Jaime, Luciana; Batllori, Enric; Ferretti, Marco; [et al.]. «Climatic and stand drivers of forest resistance to recent bark beetle disturbance in European coniferous forests». Global change biology, Vol. 28, Issue 8 (April 2022), p. 2830-2841. DOI 10.1111/gcb.16106

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

Running title: Forest resistance to bark beetle disturbance

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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 increase of extreme heat and drought episodes. Under this context, the environmental position of host tree populations within the species' climatic niche (central *vs*. marginal populations) is expected to be a determinant in the dynamics of insect-host systems. Here, we analyzed the recent patterns of bark beetle disturbance and forest resistance across European coniferous forests during the 2010-2018 period. We obtained bark beetle attack and tree mortality data from successive continental-scale forest condition surveys on 130 plots including five host trees and five bark beetle species, and characterized the climatic niche of each species. Then, we analyzed the overall forest resistance and species-specific responses, in terms of bark beetle attack and induced tree mortality, in relation to the distance to the niche optimum of both host tree and beetle species, previous drought events, and plot characteristics. Regional patterns of recent disturbance revealed that forests in Central, North, and East of Europe could be at risk under the attack of multivoltine bark beetle species. We found that overall forest resistance to beetle attack was determined by several driving factors, which varied among species responses. Particularly, the environmental position of the affected forest within the host and beetle species' climatic niche and plot characteristics mediated the influence of drought on the resistance to beetle attack. In turn, forest resistance to induced tree mortality was determined exclusively by the maximum intensity and duration of drought events. 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 European coniferous forests, even in those tree populations close to their species' climatic optimum.

Keywords: ICP-Forests, biotic disturbance, drought, SPEI, species climatic niche, insect-host system.

1. INTRODUCTION

Global warming and the increasing recurrence of extreme drought events are inducing widespread forest mortality around the globe (Allen, Breshears, & McDowell, 2015; Senf et al., 2018). Such widespread mortality has impacts on forest structure and composition (Batllori, Lloret, Aakala, Anderegg, & Aynekulu, 2020), carbon balance (Seidl, Schelhaas, Rammer, & Verkerk, 2014; Sippel et al., 2018), and hydrological cycles (Anderegg et al., 2013), as well as 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 insect outbreaks (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 disturbance regimes under climate change could alter forests' response and reduce their resilience capacity especially under the influence of concurrent disturbances (Buma, 2015; Seidl & Rammer, 2017). For instance, the interaction between extreme weather 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 (Biedermann et al., 2019), it is crucial to better understand the mechanisms that determine when, where, and how changing disturbance regimes may surpass forest resilience and cause irreversible changes in forest persistence (Thom, Rammer, & Seidl, 2017).

Bark beetles typically exhibit low, endemic population levels within forests, causing limited tree mortality, since specialized physical and chemical host tree defenses hinder infestation success (Raffa, Andersson, & Schlyter, 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, overcoming host defenses and killing trees across large areas (Raffa et al., 2008). 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, Sapes, Sala, & Hood, 2015). The overall resistance of forests to beetle disturbance could be approximated in terms of the likelihood of bark beetle attack and induced host tree mortality (Hood, Baker, & Sala, 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, Batllori, Margalef-Marrase, Pérez Navarro, & Lloret, 2019; Jaime et al., 2021; Lloret & Kitzberger, 2018). According to the niche theory, species performance declines from the niche optimum (or center) to the edge (or margin) of the species' niche (Carscadden, Emery, Arnillas, Carlos, & Cadotte, 2020; 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. Accordingly, 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, Gentili, Mondoni, Orsenigo, & Rossi, 2014; Martínez-Meyer, Díaz-Porras, Peterson, & Yáñez-Arenas, 2013; Sexton, McIntyre, Angert, & Rice, 2009). This enhanced resistance would be the result of a greater host tree defense capacity. However, forest resistance would diminish in such a site if the site is also located 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 niche of the host tree and insect, affecting tree performance, its defense capacity, and beetle development. Therefore, under extreme weather episodes, forests located close to the niche optimum of the host tree could become susceptible to bark beetle disturbance (Kleinman, DeGomez, Snider, & Williams, 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, Voelker, DeRose, & Burton, 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., 2017; Rouault et al., 2006; Seidl et al., 2016). In addition, some bark beetle species are infesting with unexpected aggressiveness and outside of their historical distribution range (Siitonen, 2014). These facts highlight that the resistance of European forests to a wide variety of bark beetle species might be declining, and this trend is likely to continue under more frequent extreme events of drought and heat in the coming decades (Buras & Menzel, 2019; Gazol & Camarero, 2021).

Here, we analyzed forest resistance to bark beetle attack and beetle-induced mortality, with the combined effect of drought, in European coniferous forests during the 2010-2018 period. We used plot-level data of beetle attack and tree mortality caused by five bark beetle species (*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) the driving factors of overall forest resistance to bark beetle attack and induced tree mortality considering the distance to the niche optimum of both host tree and beetle species, the characteristics of previous droughts (duration, intensity, and time since maximum drought), and plot characteristics (host tree proportion and species tree richness), and (2) the driving factors of species-specific forest resistance to bark beetle attack and tree mortality. We expected a decreased forest resistance in locations close to the host tree niche optimum that recently experienced extreme drought events and which are also 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 tree 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 differences in the drivers of forest resistance among host tree species due to feedbacks driving the dynamics of the different bark beetle species or to differences in the resistance capacity among host tree species (Reed & Hood, 2021).

2. DATA AND METHODS

2.1. Bark beetle attack and tree mortality data

We used data from the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests) Level I tree condition survey, conducted annually on ca. 6,000 plots distributed in a 16 km^2 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 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 assessed here (*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, Day, Battisti, Grégoire, & Evans, 2004). The main host tree species attacked by the five 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 to analyze 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 resulted in a total of 130 infested plots (Table S1), 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).

2.2. Drought characterization

To characterize the drought conditions experienced in each plot, we used the Standardized Precipitation-Evapotranspiration Index (SPEI; Vicente-Serrano, Beguería, & López-Moreno, 2010). SPEI is a multi-scalar index based on the difference between precipitation and potential evapotranspiration, which calculates climatic drought deviations within a temporal period considering different time-scales. In our case, we took the 1960-2018 period as temporal span and a 12-month SPEI scale. We chose the 12-month scale assuming it is suitable to identify prolonged droughts with negative effects on tree defense capacity (Rissanen et al., 2021). To compute annual SPEI values, we used climate data at 4 km^2 resolution obtained from TerraClimate database v.1.2 (Abatzoglou, Dobrowski, Parks, & Hegewisch, 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 < -1.5 as indicators of severe drought conditions (Paulo, Rosa, & Pereira, 2012). From this, we calculated the following SPEI-derived variables: (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 attack or mortality period in each plot.

2.3. Niche characterization and distance to the species' climatic niche optimum

To characterize the climatic niche of each considered species, we collected occurrence data for the five host tree species from the European Forest Data (Mauri, Strona, & San-Miguel-Ayanz, 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 (Table S2).

We obtained monthly precipitation, maximum, and minimum temperatures from TerraClimate 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, Phillips, Leathwick, & Elith, 2012). These bioclimatic variables included: annual mean temperature, mean diurnal range, isothermality, temperature seasonality, maximum temperature of warmest month, minimum 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 five bark beetle species 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, which accounted for 66.1% of the variability within the original variables (Figure S1). To characterize each species climatic niche, we used the scores of the first and second PCA axes to project the climatic values of each species' occurrences into the two-dimensional environmental space. Subsequently, we applied kernel density functions (Broennimann et al., 2012; ks R package, 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 0.05 highest percentile within each species' climatic niche (Figure S2).

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 attack or mortality was recorded (Figure S3). 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 (Figure S4).

2.4. 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 examine 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 among species. For 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.

2.5. 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 responses 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 tree mortality induced by beetle attack as the proportion of dead infested trees in relation to total host trees. In plots with more than one consecutive year of attack or mortality, we pooled together the data of the different involved years. Then, the bark beetle attack and tree mortality were examined in relation to the following plot-level explanatory variables: (1) distance at a given time to the host tree climatic niche optimum, (2) distance at a given time to the bark beetle climatic niche optimum; (3) drought duration, maximum drought intensity, and time since maximum drought (SPEI-derived variables), and (4) host tree proportion and tree species richness (plot characteristics). For each plot, we computed the distance between the plot position and the respective niche optimum of both host tree and bark beetle species during the year of attack or mortality.

In cases where the attack 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, to capture the most stressful conditions experienced by the host. All explanatory variables were centered and rescaled (z-score transformation) to improve the subsequent model stability and permit a direct comparison of effect sizes. We checked model fit and performance (see below) by inspecting model assumptions and overdispersion (blmeco R package; Korner-Nievergelt et al., 2015).

To analyze overall bark beetle attack and tree 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 (Table 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 (MuMIn R package; Nakagawa & Schielzeth, 2013). The R^2 marginal represents the proportion of variance explained only by fixed effects and R^2 conditional represents 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 (interactions R package, 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 GLM for each beetle species was selected based on the Akaike Information Criteria (AIC) and considering the highest R^2. In these GLMs, we analyzed together *I. sexdentatus* with *I. acuminatus*, and *T. piniperda* with *T. minor* to have enough plots with tree mortality induced by beetle attack. This grouping considered the similarity among the species biology and the main host tree attacked.

3. RESULTS

3.1. Patterns of recent bark beetle disturbance in Europe

In total, we analyzed 2,805 host trees distributed across 130 plots in 16 countries of Europe. Among them, 1,522 (54.3%) trees were non-infested, 825 (29.4%) infested, 288 (10.3%) dead non-infested, and 170 (6%) dead infested during the entire 2010-2018 period. During this period, the percentage of cumulative bark beetle attack and tree mortality at the plot-level showed geographical variations, with beetle attack hotspots in central, south-eastern, and northern Europe (Figure 1A), and mortality hotspots in south-eastern and northern Europe (Figure 1B). Considering all the species, time-series patterns of average bark beetle attack (black lines in Figure 1C-D) revealed that 2010 had the highest percentage of infested trees, ~10%. Then, the average beetle attack decreased to 1% for 2014-2017 and increased to 6% in 2018. However, the temporal patterns of beetle attack varied substantially according to the different host tree and bark beetle species with values below and over the average beetle attack (color lines, Figure 1C-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 found 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 tree mortality (Table 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 tree mortality rates occurred in *P. abi*es plots, followed by *P. sylvestris*, *P. pinaster*, and *P. nigra*. 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*. About tree mortality rates, plots with *I. acuminatus* exhibited the highest value, followed by *I. typographus*, *I. sexdentatus*, *T. piniperda*, and *T. minor*.

3.2. Forest resistance: bark beetle attack and tree mortality responses

The likelihood of overall bark beetle attack was significantly determined by host tree abundance (host proportion) and tree species richness in the plots, distance to the climatic niche optimum of the host and the beetle, and drought conditions (Table 2). Higher values of beetle attack, and therefore lower forest resistance, occurred in locations with a lower abundance of host trees, lower richness, and drought events with less intensity but with longer duration during the ten years before the attack (minimum SPEI value 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. Importantly, the positive interaction between these two variables showed that plots' environmental distance to beetle niche optimum modulated the effect of the distance to host niche optimum on the forest resistance to 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 (Figure S5).

In contrast to bark beetle attack, the likelihood of tree mortality was only significantly explained by the maximum drought intensity and the duration of drought conditions (i.e., the minimum SPEI value and the number of months with SPEI values < -1.5, respectively; Table 2). Forest resistance to tree mortality induced by beetle attack decreased with the maximum intensity and the duration of drought events. In addition, the variance explained in the tree 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; R^2 conditional = 0.56 in the mortality model), mostly due to bark beetle species.

Patterns of bark beetle attack varied among species (Figure 2A) For *I. typographus*, the likelihood of beetle attack was negatively determined by plot characteristics (host 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 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 drought events of low intensity but more duration. Tree mortality patterns also varied among bark beetle species (Figure 2B), but in all cases, it was determined by drought characteristics. Particularly, for *I. typographus*, the likelihood of tree mortality increased with 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. 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. DISCUSSION

Bark beetle attack and eventual beetle-induced 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 (i.e., climatic niche). Drought conditions, both duration and maximum intensity, had a critical role on recent bark beetle disturbance patterns, suggesting they have been key in modulating 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, Panassiti, Pennerstorfer, & Matthews, 2019; Neumann, Mues, Moreno, Hasenauer, & Seidl, 2017; Rouault et al., 2006). However, our analysis revealed that the influence of drought on forest resistance to bark beetle attack is mediated by the environmental position of the affected forest within the host tree and beetle species climatic niche. We found that forest resistance was modulated by the joint influence of the proximity of both the host tree and beetle species to the respective climatic optimum. This highlights the potential of integrating host and beetle niche characterization into a common environmental space to better understand the spatio-temporal patterns of forest resistance to bark beetle disturbance at regional scales under changing climates.

4.1. 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 European latitudes, 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, Appelberg, Harding,

& Bärring, 2009; Siitonen, 2014). This, in combination with recent 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. This 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, Battisti, Schroeder, & Faccoli, 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.

4.2. Forest resistance

Overall, forest resistance to beetle attack was determined by the confluence of diverse factors that predispose trees to be attacked by bark beetles, such as the forest environmental position in relation to the host and beetle climatic niche optimums, previous droughts, and plot characteristics. At the time of beetle attack, plots located climatically closer to both 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 the host climatic optimum. In addition, under current climatic trends, a displacement of beetles' populations during the study period (2010-2018) towards more suitable conditions for their development (Figure S6) may have increased the likelihood of beetle attack in plots far from the historical (1960-2000) beetle optimum.

Although higher tree defense capacity may be expected in host tree populations located close to their climatic optimum due to a better species performance (Abeli et al., 2014; Martínez-Meyer et al., 2013; Sexton et al., 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 droughts with a moderate maximum intensity during the ten-years before the 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, Latimer, Mortenson, Fettig, & North, 2021). But, long-lasting drought stress can compromise 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, Kane, & Mitton, 2014). In consequence, under recurrent drought conditions, vigorous trees established in locations environmentally close to the species 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 the attack success (Boone, Aukema, Bohlmann, Carroll, & Raffa, 2011).

Concerning plot characteristics, plots with low tree species richness 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. This may reflect 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, the selection started from the center of circular plots/satellites of cross-cluster plots and the survey effort focused 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.

Forest resistance to beetle-induced tree mortality was exclusively driven by the duration and maximum intensity of droughts undergone during the ten-years before the mortality. Independently of plot characteristics and the environmental location within the host and beetle climatic niche at the time of mortality, trees in plots that previously experienced long-duration 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, 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, 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 intensity and duration of drought conditions before beetle attack, which has strong implications in the context of ongoing climate change and the expected increase in extreme climatic events.

Species-specific patterns showed 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 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, Das, Ampersee, Bulaon, & Yee, 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 previous, intense 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*, the occurrence of prolonged droughts with a moderate maximum intensity in pine populations close to their climatic optimum was necessary for reducing 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 drought conditions and intense drought stress before 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.

This study reveals that the resistance of European coniferous forests to bark beetle disturbance is modulated by the joint host-insect climatic suitability and by beetle-drought interactions. The expected increase in the frequency of extreme drought events in the coming decades, particularly under the threat of multivoltine bark beetle species activity, may increase beetle attack success and beetle-induced tree mortality jeopardizing forest resistance. We suggest that an approach incorporating the magnitude and duration of drought events and stand characteristics (i.e., structure and composition), integrated within the framework of insect-host species climatic niche, would allow more accurate predictions of the rates and patterns of forest resistance to bark beetle attack and induced mortality into the future.

ACKNOWLEDGMENTS

The research was supported by the Spanish Ministry of Science and Innovation through the RESIBIO (PID2020-115264RB-I00) and BIOCLIM projects (CGL2015-67419-R), and by AGAUR (Government of Catalonia) through the 2017 SGR 1001 grant. We acknowledge the data access and support provided by the Programme Coordinating Centre and the Expert Panels of ICP Forests. The evaluation was based on data that was collected by partners of the official UNECE ICP Forests Network (http://icp-forests.net/contributors). Part of the data was co-financed by the European Commission (Data achieved at 10.12.2020).

DATA AVAILABILITY STATEMENT

The plot data that support the findings of this study were obtained from UNECE ICP Forests Network and can be requested (http://icp-forests.net/page/data-requests). Tree species' occurrences were extracted from the EU-Forest occurrence dataset that is available at Mauri et al. 2017 (https:// doi.org/10.1038/sdata.2016.123). Bark beetle species' occurrences were obtained from the openly GBIF database (http://www.gbif.org). Climatic variables are openly available in TerraClimate (https://www.climatologylab.org/terraclimate.html). R-code and other datasets that support the findings of this study are available from the corresponding author upon reasonable request.

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Table 1. Average annual bark 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.

Table 2. GLMMs results of the overall likelihood of bark beetle attack and induced 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.

Table 1.

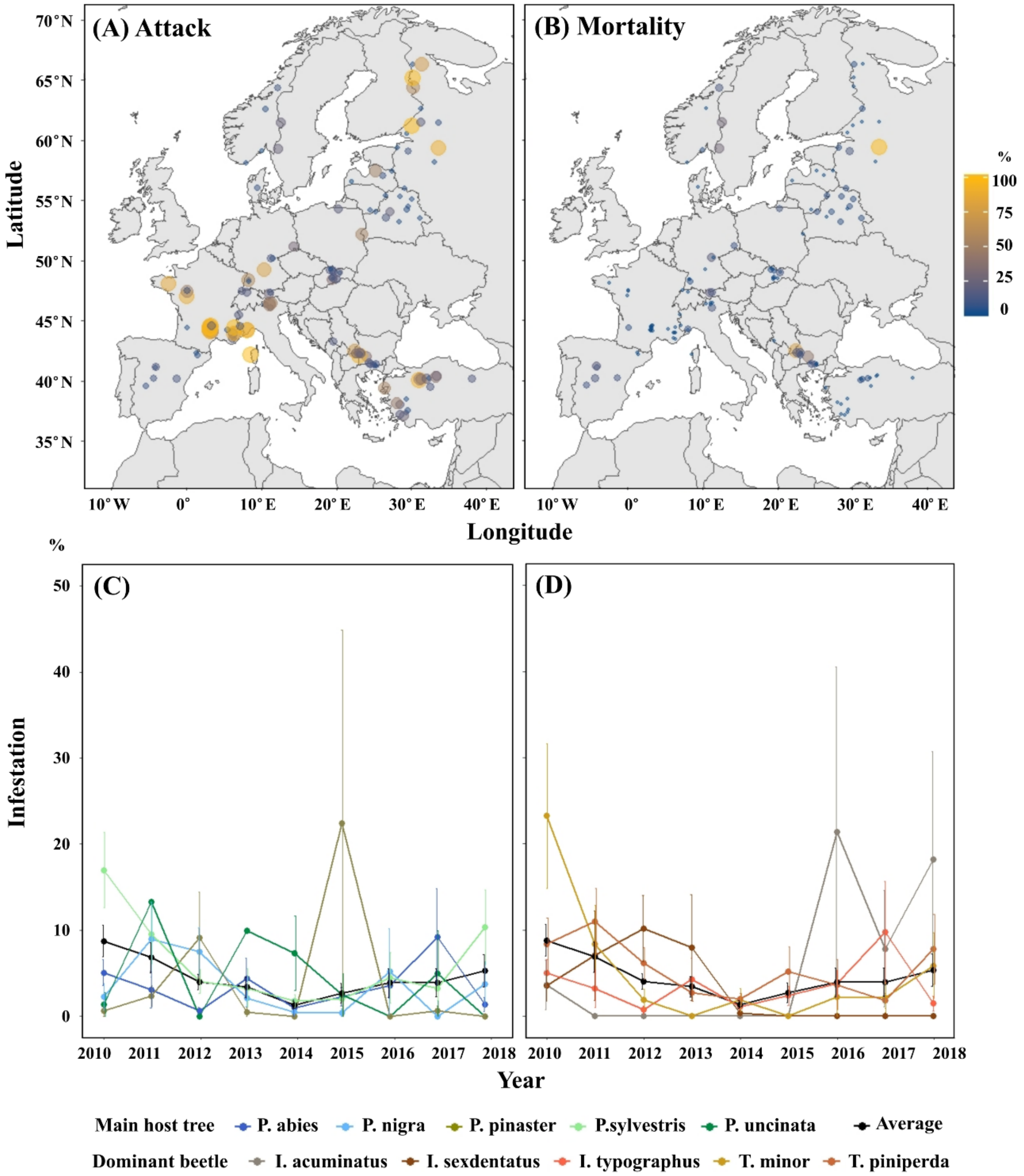
Role	**Species**	**N plots**	**Attack (% yr^{-1})**	**Mortality (% yr^{-1})**
Main host tree	*Picea abies*	47	3.42	1.12
	Pinus sylvestris	52	6.23	0.95
	Pinus nigra	20	3.42	0.06
	Pinus uncinata	3	4.40	0.00
	Pinus pinaster	8	3.98	0.64
Bark beetle	*Ips typographus*	46	3.50	1.16
	Ips sexdentatus	16	3.22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

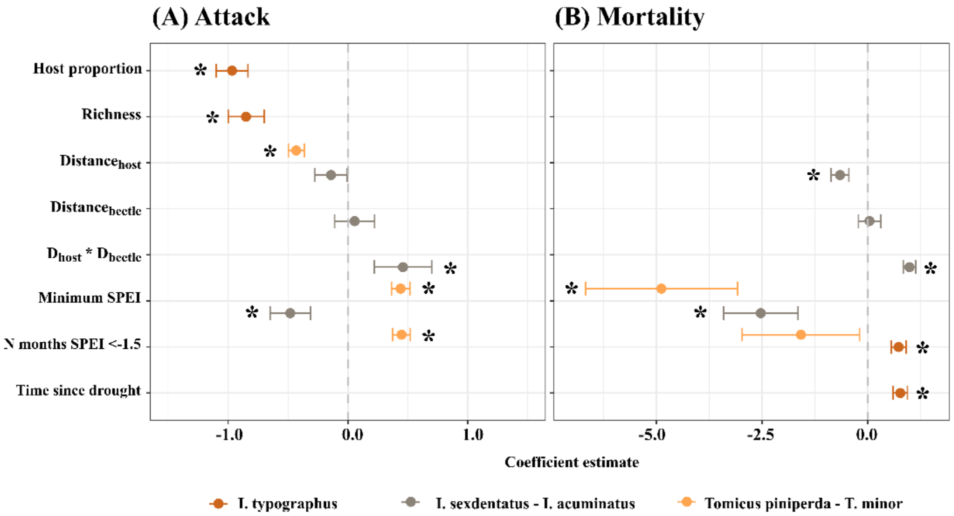
Table 2.

	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	0.079
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		

Figure 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. (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).

Figure 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 beetle attack 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.


(A) Attack
(B) Mortality
Latitude
70° N
65° N
60° N
55° N
50° N
45° N
40° N
35° N
10° W
0°
10° E
20° E
30° E
40° E
Longitude
%
100
75
50
25
0
(C)
(D)
%
Infestation
50
40
30
20
10
0
2010
2011
2012
2013
2014
2015
2016
2017
2018
Year
Main host tree
P. abies
P. nigra
P. pinaster
P.sylvestris
P. uncinata
Average
Dominant beetle
I. acuminatus
I. sexdentatus
I. typographus
T. minor
T. piniperda


(A) Attack
(B) Mortality
Host proportion
Richness
$\text{Distance}_{\text{host}}$
$\text{Distance}_{\text{beetle}}$
$D_{\text{host}} * D_{\text{beetle}}$
Minimum SPEI
N months SPEI <-1.5
Time since drought
*
-1.0
0.0
1.0
-5.0
-2.5
0.0
Coefficient estimate
I. typographus
I. sexdentatus - I. acuminatus
Tomicus piniperda - T. minor