, this approach allowed assessing the influence of inter-annual variability in the species climatic niche, which could also be relevant to improve the analysis of host tree population performance, especially in fluctuating environments (Perez-Navarro et al., 2020). Moreover, the common environmental space built for several species allowed the comparison of the performance between the different the insect-host systems assessed here.

In the conceptual framework of this Thesis, it was assumed the correspondence between population performance and its relative position within species niche (MacArthur, 1972; Sexton et al., 2009). That is, that species performance was expected to decline from the niche optimum towards the edge of the species' climatic niche (Carscadden et al., 2020; Hirzel & Le Lay, 2008; Hutchinson, 1957). However, the results found in Chapters 2, 3, and 4, contradict the hypothesis that host tree populations close to their species climatic optimum or in locations historically suitable should present higher capacity to cope with bark beetles. Biotic interactions involving multiple species (e.g., host, beetle, fungi), microlocal climatic variability, recent extreme events, or species adaptation and acclimation mechanisms could explain that this correlation between species' performance and niche position (core *vs*. periphery) is not fulfilled, as other studies have observed (Csergő et al., 2017; Dallas & Hastings, 2018). Moreover, the use of species occurrence or abundance to define the species climatic niche, rather than population growth rates, as defined by the Hutchinsonian niche (1957), may not accurately represent the response of population performance to environmental variation (Carscadden et al., 2020; Pagel et al., 2020). However, these problems do not completely invalidate the capability of climatic niche estimates to explain populations response to disturbances, as we found. Indeed, the overall results of this Thesis strongly support the validity of this approach, thus backing our knowledge about processes that are highly influenced by climate, as those determining the insect-host systems dynamics. The pattern consistently found in the three chapters reveals the vulnerability of tree populations living close to their climatic optimum can be explained by several mechanisms, such as lower tree defense investment under favorable conditions for tree growing, combined with higher nutritional quality for beetles, and the vulnerability of host trees to drought episodes due to past investment of tree structures requiring maintenance, as discussed previously.

Regardless of the conceptual and technical shortcomings outline above, the results presented in this Thesis showed that the use of indices of climatic suitability (Chapter 2 and 3) and distances to species climatic niche optimum (Chapter 4) were appropriate standardized measures to integrate and analyze the response of diverse insect-host systems at different spatiotemporal scales, particularly to extreme weather conditions. Likewise, combining the climatic niche characterization and the populations' position in the niche space of both the host tree and insect species seems a promising method to guide future research and experiments for anticipating tree mortality episodes driven by beetle disturbance under future climate change scenarios.

5.2. Conclusions.

Chapter 2. Factors that determine host tree mortality and infestation at tree- and stand-scale.

- Tree mortality was positively determined by the historical climatic suitability of the host tree populations and the intensity of bark beetle attack, and negatively by tree size.
- Stand infestation was positively determined by both historical climatic suitability of host tree and bark beetle populations, negatively determined by host tree density and basal area, and positively by tree species richness.
- Particularly, locations historically more suitable for both host tree and bark beetle species were the most infested.
- The index of historical climatic suitability derived from Species Distribution Models was revealed as a useful approach to explain patterns of tree mortality and the success of stand infestation.

Chapter 3. Factors driving outbreak dynamics at regional scale.

- Overall outbreak was positively determined by the historical and episode climatic conditions experienced by host tree populations.
- The combination of suitable climatic conditions for the beetle during the outbreak episode and high historical suitability for the host explained the locations of the initiation of outbreaks.
- Year-to-year patterns revealed that the amounts of outbreak initiation and spread were determined by the spatiotemporal variability in climatic conditions. Particularly, years with low amounts of outbreak initiation and spread were determined by high host historical climatic suitability, with high interannual variability, and a modest reduction of suitability during the episode; while years with massive outbreak initiation and spread were promoted by suitable conditions for the beetle.

- Forest structure, characterized by dense forest with large trees, mediated the transition to widespread outbreak levels under suitable conditions for the beetle.
- The estimation of indices inferred from Species Distribution Models that quantified the historical climatic conditions (HCS), its environmental stability (HCS-SD), and measured the climatic suitability experienced by populations during the adverse episode (ECS) were useful to assess processes determined by climatic variability at different temporal scales.

Chapter 4. Factors that determine forest resistance to bark beetle disturbance considering different insect and host tree species.

- Overall forest resistance in terms of infestation (as the first stage of bark beetle attack) was positively determined by the distance to the niche optimum of the host tree and beetle species, negatively by duration and intensity of previous drought events, and positively by stand characteristics, such as tree richness.
- In addition, species-specific responses of forest resistance, in terms of infestation, varied among species, likely due to the existence of critical feedbacks governing the dynamics of the different bark beetle species involved.
- The attack success of aggressive bark beetle species was determined by plot characteristics. In contrast, promoting factors were necessary to surpass forest resistance by less aggressive or monovoltine species. These factors included suitable climatic conditions for beetle development or previous drought events that reduced host defense capacity.
- Overall and species-specific forest resistance, in terms of mortality caused by bark beetles, was exclusively driven by the magnitude and duration of previous drought events. Particularly, forest resistance decreased under intense and long-lasting drought conditions, leading to a quick death of host trees once they were first attacked.

- Distances to species niche optimum obtained from niche characterization demonstrated to be an appropriate tool to explain the role of inter-annual climatic variability on forest resistance to bark beetle attack.

Appendix A

Chapter 2

Figure A1. Description of each studied stand.

Stand	Lat (N)	Lon (E)	Elevation (m a.s.l.)	Slope (%)	Orientation	Mean temp. (°C)	Max. temp. (°C)	Min. temp. (°C)	Mean annual precip. (mm)	N	Main vegetation
1	42° 9.9'	1° 34.6'	1538	21	NE	7.2	20.5	-2.7	1034	116	*Buxus sempervirens, Juniperus communis*
2	42° 6.3'	1° 32.6'	1233	16	NW	8.9	22.3	-1.4	920	29	*Buxus sempervirens, Juniperus communis*
3	42° 13.2'	1° 34.4'	1240	15	NW	8.7	22.1	-1.6	940	79	*Buxus sempervirens, Juniperus communis*
4	42° 19.1'	1° 38.5'	1323	29	NE	8.2	21.6	-2	979	30	*Buxus sempervirens, Juniperus communis*
5	42° 18.8'	1° 39.2'	1457	27	NW	7.5	20.8	-2.5	1027	42	*Buxus sempervirens, Juniperus communis*
6	42° 20.2'	1° 37.5'	1466	11	N	7.4	21.4	-2.1	1031	23	*Juniperus communis, Amelancher ovalis*
7	42° 23.0'	1° 34.0'	1495	17	N	7.1	20.5	-2.8	1053	31	*Buxus sempervirens, Juniperus communis*
8	42° 19.9'	1° 42.6'	1618	9	NW	6.6	19.8	-3.1	1084	33	*Amelancher ovalis*
9	42° 14.6'	1° 19.4'	1561	25	NW	6.8	20.2	-3.3	1059	101	*Juniperus communis, Arctostaphilos uva-ursi*
10	42° 15.9'	1° 19.0'	1371	4	N	7.8	21.3	-2.5	999	32	*Buxus sempervirens, Juniperus communis*
11	42° 18.5'	1° 16.9'	1301	23	N	8.1	21.7	-2.3	988	68	*Buxus sempervirens*
12	42° 05.5'	1° 31.8'	1220	10	SW	9	22.4	-1.3	915	74	*Buxus sempervirens, Juniperus communis, Quercus ilex*
13	42° 11.1'	1° 33.6'	1478	16	NE	7.5	20.8	-2.5	1019	47	*Buxus sempervirens, Juniperus communis*
14	41° 55.3'	2° 23.0'	628	5	SW	12.8	25.4	2.5	845	36	*Erica arborea, Arbutus unedo*
15	41° 50.9'	2° 19.5'	744	19	NW	12.2	24.6	1.9	824	27	*Erica arborea, Juniperus communis*
16	41° 50.0'	2° 19.1'	932	6	SW	11.2	23.9	1.3	864	23	*Quercus sp., Cistus laurifolius*
17	41° 55.6'	2° 21.5'	712	19	N	12.3	25	2.1	842	23	*Arbutus unedo, Erica arborea, Quercus sp.*
18	42° 20.9'	1° 05.3'	1083	24	N	9.1	23.1	-1.8	941	46	*Amelancher ovalis*
19	42° 21.8'	1° 05.3'	729	24	N	11	25.2	-0.5	811	19	*Buxus sempervirens, Quercus sp.*
20	42° 21.2'	1° 03.0'	1166	33	NE	8.6	22.5	-2.2	975	39	*Buxus sempervirens*
21	42° 21.9'	1° 03.1'	1138	16	N	8.8	22.7	-2.1	966	40	*Lonicera xylosteum*
22	41° 20.3'	1° 00.5'	811	23	NE	11.9	25.7	0.7	688	10	*Arbutus unedo, Erica arborea, Quercus sp.*

Appendix B

Chapter 3

Table B1. The data layers and attributes used to examine spatiotemporal development of spruce beetle outbreak in the SRME.

Data	Description	Original source	Type / Units	Year(s)	Rationale
1. Occurrence data used to build SDMs					
Spruce beetle	Infestation records across Alaska, Yukon, British Columbia, and western CONUS range distribution.	ADS and AOS (Koot, 1997; McConnell et al., 2000)	Polygon / stratified random points with a minimum distance of 1 x 1 km	2001 - 2014	Used to build the Species Distribution Models as occurrence data.
Engelmann spruce	Natural history records of Engelmann spruce range distribution.	FIA + GBIF (ForeCASTS, 2014)	Point records / minimum distance of 1 x 1 km	Inventories data since the 1920s	Used to build the Species Distribution Models as occurrence data.
2. Climate variables used to build Engelmann spruce SDMs					
Temperature seasonality (bio4)	Temperature variation over a given period based on the ratio of the standard deviation of the monthly mean temperatures to the mean monthly temperature.	CHELSA (Karger et al., 2017)	1 x 1 km raster / standard deviation in ^{0}C x 100	1969 - 2013	Indicator of seasonal temperature variation. This species has a broad temperature tolerance range, withstanding extreme temperatures of more than -45°C to above 32°C (Alexander, 1987). Therefore, areas with large seasonal changes in temperature (i.e., continental climate conditions) may increase the probability of Engelmann spruce occurrence.
Mean temperature of the wettest quarter (bio8)	Mean temperatures during the wettest three months of the year.	CHELSA (Karger et al., 2017)	1 x 1 km raster / ^{0}C	1969 - 2013	Indicator of the cold/warm limits in the wettest season that determine the probability of species occurrence. Cool temperatures in the wettest season may affect positively the seedling establishment (Andrus et al., 2018) and the following growing season (Billah & Goldblum, 2019).
Mean temperature of the driest quarter (bio9)	Mean temperatures during the driest three months of the year.	CHELSA (Karger et al., 2017)	1 x 1 km raster / ^{0}C	1969 - 2013	Indicator of the cold/warm limits in the driest season that determine the probability of species occurrence. The combination of low temperature and precipitation may affect negatively the growing season (Truettner et al., 2018). On the contrary, warm temperature with low precipitation may promote tree radial growth and seed production (Billah & Goldblum, 2019; Buechling et al., 2016) before a threshold temperature level (Buechling et al., 2017).

Table B1. Continuation.

Data	Description	Original source	Type / Units	Year(s)	Rationale
Precipitation seasonality (bio15)	Ratio of the standard deviation of the monthly total precipitation to the mean monthly total precipitation.	CHELSA (Karger et al., 2017)	1 x 1 km raster / percent* *in some regions the value exceeds 100 percent	1969 - 2013	Indicator of seasonal precipitation variation. This species lives in a wide range of seasonal precipitation, but with moderate or no seasonal deficiency (Alexander & Shepperd, 1984). Therefore, areas with large seasonal changes in precipitation (i.e., continental climate conditions) may increase the probability of Engelmann spruce occurrence.
Precipitation warmest quarter (bio18)	Total precipitation during the warmest three months of the year.	CHELSA (Karger et al., 2017)	1 x 1 km raster / mm	1969 - 2013	Indicator of warm-season precipitation limits that determine the probability of species occurrence. The combination of high values of precipitation in the warm season may limit Engelmann spruce radial growth (Billah et al., 2019).
Precipitation coldest quarter (bio19)	Total precipitation during the coldest three months of the year.	CHELSA (Karger et al., 2017)	1 x 1 km raster / mm	1969 - 2013	Indicator of cold-season precipitation limits that determine the probability of species occurrence. High values of precipitation in the coldest months may reduce growing season at northern locations (Billah & Goldblum, 2019). On the contrary, high precipitation may have positive effects at southern locations (Truettner et al., 2018).
3. *Climate variables used to build spruce beetle SDMs*					
Mean diurnal range (bio2)	Mean of the monthly temperature ranges (maximum monthly minus monthly minimum). It reflects temperature fluctuation within a month to capture the diurnal temperature range.	CHELSA (Karger et al., 2017)	1 x 1 km raster / ^{0}C	1997 - 2013	Indicator of diurnal temperature fluctuation, which influences the degree-day accumulation and can affect to beetle development rate and voltinism (Chen et al., 2015). A higher temperature range that increments the accumulated growing degree-days may shorten the duration of beetle generations (Dell & Davis, 2019), increasing the likelihood of a spruce beetle outbreak occurrence.

Table B1. Continuation.

Data	Description	Original source	Type / Units	Year(s)	Rationale
3. Climate variables used to build spruce beetle SDMs					
Mean temperature of warmest quarter (bio10)	Mean temperatures that prevail during the warmest three months of a given year.	CHELSA (Karger et al., 2017)	1 x 1 km raster / ^{0}C	1997 - 2013	Indicator of the mean summer temperatures, whose higher values may accelerate beetle population growth (Hansen & Bentz, 2003; Hansen et al., 2001) and increase the probability of a spruce beetle outbreak occurrence (Berg et al., 2006; DeRose et al., 2013; O'Connor et al., 2015).
Mean temperature of coldest quarter (bio11)	Mean temperatures that prevail during the coldest three months of a given year.	CHELSA (Karger et al., 2017)	1 x 1 km raster / ^{0}C	1997 - 2013	Indicator of the mean winter temperatures, whose higher values may increase the survival rates of overwintering beetles (Miller & Werner, 1987; Schmid & Frye, 1977) and promote a spruce beetle outbreak occurrence (DeRose et al., 2013; DeRose & Long, 2012; Hart et al., 2014).
Precipitation driest quarter (bio17)	Total precipitation that prevails during the driest three months of a given year.	CHELSA (Karger et al., 2017)	1 x 1 km raster / mm	1997 - 2013	Lower values of precipitation promote indirectly the probability of spruce beetle outbreak occurrence (Csank et al., 2016; Hebertson & Jenkins, 2008) by predisposing host trees to beetle attack (Mattson & Haack, 1987; Werner et al., 2006).
Precipitation warmest quarter (bio18)	Total precipitation during the warmest three months of a given year.	CHELSA (Karger et al., 2017)	1 x 1 km raster / mm	1997 - 2013	Indicator of warm-season precipitation. Lower values of precipitation may reduce host tree vigor and increase the probability of spruce beetle outbreak occurrence (Csank et al., 2016; Hart et al., 2014, 2017; Sherriff et al., 2011).
Precipitation coldest quarter (bio19)	Total precipitation during the coldest three months of a given year.	CHELSA (Karger et al., 2017)	1 x 1 km raster / mm	1997 - 2013	Indicator of cold-season precipitation. Winter drought increases the probability of spruce beetle outbreak occurrence (Hart et al., 2017).

Table B1. Continuation.

Data	Description	Original source	Type / Units	Year(s)	Rationale
4. Forest attributes to build outbreak models					
Stand density	Landsat-based maps of percent tree cover. The percent of each pixel covered by vegetation > 3m in height.	Landsat (J. O. Sexton et al., 2013)	Polygon / percent of tree cover in a grid of 1 x 1 km, then converted to a raster.	2000	Used as an indicator of stand density. Denser stands are linked to higher susceptibility to infestation (Jenkins et al., 2014; Schmid & Frye, 1977).
Dominance of large trees	Proportion of tree cover classify as small (S), medium (M) or large (L) trees within spruce-fir cover. S trees (> 2.5 cm to < 12,5 cm). M trees (>12,5 cm to < 22 cm). L trees (> 22 cm).	USFS (2003)	Polygon / proportion of spruce-fir tree cover classify as large in a grid of 1 x1 km, then converted to a raster	2002	Used as an indicator of the dominant tree size, since larger tree diameters have been linked to a higher susceptibility to infestation (Jenkins et al., 2014; Schmid & Frye, 1977; Schmid & Hinds, 1974).
5. Spruce beetle outbreak maps to build outbreak models					
Spruce beetle activity	The presence/absence of gray stands inferred to be affected by spruce beetles based on Landsat imagery.	Hart and Veblen, 2015	30 x 30 m raster / conversion to 1 x 1 km	2000 - 2014	Used in conjunction with ADS data to create maps of spruce-fir forest affected and unaffected by spruce beetle outbreak
ADS Damage causal agent	Spruce beetle causing damage at the SRME.	McConnell et al. (2000)	Polygon	1997 - 2013	Used to improve Landsat-based estimates of the presence/absence of spruce beetle activity. Mask to consider any given pixel as a 'true' pixel of presence of spruce beetle outbreak.
Blowdown	The presence/absence of blowdown derived from 1988-1989 and 1997 aerial imagery.	Lindemann and Baker (2001)	Polygon	1997	Used to remove areas of blowndown, which may be misclassified as outbreak, from maps of spruce beetle activity.
Fire	Burned area boundaries.	MTBS Project (2017)	Polygon	1988 - 2014	Used to remove areas of wildfire, which may be misclassified as outbreak, from maps of spruce beetle activity.
FACTS Timber Harvest	The presence/absence activities accomplished as part of the timber harvest program, based on aerial imagery or GPS positions.	USFS (2016)	Polygon	1989 - 2014	Used to remove areas of timber harvest, which may be misclassified as outbreak, from maps of spruce beetle activity.

Table B2. Description and evaluation of the built SDMs. The model description includes: algorithm used (Algorithm); number of occurrences (N occur.); number of pseudo-absences (N pseudo-absences); method of partitioning data in training and testing dataset (Part.); number of climatic variables used (N variables). The model evaluation includes: the mean area under the receiver operating characteristic curve (mean AUC).

Model fitting						**Model evaluation**
Species	Algorit.	N. presences	N. pseudo-absences	Partitioning	Variables	Mean AUC
Picea engelmannii	GLM	2,945	10,000	70 calibrating / 30 validation 5-fold for training/testing	6	0.93 ± 0.004
	GAM		10,000			0.94 ± 0.003
	RF		2,945			0.96 ± 0.001
	MAXENT		10,000			0.94 ± 0.001
Dendroctonus rufipennis	GLM	25,874	30,000	70 calibrating / 30 validation 5-fold for training/testing	6	0.85 ± 0.001
	GAM		30,000			0.87 ± 0.001
	RF		25,874			0.95 ± 0.001
	MAXENT		30,000			0.85 ± 0.001

Spatial autocorrelation test

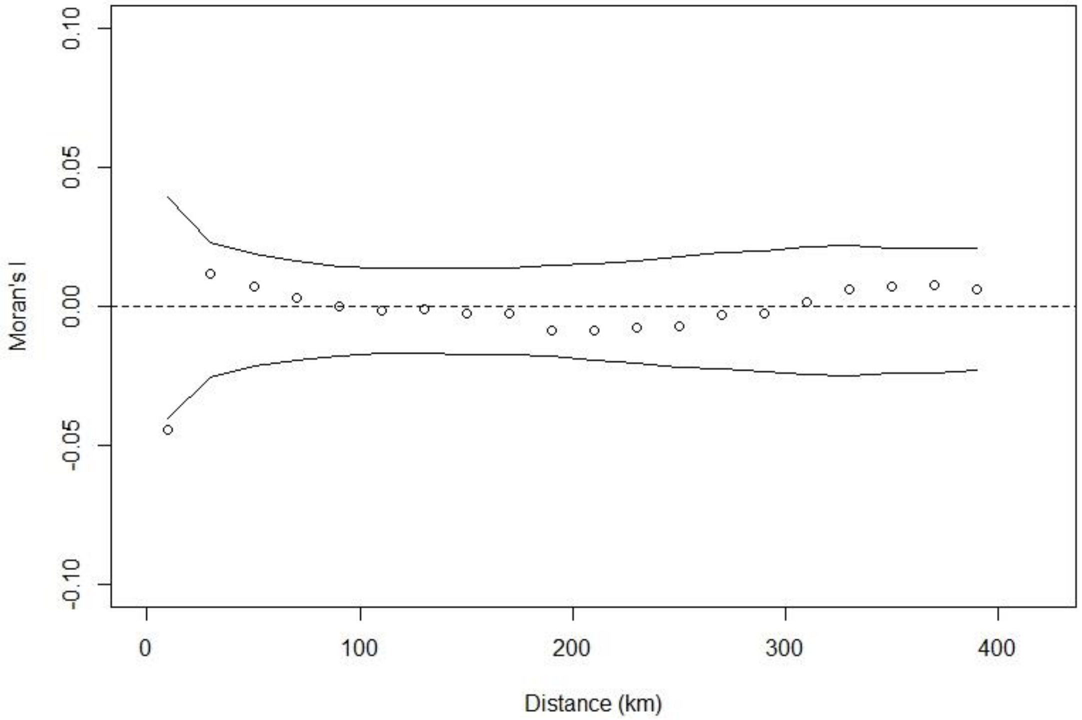


Figure B1.1 Correlogram of mean residuals of generalized linear models of the overall spruce beetle outbreak in the entire period (2000-2013). Gap distance between points of 10 km.

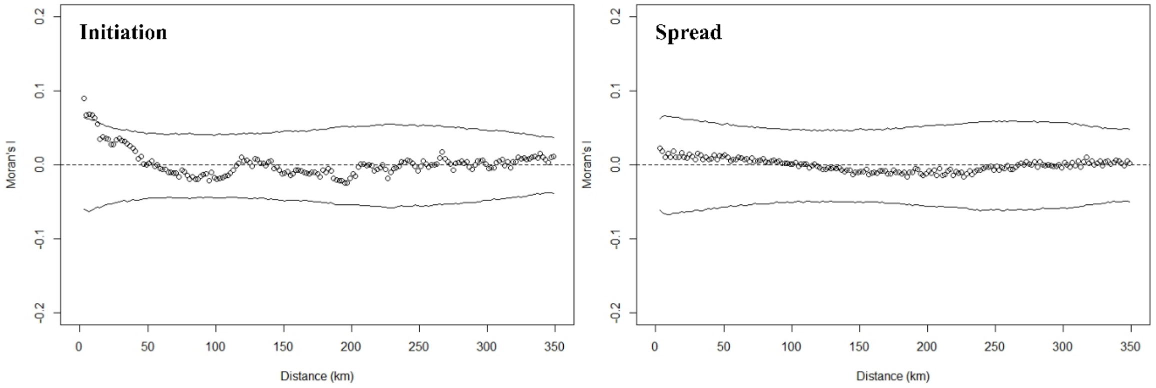


Figure B1.2. Correlograms of mean residuals of generalized mixed models of the overall outbreak initiation and spread response for the entire period (2000-2013). Gap distance between points of 2 km.

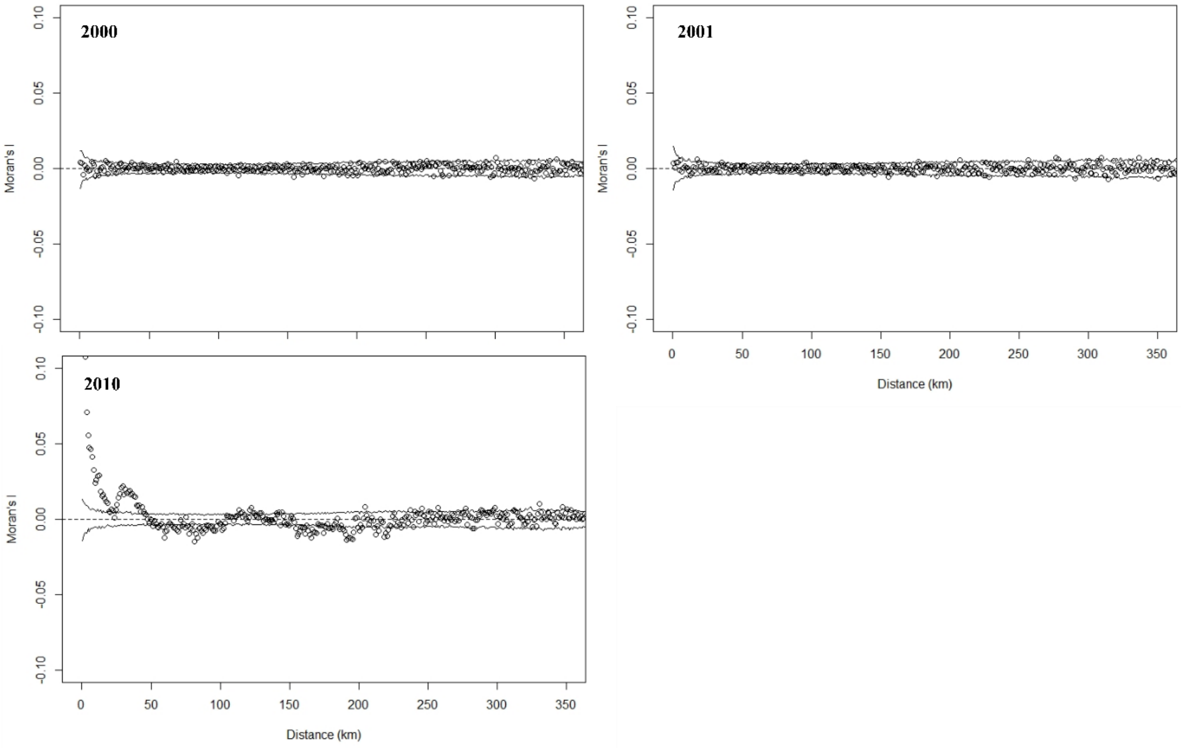


Figure B1.3. Correlograms of mean residuals of CAR models of the outbreak initiation for each year of the study period (2000-2013). Gap distance between points of 1 km.

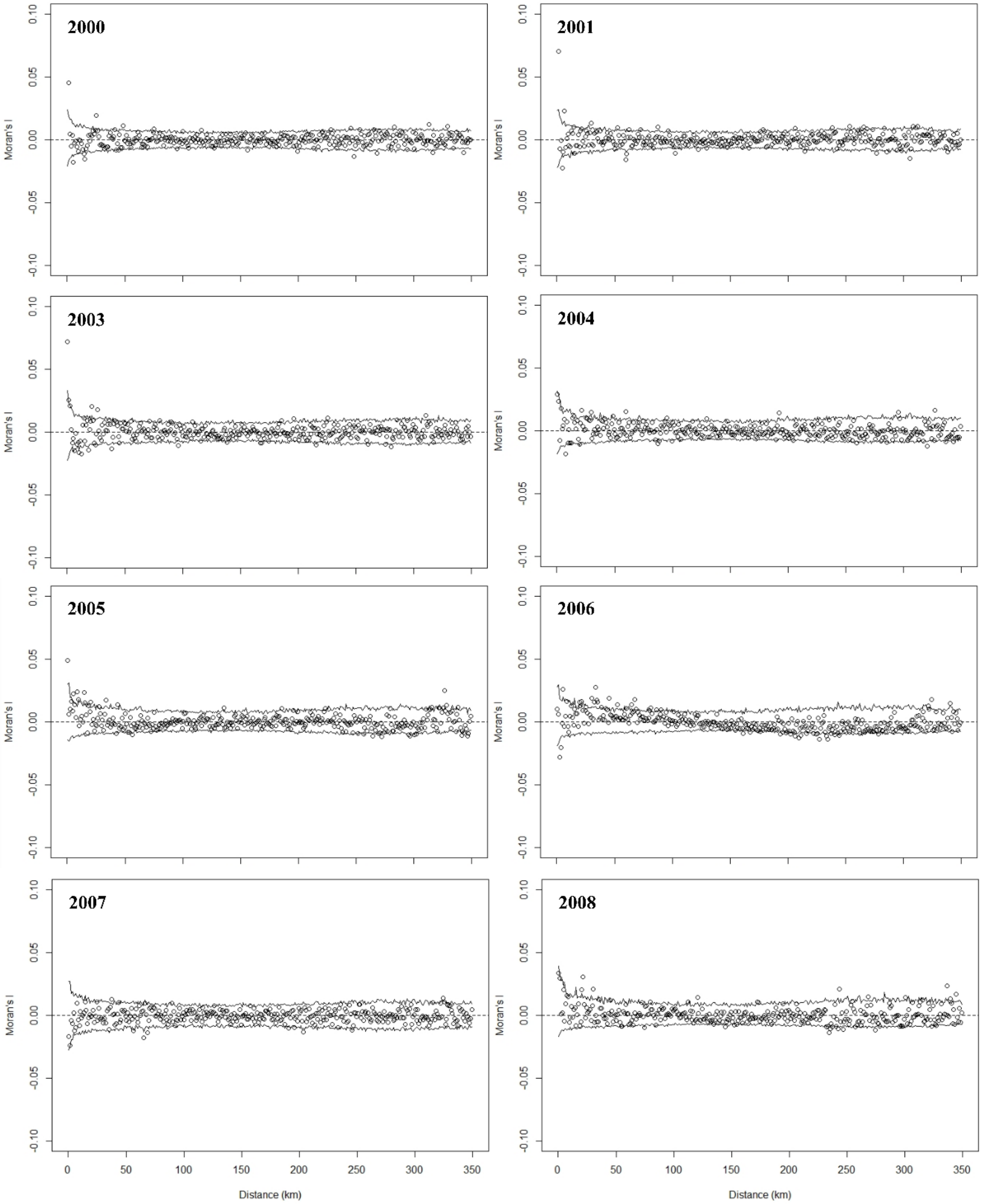


Figure B1.4. Correlograms of mean residuals of CAR models of the outbreak spread for each year of the study period (2000-2013). Gap distance between points of 1 km.

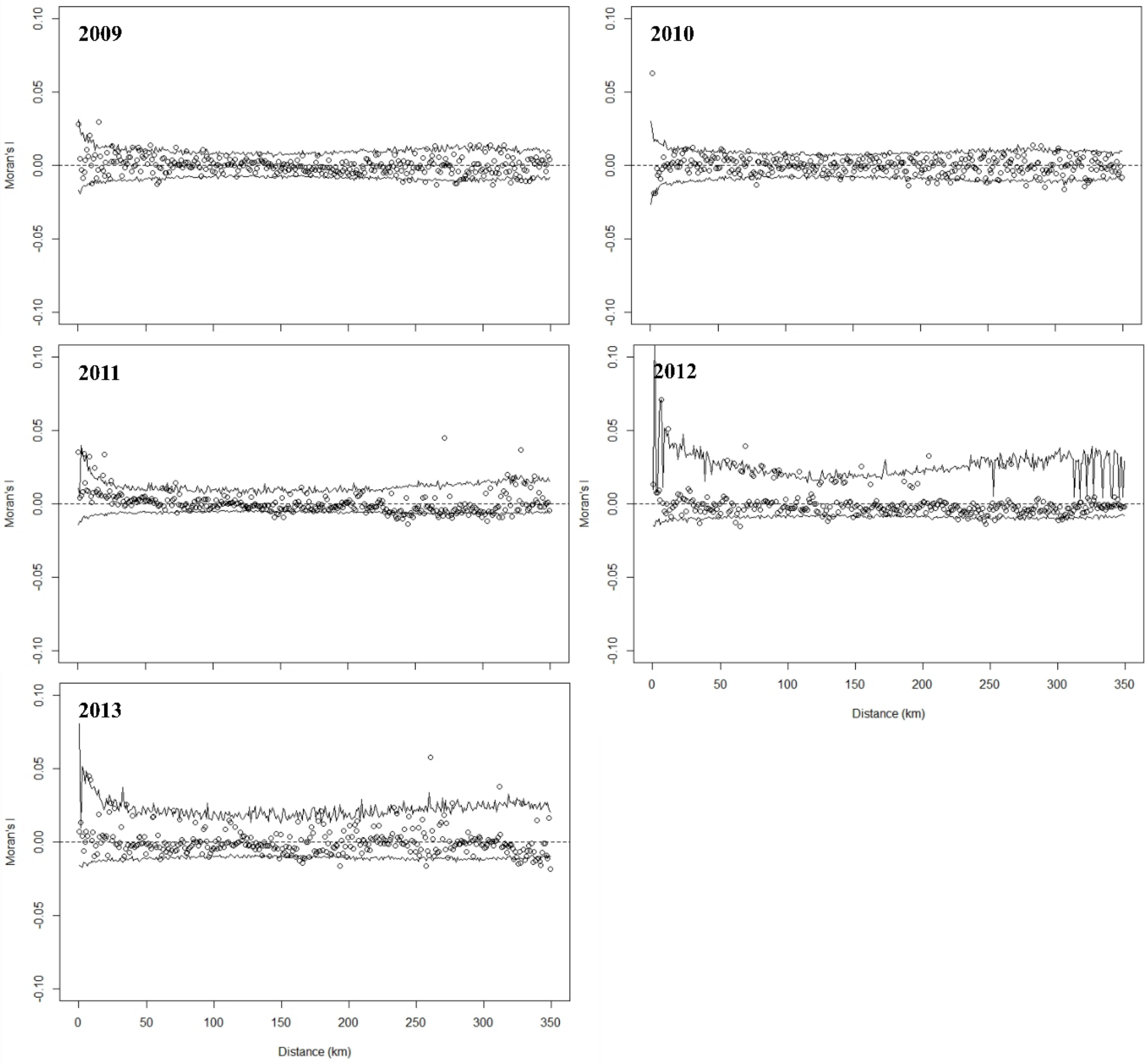


Figure B1.4. Continuation.

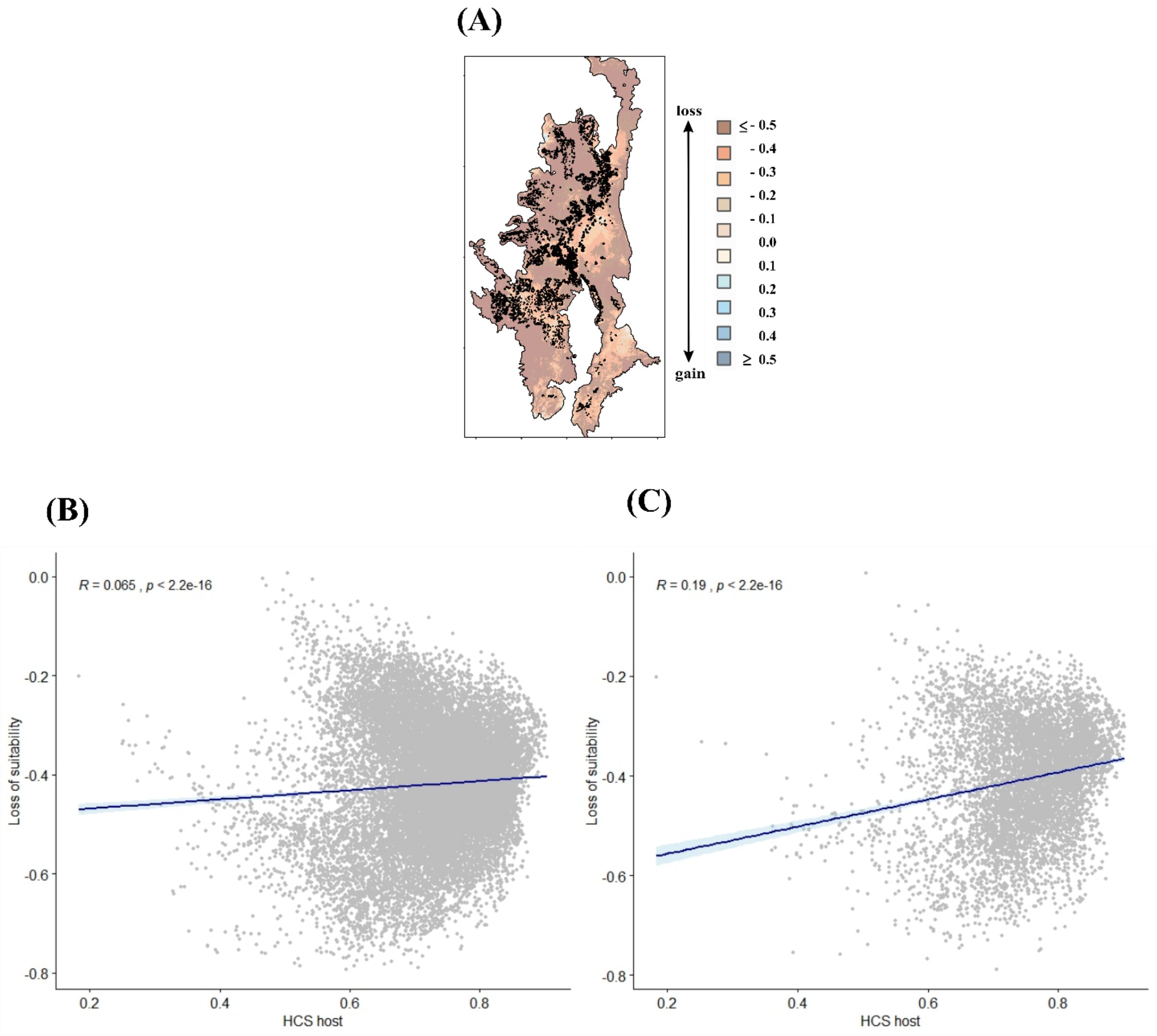


Figure B2. (A) Relative loss of climatic suitability ($aECS_{host}$-HCS_{host}/HCS_{host}) during the 2000-2013 episode. Black dots indicate cumulative outbreak pixels. (B) Correlation between the relative loss of suitability and the HCS_{host} for all pixels (unaffected and affected by spruce beetle outbreak) (C) Correlation between loss of suitability and HCS_{host} for affected pixels by spruce beetle outbreak. Plotted in the original scale.

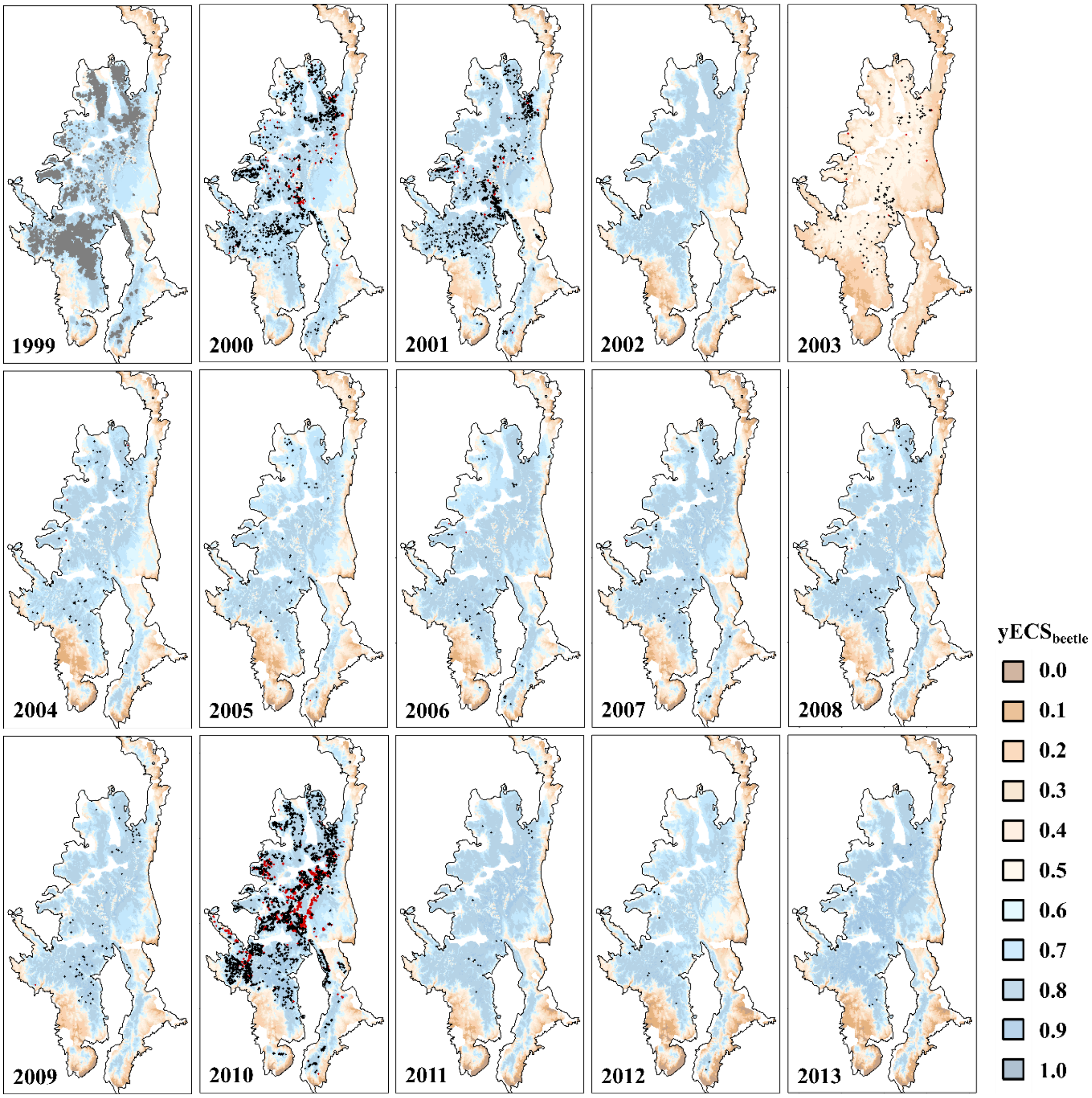


Figure B3. New affected pixels per year in relation to the climatic suitability of the bark beetle during the study period (2000-2013). 1999 was taken as a reference to the previous affectation (grey dots) to consider the newly affected pixels in the following years. Black dots indicate outbreak spread pixels of each year and red dots outbreak initiation pixels. Brown to dark blue colors shows low to high climatic suitability values, respectively. Number of new pixels per year (initiation/spread): 2000 (170/1115); 2001 (73/863); 2002 (0/0); 2003 (0/134); 2004 (1/57); 2005 (1/49); 2006 (2/43); 2007 (2/41); 2008 (1/38); 2009 (1/50); 2010 (1465/2565); 2011 (1/12); 2012 (0/9); 2013 (2/13).

Appendix C

Chapter 4

Table C1. List of the 130 study plots. Total dead, dead infested and infested during the whole period. Host proportion and tree species richness at the beginning of the infestation process (i.e., first time of bark beetle attack).

Plot	**Lat**	**Lon**	**Infestation period**	**Mortality period**	**Main host**	**Attacking bark beetle**	**Total dead**	**Total dead infested**	**Total infested**	**Host proportion**	**Richness**
site_12	37.38	29.32	2012	------------	*P. nigra*	*T. minor*	0	0	1	0.75	5
site_15	37.55	29.42	2012	------------	*P. nigra*	*T. minor*	0	0	1	0.63	2
site_16	38.02	28.47	2011	------------	*P. nigra*	*T. minor*	0	0	5	1.00	1
site_17	38.47	29.39	2011	------------	*P. nigra*	*T. minor*	0	0	1	1.00	1
site_18	39.4	26.4	2010-2016	------------	*P. nigra*	*T. piniperda*	1	0	13	1.00	1
site_19	39.51	32.47	2012	------------	*P. nigra*	*I. sexdentatus*	0	0	3	0.83	2
site_21	39.58	-5.4	2012	2012	*P. pinaster*	*I. sexdentatus*	3	2	2	1.00	1
site_22	40.07	31.06	2011-2012	2015	*P. nigra*	*I. sexdentatus*	1	1	17	0.75	3
site_23	40.16	31.28	2010-2014	2014	*P. nigra*	*I. sexdentatus*	1	1	7	0.88	3
site_24	40.16	31.17	2012-2013	------------	*P. nigra*	*I. sexdentatus*	5	0	12	1.00	1
site_25	40.19	38.03	2012	------------	*P. sylvestris*	*T. piniperda*	0	0	4	0.96	2
site_28	40.24	-4.37	2011	2011-2012	*P. pinaster*	*I. sexdentatus*	3	2	2	0.72	2
site_29	40.25	32.02	2010-2013	2013	*P. sylvestris*	*I. sexdentatus*	3	1	25	1.00	1
site_30	40.25	32.36	2013	------------	*P. nigra*	*I. sexdentatus*	4	0	1	0.79	3
site_31	40.34	33.21	2012-2018	------------	*P. nigra*	*I. sexdentatus*	1	0	9	0.92	2
site_32	40.42	33.32	2010	------------	*P. nigra*	*I. sexdentatus*	5	0	2	0.35	2
site_33	41.1	-4.12	2011	2011	*P. pinaster*	*I. sexdentatus*	10	1	1	0.79	2
site_34	41.19	-4.14	2011	2011-2013	*P. pinaster*	*I. sexdentatus*	8	4	4	1.00	1
site_35	42.18	1.43	2014	------------	*P. uncinata*	*T. piniperda*	0	0	1	0.58	3
site_36	42.23	23.08	2010	2012	*P. sylvestris*	*T. piniperda*	15	1	3	1.00	1
site_37	42.29	1.36	2010	------------	*P. uncinata*	*I. acuminatus*	0	0	1	1.00	1
site_39	42.34	22.57	2010-2018	2015-2018	*P. sylvestris*	*I. acuminatus*	7	6	11	1.00	1
site_40	42.34	23.11	2010	2013-2018	*P. sylvestris*	*T. piniperda*	17	6	13	1.00	1
site_41	43.43	6.41	2014	------------	*P. sylvestris*	*T. piniperda*	0	0	1	1.00	1
site_42	43.53	6.18	2012	------------	*P. nigra*	*T. piniperda*	0	0	4	1.00	1
site_43	44	6.42	2012-2016	------------	*P. sylvestris*	*T. piniperda*	1	0	3	0.25	2
site_44	44.01	6.18	2011-2014	------------	*P. sylvestris*	*T. piniperda*	0	0	6	1.00	1
site_45	44.01	6.3	2010-2013	------------	*P. sylvestris*	*T. piniperda*	0	0	12	0.70	4
site_46	44.14	3.19	2011-2017	------------	*P. sylvestris*	*T. piniperda*	0	0	17	1.00	1
site_47	44.14	3.43	2012-2018	------------	*P. sylvestris*	*T. piniperda*	0	0	12	1.00	1
site_49	44.19	8.04	2010	------------	*P. sylvestris*	*T. minor*	1	0	20	0.69	2
site_51	44.23	3.07	2011-2018	------------	*P. sylvestris*	*T. piniperda*	0	0	16	1.00	1

Table C1. Continuation.

Plot	Lat	Lon	Infestation period	Mortality period	Main host	Attacking bark beetle	Total dead	Total dead infested	Total infested	Host proportion	Richness
site_52	44.23	3.19	2010-2015	------------	*P. sylvestris*	*T. piniperda*	0	0	19	1.00	1
site_54	44.28	5.44	2010	------------	*P. sylvestris*	*T. piniperda*	1	0	1	0.75	2
site_55	44.29	8.15	2010-2018	2015	*P. sylvestris*	*T. piniperda*	1	1	13	0.50	2
site_56	44.31	3.31	2012-2013	------------	*P. nigra*	*T. piniperda*	0	0	2	1.00	1
site_57	44.39	0.18	2010	2011	*P. pinaster*	*I. sexdentatus*	2	1	1	1.00	1
site_58	44.4	3.2	2011	------------	*P. sylvestris*	*T. piniperda*	0	0	20	1.00	1
site_59	44.4	3.32	2011-2012	------------	*P. sylvestris*	*T. piniperda*	0	0	20	1.00	2
site_60	44.43	6.46	2011-2017	------------	*P. uncinata*	*T. piniperda*	0	0	20	1.00	2
site_61	44.49	3.2	2011-2017	------------	*P. sylvestris*	*T. minor*	0	0	19	1.00	1
site_62	44.54	7.15	2011-2013	------------	*P. sylvestris*	*T. piniperda*	1	0	3	0.49	4
site_63	44.57	3.32	2010-2014	------------	*P. sylvestris*	*T. piniperda*	0	0	19	1.00	1
site_64	44.57	3.44	2010-2014	------------	*P. abies*	*I. typographus*	0	0	4	1.00	2
site_66	45.45	7.02	2011	------------	*P. sylvestris*	*T. minor*	1	0	4	0.96	2
site_67	46.27	11.09	2010	------------	*P. sylvestris*	*T. minor*	0	0	3	0.19	2
site_69	46.43	11.38	2010-2011	------------	*P. sylvestris*	*T. piniperda*	0	0	3	0.38	6
site_70	46.43	11.13	2010	------------	*P. abies*	*I. typographus*	0	0	14	1.00	1
site_71	51.20	14.25	2011-2016	2012	*P. abies*	*I. typographus*	1	1	4	0.54	3
site_72	47.4	0.11	2012-2017	------------	*P. pinaster*	*T. piniperda*	0	0	10	1.00	1
site_73	47.49	0.11	2012	------------	*P. pinaster*	*T. piniperda*	0	0	2	1.00	1
site_74	47.49	7.33	2012	------------	*P. sylvestris*	*T. minor*	1	0	1	0.25	5
site_75	48.41	8.24	2016	------------	*P. sylvestris*	*T. minor*	0	0	3	0.21	5
site_76	48.38	19.44	2010	------------	*P. abies*	*I. typographus*	1	0	3	0.17	3
site_77	47.39	8.12	2014	------------	*P. sylvestris*	*T. minor*	0	0	2	0.46	4
site_78	48.46	19.54	2013	------------	*P. abies*	*I. typographus*	6	0	1	0.84	3
site_79	48.46	20.07	2013	------------	*P. abies*	*I. typographus*	0	0	7	0.80	2
site_80	48.55	19.41	2010	------------	*P. abies*	*I. typographus*	2	0	4	1.00	1
site_81	48.55	19.55	2013	2015	*P. abies*	*I. typographus*	3	1	10	1.00	1
site_82	49.03	20.47	2010	------------	*P. abies*	*I. typographus*	1	0	1	0.93	3
site_83	49.04	20.34	2010	2012	*P. abies*	*I. typographus*	1	1	2	0.21	4
site_84	49.12	19.55	2010-2013	2011	*P. abies*	*I. typographus*	37	1	6	1.00	1
site_86	49.2	19.42	2010	2011-2016	*P. abies*	*I. typographus*	1	0	3	1.00	1
site_87	49.21	19.03	2010-2013	------------	*P. abies*	*I. typographus*	9	2	7	1.00	1
site_88	49.29	19.16	2010	------------	*P. abies*	*I. typographus*	0	0	1	1.00	1

Table C1. Continuation.

Plot	Lat	Lon	Infestation period	Mortality period	Main host	Attacking bark beetle	Total dead	Total dead infested	Total infested	Host proportion	Richness
site_92	53.2	28.41	2011	2011	*P. sylvestris*	*T. piniperda*	1	1	1	1.00	1
site_93	53.57	26.56	2010	------------	*P. abies*	*I. typographus*	0	0	2	0.58	2
site_94	54.05	25.27	2011	2011	*P. sylvestris*	*T. piniperda*	3	1	1	0.86	2
site_95	54.06	27.12	2010	2015	*P. abies*	*I. typographus*	3	1	5	0.88	2
site_96	54.16	24.57	2011	------------	*P. abies*	*I. typographus*	0	0	1	0.88	2
site_97	54.26	20.33	2010	2010	*P. abies*	*I. typographus*	1	1	2	0.29	3
site_98	37.11	29.01	2011	------------	*P. nigra*	*T. minor*	0	0	7	1.00	1
site_99	37.19	28.49	2011	------------	*P. nigra*	*T. piniperda*	0	0	2	0.42	3
site_100	54.49	29.57	2010	2011	*P. abies*	*I. typographus*	2	1	1	0.79	4
site_102	55.07	30.11	2013	2013	*P. abies*	*I. typographus*	3	1	1	0.96	2
site_104	55.34	28.52	2010	2010	*P. sylvestris*	*I. sexdentatus*	2	1	1	0.83	2
site_105	55.43	26.52	2010	2010	*P. sylvestris*	*I. sexdentatus*	1	1	1	1.00	1
site_107	56.01	29.08	2010	2010	*P. sylvestris*	*I. sexdentatus*	1	1	1	0.92	3
site_111	56.58	22.04	2012	------------	*P. abies*	*I. typographus*	1	0	1	0.86	3
site_114	57.07	26.19	2012	------------	*P. abies*	*I. typographus*	1	0	1	0.37	3
site_118	57.39	27.47	2010	------------	*P. sylvestris*	*T. piniperda*	0	0	1	1.00	1
site_122	57.46	25.21	2010	------------	*P. abies*	*I. typographus*	0	0	1	0.13	3
site_128	58.12	8.00	2010	------------	*P. sylvestris*	*T. piniperda*	0	0	1	0.61	2
site_130	58.21	33.13	2011	------------	*P. abies*	*I. typographus*	0	0	1	0.59	3
site_137	59.07	29.56	2011	2011	*P. abies*	*I. typographus*	7	3	3	0.68	4
site_140	59.15	10.03	2010	2010	*P. abies*	*I. typographus*	2	1	1	0.94	3
site_144	59.38	33.55	2011	2011	*P. abies*	*I. typographus*	29	23	23	0.81	2
site_145	59.41	28.12	2011	2011	*P. abies*	*I. typographus*	1	1	1	0.81	3
site_149	60.58	29.38	2011	------------	*P. sylvestris*	*T. piniperda*	10	0	1	0.97	2
site_150	61.16	30.13	2010	------------	*P. sylvestris*	*T. minor*	0	0	24	0.92	2
site_151	61.48	33.53	2010	------------	*P. sylvestris*	*T. minor*	0	0	2	0.96	2
site_152	61.5	31.27	2011	------------	*P. abies*	*I. typographus*	0	0	1	0.17	2
site_153	62.58	10.52	2010	------------	*P. abies*	*I. typographus*	1	0	1	1.00	1
site_154	62.59	31.31	2011	2011	*P. sylvestris*	*T. minor*	1	1	1	0.81	3
site_155	64.44	30.15	2010	------------	*P. sylvestris*	*T. minor*	0	0	14	0.80	2
site_156	65.18	30.15	2010-2011	------------	*P. sylvestris*	*T. minor*	0	0	24	1.00	1
site_157	66.27	30.16	2011	2011	*P. abies*	*I. typographus*	1	1	1	0.64	3
site_158	66.27	31.43	2010	------------	*P. sylvestris*	*T. minor*	0	0	18	0.80	2

Table C1. Continuation.

Plot	Lat	Lon	Infestation period	Mortality period	Main host	Attacking bark beetle	Total dead	Total dead infested	Total infested	Host proportion	Richness
site_159	46.11	11.2	2016	2016	*Picea abies*	*I. typographus*	4	1	1	0.89	2
site_160	52.13	23.47	2015	------------	*P. sylvestris*	*T. piniperda*	0	0	12	1.00	1
site_162	46.35	10.48	2016	------------	*P. abies*	*I. typographus*	4	0	1	0.75	2
site_163	40.2	-1.29	2016-2017	2017	*P. sylvestris*	*I. acuminatus*	3	2	3	0.92	2
site_165	42.47	22.43	2016-2018	2016-2018	*P. sylvestris*	*I. acuminatus*	88	65	66	1.00	1
site_166	49.21	10.34	2017	------------	*P. abies*	*I. typographus*	1	0	4	0.22	5
site_169	47.29	11.02	2015-2017	2015	*P. abies*	*I. typographus*	2	2	3	0.42	5
site_170	47.38	11.28	2017	2018	*P. abies*	*I. typographus*	1	1	1	0.38	5
site_172	48.24	8.37	2018	2018	*P. abies*	*I. typographus*	1	1	1	0.88	2
site_175	50.22	11.26	2016	2016	*P. abies*	*I. typographus*	3	3	3	0.75	3
site_180	42.19	8.54	2016-2018	------------	*P. nigra*	*T. piniperda*	3	0	20	1.00	1
site_181	54.26	29.38	2015	------------	*P. abies*	*I. typographus*	0	0	1	0.71	4
site_182	41.28	25.28	2016	------------	*P. sylvestris*	*T. piniperda*	25	0	1	1.00	1
site_183	38.18	28.02	2018	------------	*P. nigra*	*T. minor*	0	0	11	1.00	1
site_184	56.07	9.4	2015-2016	------------	*P. abies*	*I. typographus*	0	0	2	1.00	1
site_188	48.1	-2.37	2018	------------	*P. sylvestris*	*T. piniperda*	0	0	7	0.38	3
site_190	42.02	24.04	2017-2018	2017-2018	*P. sylvestris*	*I. acuminatus*	23	11	11	1.00	1
site_191	42.09	23.1	2016	2016	*P. abies*	*I. typographus*	5	1	14	0.38	2
site_193	53.54	31.11	2015	2015	*P. abies*	*I. typographus*	2	1	1	0.96	2
site_194	41.34	25.06	2018	2018	*P. sylvestris*	*I. acuminatus*	16	3	3	1.00	1
site_195	41.36	25.17	2018	------------	*P. nigra*	*T. minor*	6	0	1	1.00	1
site_196	42.3	23.19	2018	------------	*P. sylvestris*	*T. piniperda*	1	0	8	1.00	1
site_197	41.52	24.41	2018	------------	*P. sylvestris*	*T. piniperda*	16	0	6	1.00	1
site_198	41.42	24.47	2018	2018	*P. abies*	*I. typographus*	12	4	4	1.00	1
site_199	41.44	25.2	2018	------------	*P. nigra*	*T. minor*	12	0	4	1.00	1
site_200	43.26	19.54	2015-2016	------------	*P. abies*	*I. typographus*	0	0	4	1.00	1
site_201	50.22	11.53	2018	------------	*P. sylvestris*	*T. minor*	0	0	1	0.54	4
site_202	64.36	12.26	2018	2018	*P. abies*	*I. typographus*	1	1	1	1.00	1
site_203	48.41	8.37	2015	------------	*P.sylvestris*	*T. piniperda*	0	0	1	1.00	1
site_205	61.52	12.59	2015	2015	*P. abies*	*I. typographus*	2	1	1	0.80	2
site_206	47.06	0	2015	------------	*P. pinaster*	*T. piniperda*	0	0	18	1.00	1
site_207	59.34	12.22	2014	2014	*P. abies*	*I. typographus*	1	1	1	0.67	2

Table C2. Occurrence data obtained for each host tree and bark beetle species from 1960 to 2000 filtered by a minimum distance of 4km^2.

Role	Species	N occurrences	Source
Bark beetle	Ips typographus	1978	GBIF
Bark beetle	Ips sexdentatus	830	GBIF
Bark beetle	Ips acuminatus	333	GBIF
Bark beetle	Tomicus piniperda	1127	GBIF
Bark beetle	Tomicus minor	624	GBIF
Host tree	Picea abies	22868	EUForest
Host tree	Pinus sylvestris	23459	EUForest
Host tree	Pinus nigra	3585	EUForest
Host tree	Pinus pinaster	3128	EUForest
Host tree	Pinus uncinata	504	EUForest

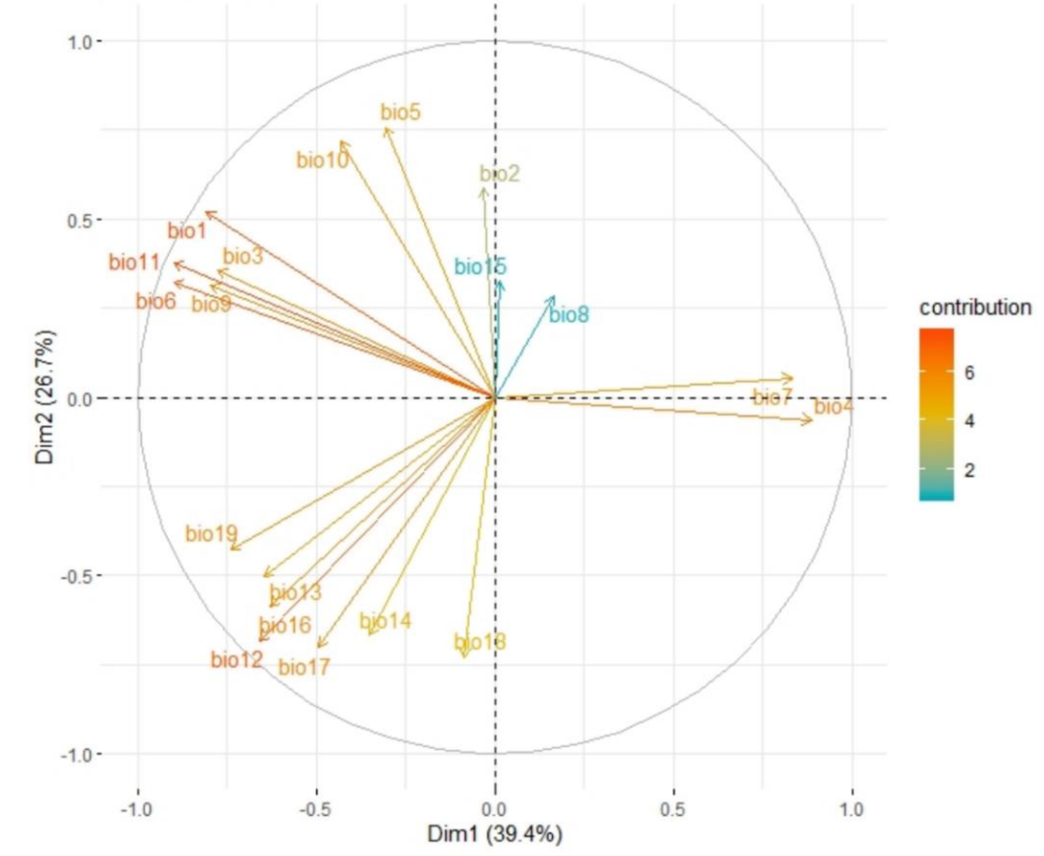
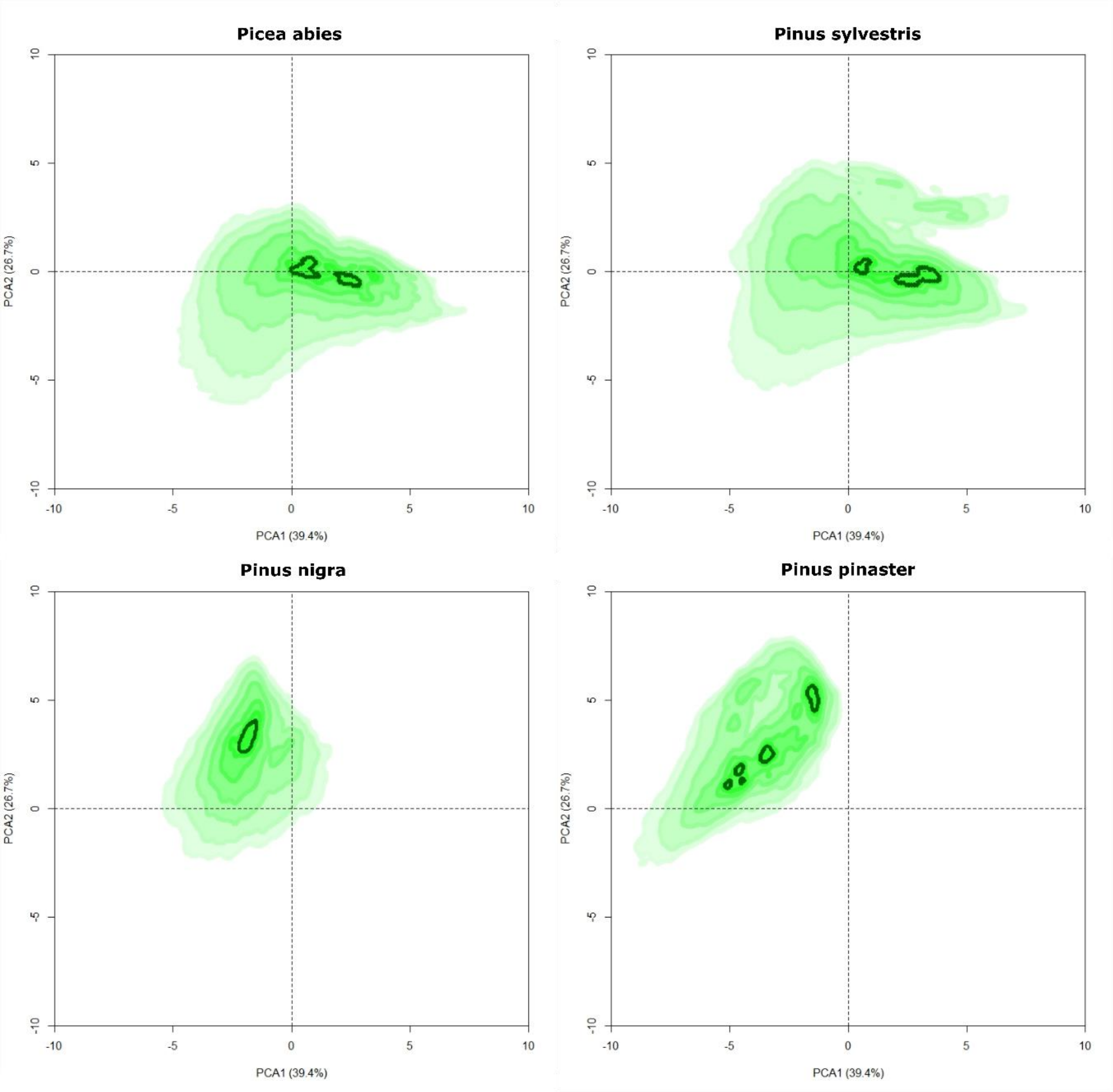


Figure C1. Correlation circle obtained from the PCA of the 19 selected bioclimatic variables. Bio1 = annual mean temperature; bio2 = mean diurnal range; bio3 = isothermality; bio4 = temperature seasonality; bio5 = max temperature of warmest month; bio6 = min temperature of coldest month; bio7 = temperature annual range; bio8 = mean temperature of wettest quarter; bio9 = mean temperature of driest quarter; bio10 = mean temperature of warmest quarter; bio11 = temperature of coldest quarter; bio12 = annual precipitation; bio13 = precipitation of wettest month; bio14 = precipitation of driest month; bio15 = precipitation seasonality; bio16 = precipitation of wettest quarter; bio17 = precipitation of driest quarter; bio18 = precipitation of warmest quarter; bio19 = precipitation of coldest quarter. The PCA was calibrated using climatic data from the total 58,436 occurrences from the 10 sampled species (5 of host trees and 5 of bark beetles). First and second axes contained 66.1% of explained variability. The variables' color represents the percentage of contribution of each variable to the PCA.



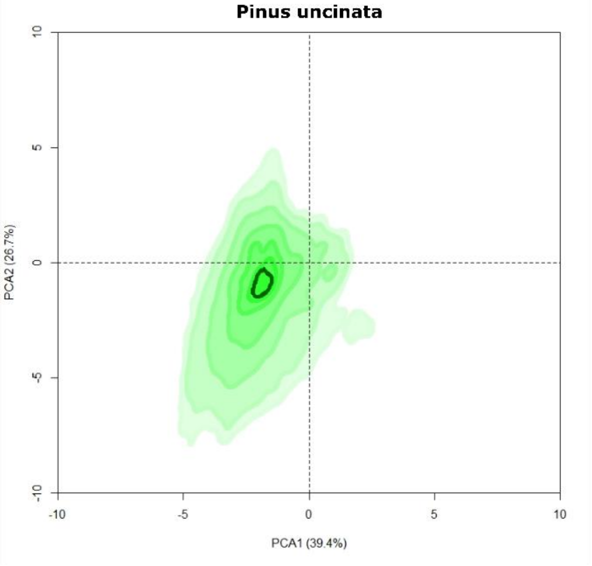
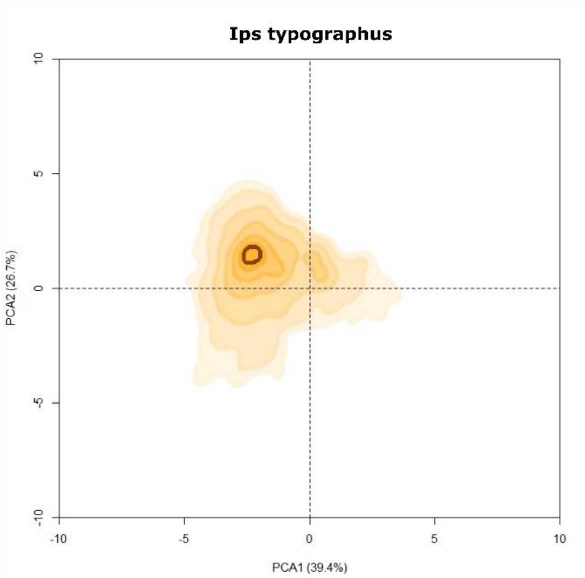
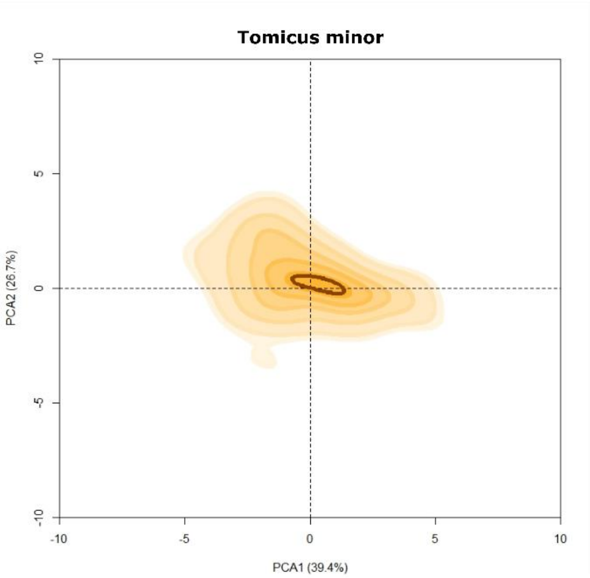
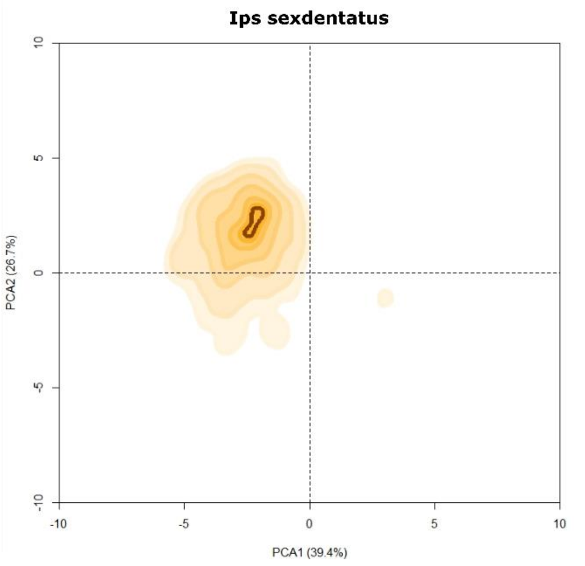
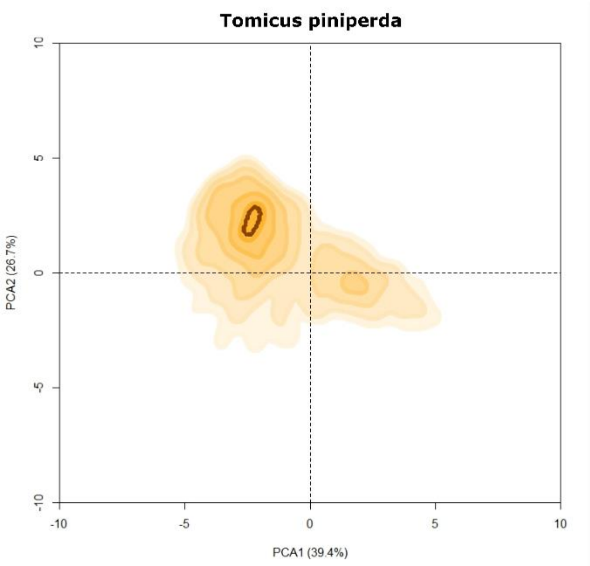


Figure C2. Species climatic niche determined by the two PCA environmental axes for each of the studied species. Green palette indicates the climatic niche of host tree species and orange palette indicate the climatic niche of bark beetle species. Dark green and dark orange lines represent the climatic optimum for each species based on the highest 0.05 % percentile obtained from Gaussian kernel functions. Bandwiths depicted at 0.05, 0.10, 0.25, 0.50, 0.75, 0.90 and 0.95.









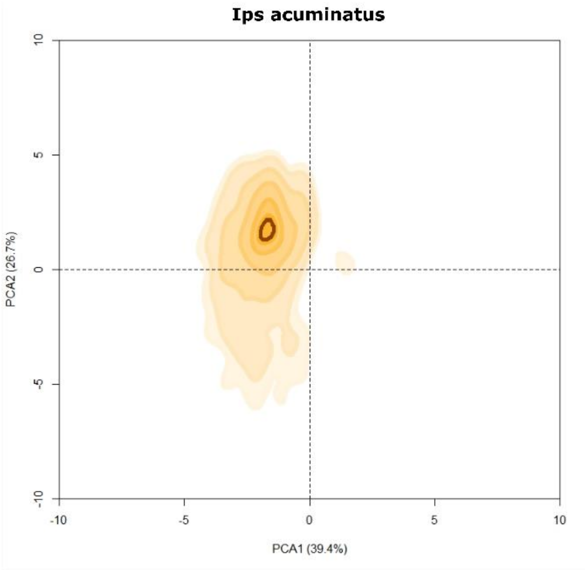


Figure C2. Continuation.

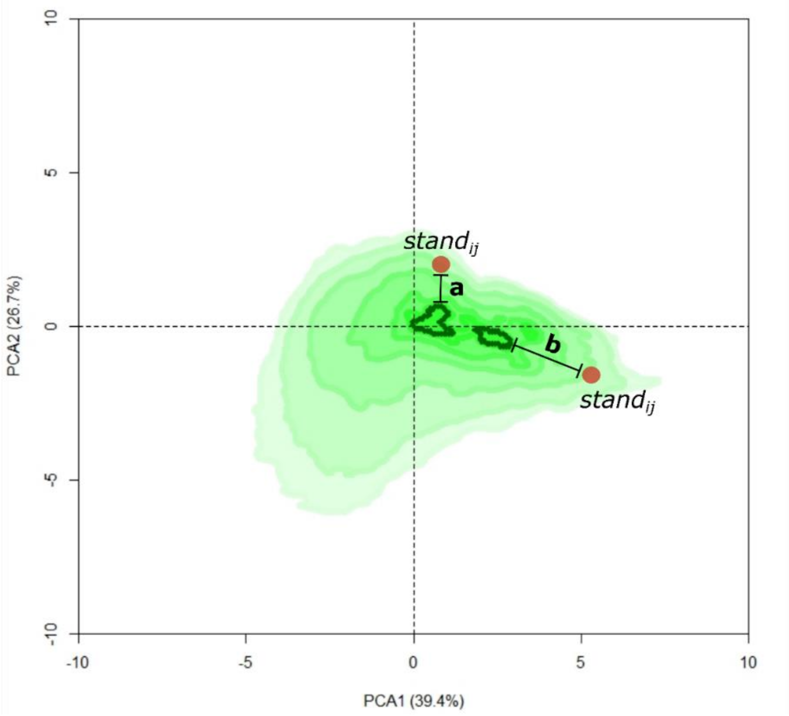


Figure C3. Example of distances measured in a species climatic niche. In cases in which the niche optimum was divided in two, the distance between a particular study site and the niche optimum was calculated considering the closest part of the niche optimum. Stands are represented by the red dots and the distances by “a” and “b”. Stand$_{ij}$: *i* (particular stand location), *j* (year of bark beetle attack or mortality during the 2010-2018 period).

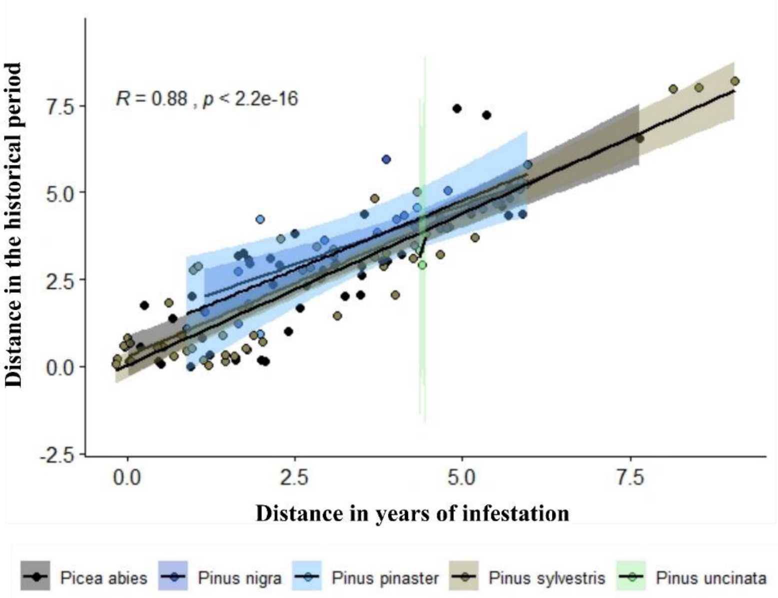


Figure C4. Pearson correlation between the distance to the niche optimum of the host tree species during the historical period (1960-2000) and the distance to the niche optimum of host tree species during the years of infestation as bark beetle attack (2010-2018).

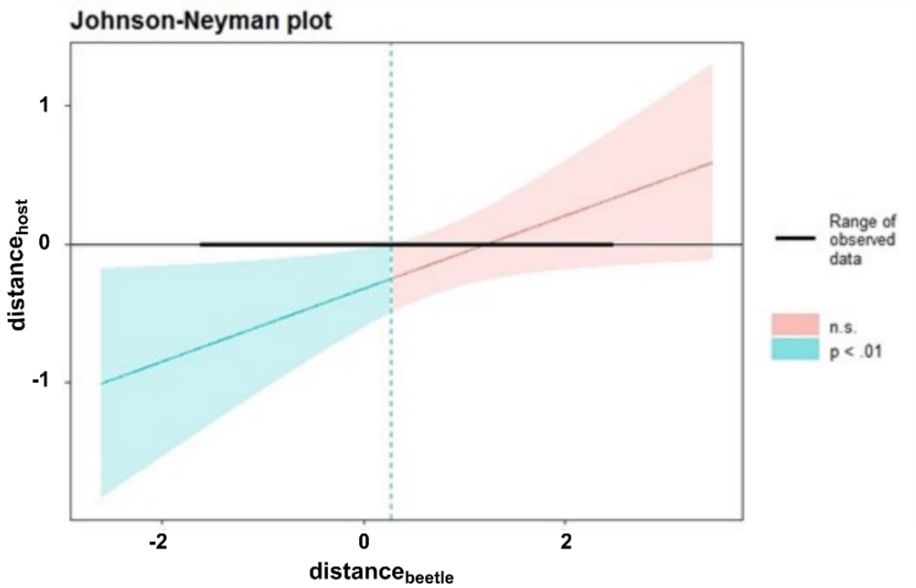


Figure C5. Johnson-Neyman interval for the interaction effect between the distance to host climatic optimum and the distance to the beetle climatic optimum. This plot provides the range of values of the moderator ($\text{distance}_{\text{beetle}}$) in which the slope of the predictor ($\text{distance}_{\text{host}}$) is significant vs. non-significant.

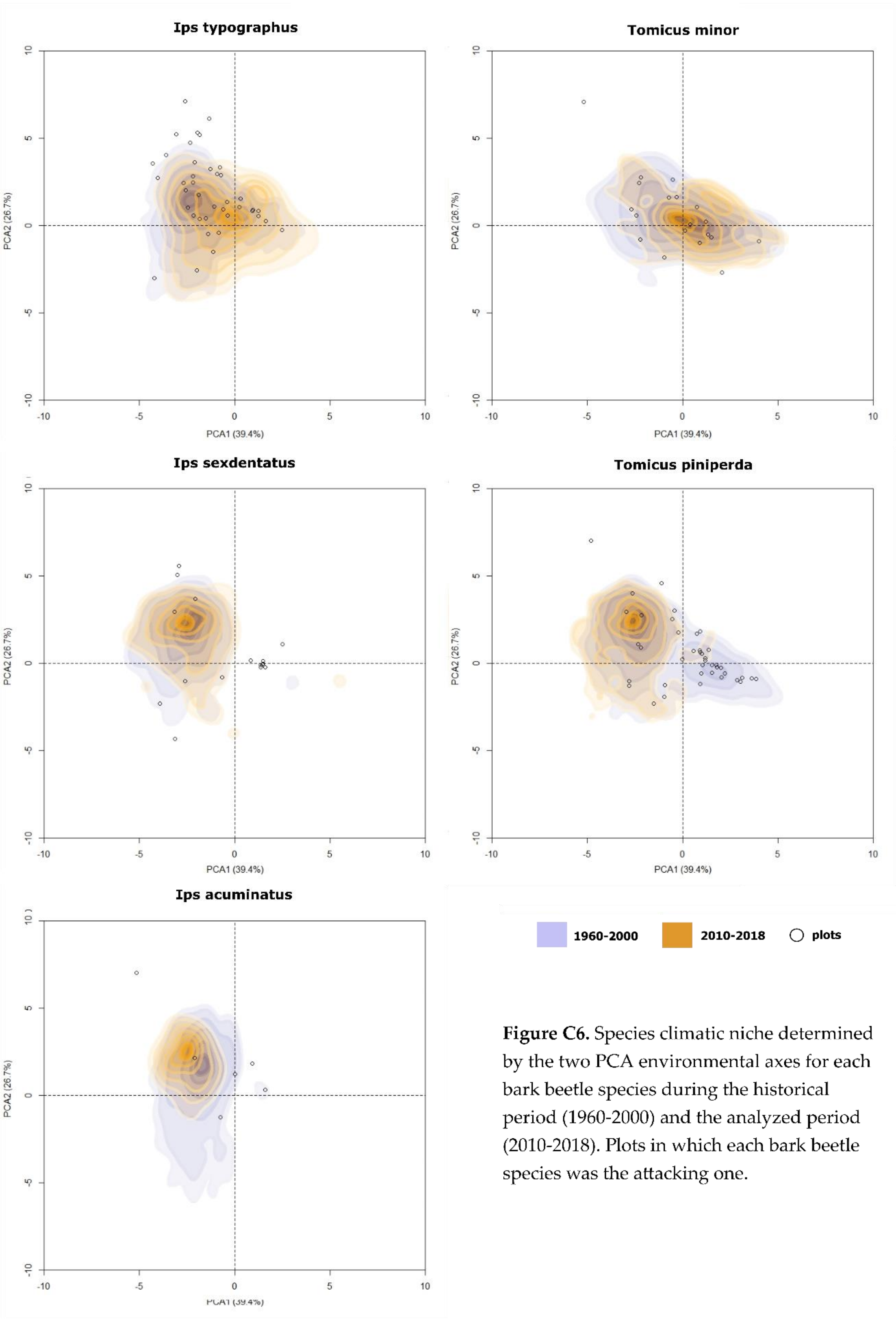


Figure C6. Species climatic niche determined by the two PCA environmental axes for each bark beetle species during the historical period (1960-2000) and the analyzed period (2010-2018). Plots in which each bark beetle species was the attacking one.

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