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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. So, the consequences of infestation would likely be more intense in tree populations living closer to the limits of 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 (*Pinus sylvestris* L.) 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 trees and bark beetles. Climatic suitability values were estimated by using species distribution models (MaxEnt). Then, we developed generalized linear mixed-effects models and partial least squares-generalized linear models to study tree mortality and stand bark beetle infestation in relation to host and insect suitability, intensity of bark beetle attack, tree characteristics, and stand structure. 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 probability of dying at lower values of attack intensity. At stand level, bark beetle infestation was negatively associated with the density of Scots pine and the basal area, and positively with tree species richness. Taken together, the response of Scots pine populations to tree characteristics and stand structure suggested an attack by bark beetles with a low population density that preferred weakened smaller trees. Remarkably, our results showed that Scots pine populations established in higher climatic suitability areas were more vulnerable to infestation, particularly when locations were also suitable for these insects. 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 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 climatic events.

Keywords: bark beetles; Scots pine; drought; climatic suitability; tree mortality; stand infestation; disturbance interactions.

1 Introduction

Climate change has been linked to increased mortality of coniferous tree species around the globe due to extreme 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 forest mortality has emerged as a major disturbance under the context of global climate change (Anderegg et al., 2015). Unprecedented outbreaks, in which some bark beetle species have killed billions of coniferous trees across vast areas (e.g., Bentz et al., 2010; Meddens et al., 2012; Rouault et al., 2006; Seidl et al., 2016) and the expansion of the geographic range of native beetle species into new areas (Logan and Powell, 2001; Raffa et al., 2013; Weed et al., 2013) indicate that disturbance regimes associated with insect-driven tree mortality are changing. Furthermore, extreme climatic events such as drought episodes are likely to affect local tree populations differently across their geographic distribution range (Hampe and 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 depend 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 and 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 and Berryman, 1983) according to their age, size, and the level of stress they support (Krokene, 2015). The insect-host system is also highly sensitive to climatic variability (Seidl et al., 2009). Warming increases beetles' overwinter survival and accelerates their growth rates (Bentz et al., 2010; Creeden et al., 2014; Temperli et al., 2015), whilst severe drought stress disrupts host tree defenses, thereby increasing trees' overall susceptibility to infestation (Gaylord et al., 2013; Netherer et al., 2015). 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). Therefore, the insect-host system could be modified at the edges of the geographical range of tree populations when these correspond to the limits of species' climatic tolerance (Thuiller et al., 2008). For instance, 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 (MacArthur, 1972), perturbations in the phenology, abundance, and ecological interactions of species are more evident in localities with less suitable environmental conditions and limitations on population performance due to harsher climatic conditions (Lynch et al., 2014; Morin et al., 2007; Raffa et al., 2015), which in turn often correspond to the edges of the 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 and Jump, 2017; Lloret and Kitzberger, 2018; Rehm et al., 2015), probably due to genetic adaptations and/or higher plastic responses (Aitken et al., 2008; Hampe and Petit, 2005; Jump and 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 and 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. This approach will considerably further understanding of the consequences of climate change on host-insect dynamics across biogeographical gradients and therefore improve anticipation of 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 and thus comes closer to the limits of its climatic tolerance (Carlisle and Brown, 1968). Scots pine populations situated in this region may therefore be particularly sensitive to extreme climatic events when these are combined with insect attack (Hampe and Petit, 2005; Matías and Jump, 2012). In fact, drought-induced Scots pine dieback has recently been observed in the Iberian Peninsula (Hódar et al., 2003; Martínez-Vilalta and Piñol, 2002; Galiano et al. 2010), along with a 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 post-drought tree mortality and bark beetle infestation in Scots pine populations from the northeast of the Iberian Peninsula. The assumption behind SDMs is that species occurrences represent the environmental conditions that are suitable for a given species to reproduce and survive (Soberón and Peterson, 2005). Significantly, model output can be interpreted as a species-specific index of the climatically suitable conditions across the landscape (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 and Kitzberger, 2018; Pérez Navarro et al., 2018; Sapes et al., 2017). We explore the response of tree mortality and bark beetle infestation at tree and stand level to the climatic suitability of both the host tree and insect, tree characteristics, and stand structure. Specifically, we examined whether 1) larger and closer trees with evidence of bark beetle attack have a greater probability of mortality; 2) denser and monospecific stands of the host tree are more prone to be infested; 3) trees living in localities with low values of climatic suitability are more vulnerable to die, and 4) 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 Material and Methods

2.1 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 and Jump, 2012). In 2005, the Iberian Peninsula experienced an extreme drought episode that was followed by several dry years (EEA, 2017). This drought event affected Scots pine populations in Catalonia, among other conifer species; various symptoms were detected including tree defoliation, mortality (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 on sites with contrasted climate conditions (Fig. 1). The populations' elevation ranged from 600 to 1,600 m a.s.l, with mean annual temperatures from 6.5 °C to 13 °C and annual precipitation between 700 and 1,100 mm/year (WorldClim, version 2.0., Fick and Hijmans, 2017). Sites included pure stands of Scots pine (*Pinus sylvestris* L.) and mixed stands of Scots pine and holm oak (*Quercus ilex* L.) or mountain pine (*Pinus uncinata* Ramond ex DC. in Lam. and DC) with an understory dominated by strawberry tree (*Arbutus unedo* L.), kermes oak (*Quercus coccifera* L.), boxwood (*Buxus sempervirens* L.) and common juniper (*Juniperus communis* L.).

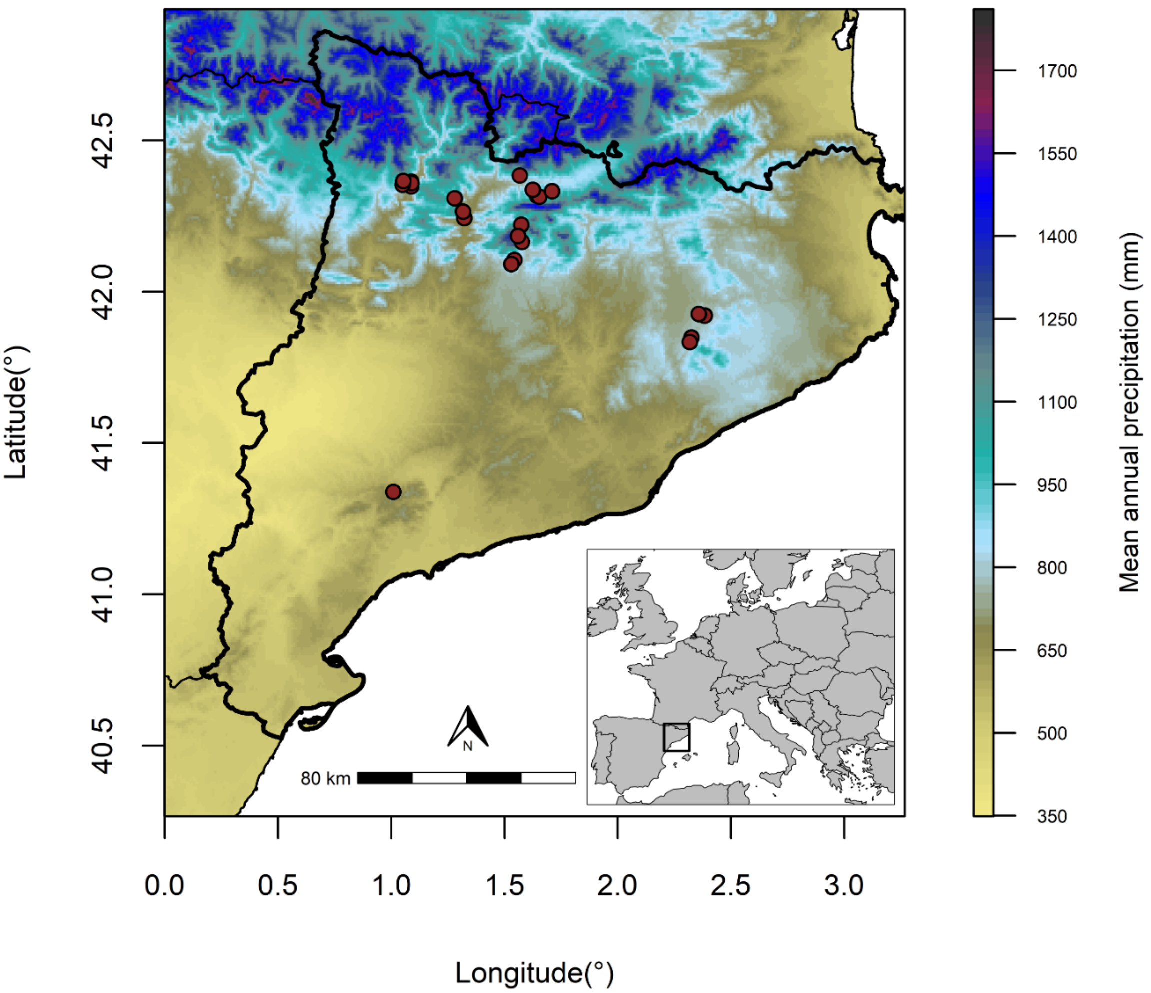

Figure 1. Map of the study area in the northeast of Spain and location of the 22 sampled Scots pine populations (red dots) across the precipitation gradient (mean annual precipitation (mm).

2.2 Field data collection and stand attributes

During 2013-2014, a circular stand (of 314 m^2) was established in each of the 22 selected populations. On each site, we recorded 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. A total of 962 Scots pines were sampled.

Scots pine trees were naturally attacked by four bark beetles species within the study region: *Ips acuminatus* (Gyll.), *Ips sexdentatus* (Börner), *Tomicus minor* (Hart.), and *Tomicus piniperda* (L.). The identification of each bark beetle species was principally based on galleries and/or bark beetle imagoes. 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., Borkowski and Skrzecz, 2016; Lieutier et al., 1995). 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. We thus opted to potentially overestimate insect attack, associated with infestation success, rather than underestimating it. Moreover, we recorded the presence/absence of bark beetle species in other parts of the tree, including signs of galleries in the branches and the upper part of the stem.

For each stand, we calculated the following forest attributes: Scots pine density (trees ha^{-1}), Scots pine basal area (m^2 ha^{-1}), tree species richness, and a nearest neighbor (R) based on the distances to the nearest neighbor recorded for all Scots pine trees (following Clark and Evans, 1954). The calculation of the nearest neighbor was used as a measure of the clustering or ordering of tree spatial distribution within each stand. 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. Finally, bark beetle infestation in each stand was considered as the proportion of dead trees presenting signs of a successful attack (i.e., bore holes and signals of maternal galleries).

2.3 Climatic suitability modeling

We assessed the contribution of the climatic suitability of the host tree and beetle species in the Scots pine mortality and infestation processes. We used species distribution models (SDMs) built at the European scale to obtain estimates of the probability of species' occurrences, both for Scots pine and bark beetles, under the climatic conditions that characterize our study sites.

Occurrence data

Scots pine records were obtained from European Forest data (Mauri et al., 2017), amounting to a total of 9,368 occurrences. For bark beetle species, we collated species occurrences from different sources, due to the scarcity of records; these sources included the Global 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 (Borkowski and Skrzecz, 2016; Gallego and Galián, 2001; Horn et al., 2009; Jankowiak, 2012; Kerdelhué et al., 2002; Kohlmayr et al., 2002; Moraza et al., 2013; Olsovsky et al., 2013; Pineau et al., 2017; Ritzerow et al., 2004; Rossi et al., 2009; Vasconcelos et al., 2006). However, 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). Despite the absence of records of the other two bark beetle species (*I. acuminatus* and *T. minor*), our analyses were not seriously compromised since the largest part of the Scots pine infestation was attributed to *I. sexdentatus* and *T. piniperda*. Furthermore, these two species are considered two of the most damaging pests in Europe and cause significant forest loss every year (Sauvard, 2004). We therefore considered them good representatives for analyzing the 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 and Hijmans, 2017) at a resolution of 30 seconds (~1 km^2). We selected them on the basis of the host tree and insect ecological requirements (Lieutier et al., 2004; Matías and Jump, 2012). To prevent multicollinearity among them, variables were also filtered by means of a Variance Inflation Factor (VIF) < 10 as a critical threshold (Quinn and 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 a small number of occurrences (Pearson et al., 2007). 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 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 and 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 habitat 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 and Bell, 1997), and we also applied jackknife test to measure percent contribution of each variable to the final model.

2.4 Tree mortality and infestation modeling

Statistical analyses were conducted at the tree- and stand-level. 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 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 probability of tree mortality as a function of tree size, distance to the nearest neighbor, intensity of bark beetle attack, and climatic suitability of Scots pine. The binary response of tree mortality (living or dead tree) was modeled as a binomial error distribution with a logit-link function (Bolker et al., 2008). We built a null model, from which we created a set of models by adding different combinations and interactions between predictors. Note that presence/absence of bark beetle species was finally not included in the models because it introduced a large amount of over-dispersion. All the GLMMs were fitted by Laplace approximation and included ‘stand’ as a random effect. After ranking our models, we selected the best one according to Akaike’s information criterion (AIC; Akaike, 1973), Bayesian information criterion (BIC; Schwarz, 1978), and the marginal and conditional R^2 (MuMln package, Nakagawa and 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 modeled the proportion of bark beetle infestation as a function of tree density, basal area, richness of tree species, nearest neighbor index, Scots pine suitability, and the suitability of the two bark beetle species (i.e. *Ips sexdentatus* and *Tomicus piniperda*). Since we found a high negative correlation between Scots pine and *I. sexdentatus* suitabilities, we used the PLS (Partial Least Squares) approach for the analysis. PLS generalizes and combines principal component analysis and multiple regression features to model relationships between the response and explanatory variables. The components are obtained through the combination of the original predictors that maximize the explained variance (R^2) in the response variable (Abdi, 2003). Furthermore, this technique is particularly useful for analyzing correlated predictor variables with a small sample compared with the number of predictors (Carrascal et al., 2009). Thus, 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 weights of the original predictors on each component. Predictors' weights explain the signal of their effect and its square value 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.

3 Results

3.1 Climatic suitability modeling

The SMDs for the two bark beetle species showed good performance accuracy, with mean AUC values higher than 0.75 and a standard deviation lower than ±0.04 (Table 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 a poorer performance than the bark beetle models, with a mean AUC value of 0.67 and a standard deviation of ±0.005 (Table 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, isothermality, and annual temperature range. 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 and Jump, 2012).

Table 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 variables with the highest contribution for the model.

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)

Standard errors are in brackets

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). *T. piniperda* occurrence in particular was expected to be more likely at higher altitudes with colder temperatures than *I. sexdentatus* occurrence. Scots pine did not present high suitability values on our study sites, probably because this tree species reaches its southern limit of distribution in the Iberian Peninsula.

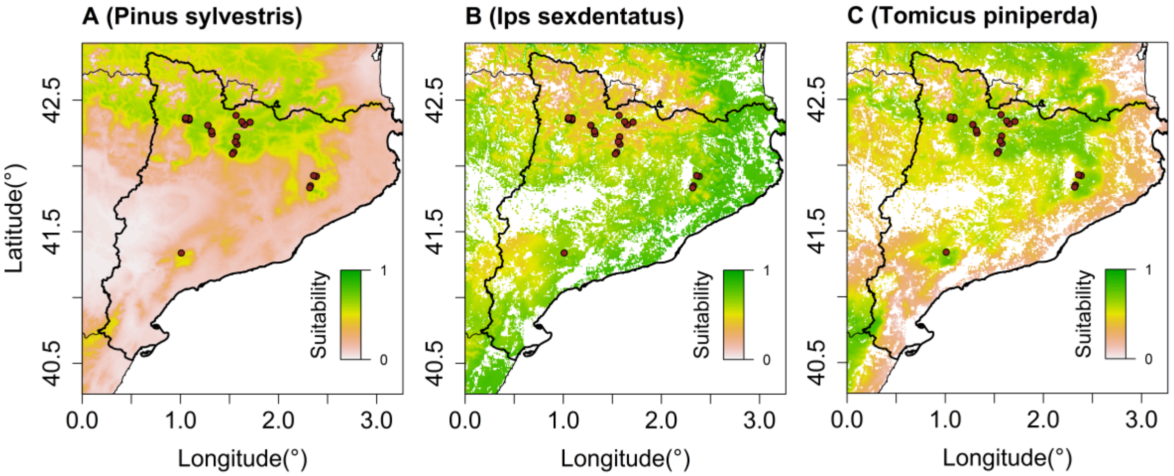

Figure 2. Habitat-suitability maps obtained in MaxEnt models for *P. sylvestris* (A), *I. sexdentatus* (B), and *T. piniperda* (C). Red dots correspond to the 22 study stands.

3.2 Determinants of tree mortality and infestation

A total of 56.2% of the sampled Scots pine trees corresponded to dead trees, of which 72% showed signs of bark beetle infestation (Table 2). In contrast, only 9% 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.

At tree level, the best GLMM model fitted to describe Scots pine mortality included tree size, distance to the nearest neighbor, intensity of attack, Scots pine suitability, and the 2-way interactions between the predictors (Table 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. 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. 3; C). In contrast, at low levels of attack intensity, Scots pine mortality tended to increase more markedly at higher rather than lower values of tree suitability (Fig. 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 3).

Table 2. Description of the tree- and stand level attributes (mean ± standard deviation) within the study sites.

	Living trees	Living infested trees	Dead trees	Dead infested trees	Total stands
Number of trees	421	37	541	387	962
Mean dbh (cm)	14.6 (±9.9)	20.9 (±12.7)	15.2 (±8.3)	15.4 (±8.1)	14.9 (±9.1)
Mean dnn (cm)	1.4 (±1.0)	1.6 (±1.3)	1.2 (±1.0)	1.2 (±1.0)	1.3 (±1.0)
Mean iat (n holes/m^2)	75 (±72)	143 (±180)	207 (±211)	284 (±198)	123 (±191)
Basal area (m^2/ha)	--	--	--	--	33.4 (±14.4)
Density (n/ha)	--	--	--	--	1429.5 (± 909.9)
Richness (n tree species)	--	--	--	--	2.9 (±1.5)
Nearest neighbor index	--	--	--	--	0.8 (±0.2)

Table 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; BIC = 884; R^2 marginal = 0.83; R^2 conditional = 0.85; Dispersion statistic = 0.90; N = 962. Standard errors are in brackets

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 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, *Ips* suitability, and the three-way interaction between Scots pine, *Ips,* and *Tomicus* suitabilities. This component was best explained by the three-way interaction, which alone retained nearly half of the information content (43%), whereas *Ips* 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.

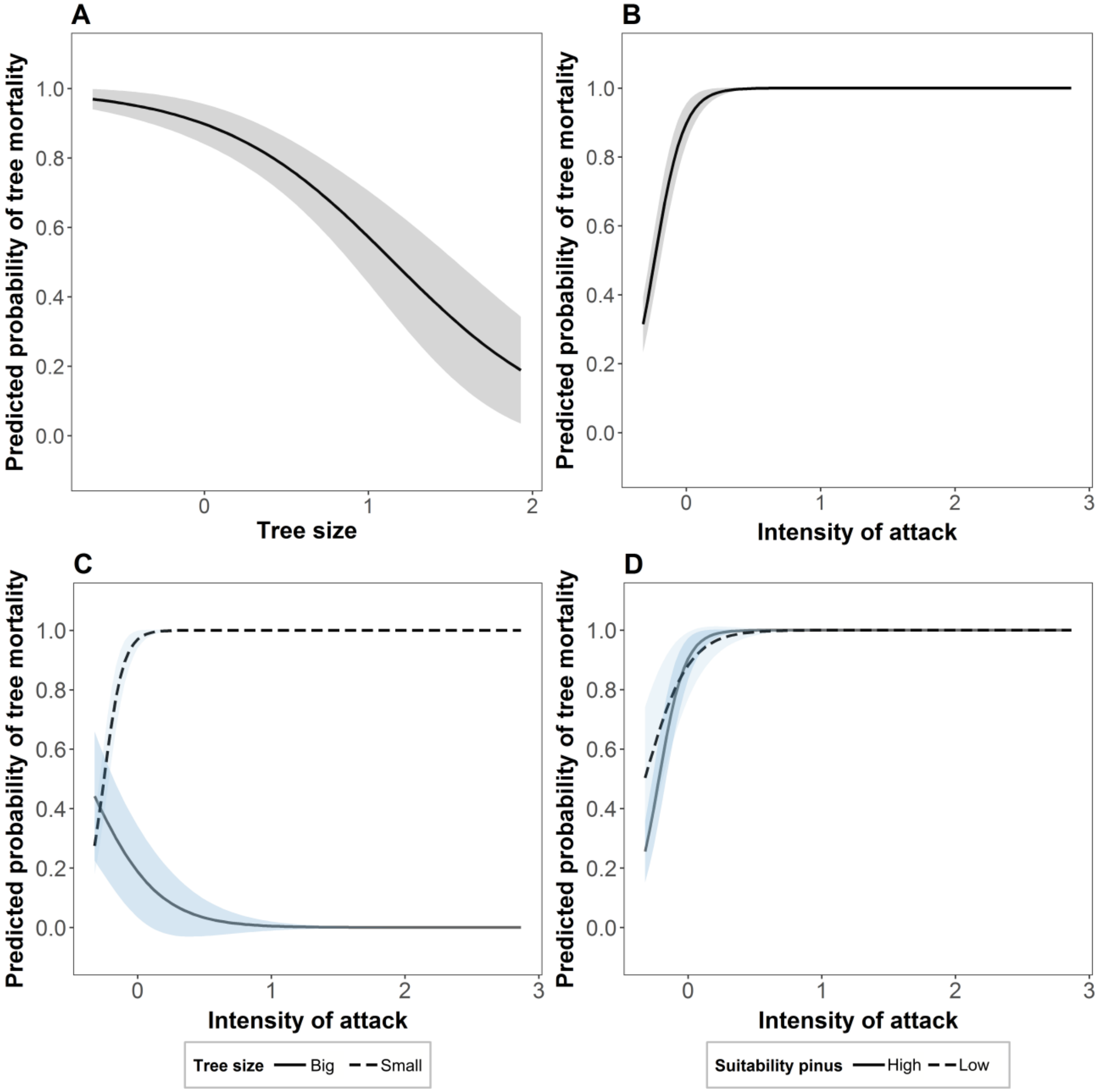

Figure 3. Plots depicting the significant relationships obtained within the tree-level mortality model. A: Correlation between tree size (dbh scaled) and predicted probability of tree mortality; B: Correlation between intensity of attack (number of holes scaled) and predicted probability of tree mortality. Black lines represent prediction of the model and gray shaded areas represent limit of the confidence intervals. C: Effect of the two-way interaction between intensity of attack (number of holes scaled) and tree size (maximum and minimum of dbh scaled) 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) on predicted tree mortality. Black and dashed lines represent predictions of the model and blue shaded areas represent limit of the confidence intervals. See methods for details on variable standardization.

Table 4. PLS-GLM weights estimates of stand-level variables to explain the proportion of dead infested trees. 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 área (ba)	**-0.28 (0.08)**	**-0.34 (0.11)**
Richness of tree species (r)	0.00 (0.00)	**+0.38 (0.15)**
Spatial pattern (sp)	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 weights in brackets

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 inconsistent with host tree populations close to reaching a beetle eruptive phase (i.e., outbreak). Previously reported predisposing factors for insect outbreak are related to the quantity (e.g., high stand basal area and high abundance of host individuals) and quality (e.g., high level of nutrients) of host trees (Negron and Wilson, 2003; Perkins and Roberts, 2003; Shore et al., 2000). Nevertheless, it is 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 and Berryman, 1983) modulate the emergence 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.

As regards 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. In contrast, the contribution of beetle attack in larger trees was scarcely relevant to any explanation of their death. This conforms to the reported effects under low beetle density, where the attack pattern on small trees is related to incipient bark beetle population levels (Boone et al., 2011). When beetle population density is too low for a cooperative attack, insects exploit weakened trees (Ryan et al., 2015), such as small and suppressed individuals with competitive disadvantages for light interception and belowground water uptake, due to their lower rooting depth (Bravo-Oviedo et al., 2006; Dawson, 1996; Lloret et al., 2004). Furthermore, the defenses in small trees are less substantial than those of larger and more vigorous trees, so the former would require lower levels of attack intensity to be successfully colonized by insects (Raffa et al., 2016). Furthermore, the absence of any significant effect exerted by the distance to the nearest conspecific neighbor supports this interpretation, as well as indicating a scattered pattern of pine mortality.

At stand level, infestation patterns and their relationship to stand structure also suggest the lack of an intense bark beetle outbreak in the studied populations. The probability of dead Scots pines being infested was negatively associated with Scots pine density and basal area, and positively related to the richness of tree species. 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 et al., 2015). However, if the beetle populations levels are incipient, they preferentially attack and kill trees in stands where the hosts are more susceptible (Bone et al., 2013), as we found at tree level, where small trees exhibited a higher vulnerability. On the other hand, the mechanisms underlying the positive relationship between richness and bark beetle infestation appear to be complex. Baier et al. (2002) found that Norway spruce from mixed stands presented lower resin defenses to deal against beetle attack. In contrast, 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, 2001). In our study populations, the absence of a significant relationship between tree spatial pattern and infestation likely reflects the lack of the typical clustered pattern of an eruptive phase (i.e. outbreak) of bark beetle attack. Furthermore, 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).

It should be noted that a relevant number of dead trees (28%) did not show any signs of bark beetle attack. Although there may be an underestimate of attacks due to the limitations of our visual survey, this value suggests that causes other than insects contributed to tree mortality on the study sites. In effect, recent drought periods have been demonstrated to be a 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 vulnerable 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 more vulnerable 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 and 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 the results of Rigling et al. (2003), 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).

Interestingly, infestation in our Scots pine populations was particularly intense on sites where the climatic suitability for *I. sexdentatus* and *T. piniperda* was greater. Therefore, maximum infestation levels were only attained when high suitability values coincided in both the beetle 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, it is known that interspecific competition between beetle species is in many cases minimized by using different parts of a common resource (Paine et al., 1981), allowing them to coexist in the same host population. *Ips 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). In an eruptive phase, these two species would probably compete for food resources and habitat, reducing coexistence within the same stand (Light et al., 1983; Rankin and 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 in trees of a different size, helping to overcome tree defenses and promoting higher infestation levels.

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 vulnerable to the attack. In fact, the stage of the infestation process also appears 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 and Jump, 2017; Lloret and Kitzberger, 2018), that tree populations situated 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. Further studies examining the climatic niche of both the insect and host species are therefore needed to better anticipate the potential effects of these interactions on future forest dynamics.

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