Margalef Marrase, Jordi; Pérez Navarro, María Ángeles; Lloret Maya, Francisco. «Relationship between heatwave-induced forest die-off and climatic suitability in multiple tree species». Global change biology, Vol. 26, Issue 5 (May 2020), p. 3134-3146. DOI 10.1111/gcb.15042

Relationship between heatwave-induced forest die-off and climatic suitability in multiple tree species

Running tittle: Species climatic suitability and forest die-off

Jordi Margalef-Marrase[1], María Ángeles Pérez-Navarro[1], Francisco Lloret[1,2]

[1]CREAF, Cerdanyola del Vallès, 08193, Spain.

[2]Unitat d'Ecologia, Univ. Autònoma Barcelona, Cerdanyola del Vallès, 08193, Spain.

Correspondence:

Jordi Margalef-Marrase, CREAF, Cerdanyola del Vallès, Spain

Phone: +34 935813345

ORCID ID: https://orcid.org/0000-0003-4369-9918

E-mail: jmargalefmarrase@gmail.com

Abstract

In recent decades many forest die-off events have been reported in relation to climate change-induced episodes, such as droughts and heat waves. To understand how these extreme climatic events induce forest die-off it is important to find a tool to standardize the climatic conditions experienced by different populations during a specific extreme climatic event, taking into account the historic climatic conditions of the site where these populations live (bioclimatic niche). In this study we used estimates of climatic suitability calculated from Species Distribution Models (SDMs) for such purpose. We studied forest die-off across France during the 2003 heat wave that affected Western Europe, by using 2,943 forest inventory plots dominated by fourteen single tree species. Die-off severity was estimated by NDVI loss using MODIS remote sensor imagery. Climatic suitability at local level during the historical 1979-2002 period (HCS), the episode time (2003) (ECS) and suitability deviance during the historical period (HCS-SD)) were calculated for each species by means of BRT models using the CHELSA climate database and occurrences extracted from European forest inventories. Low HCS-SD and high mean annual temperature explained the overall regional pattern of vulnerability to die-off across different monospecific forests. The combination of high historical and low episode climatic suitability also contributed significantly to overall forest die-off. Furthermore, we observed different species-specific relationships between die-off vulnerability and climatic suitability: Sub-Mediterranean and Mediterranean species tended to be vulnerable in historically more suitable localities (high HCS), while Euro-Siberian species presented greater vulnerability when the hot drought episode was more intense. We demonstrated that, at regional scale, past climatic legacy plays an important role in explaining NDVI loss during the episode. Moreover, we demonstrated that SDM-derived indexes, such as HCS, ECS and HCS-SD, could constitute a tool for standardizing the ways that populations and species experience climatic variability across time and space.

Keywords: Climatic suitability, canopy decay, forest die-off, extreme climatic event, hot-drought, species distribution models, hot-drought, NDVI

Introduction

Forest die-off and tree mortality events have been widely reported in recent years across many biomes, and they have been associated with hot drought episodes (Allen, Breshears, & McDowell, 2015; Allen et al., 2010; Carnicer et al., 2011; van Mantgem et al., 2009) that can be related to climate change (IPCC, 2013). The evidence of the relationship between climatic variables (basically lack of precipitation combined with high temperatures) and forest die-off – loss of green coverage, leaf browning, growth reduction, partial dieback and even tree mortality – has mostly been observed at local scale for particular species (e.g., Faber-Langendoen and Tester 2006, Bigler et al. 2007, Sarris et al. 2007, Anderegg et al. 2011, Hereş et al. 2012). However, our understanding of the variability of forest die-off patterns at regional scale in relation to climate extremes like hot-drought episodes is still limited, particularly as regards comparisons of the performances of different species (Allen et al., 2015; Steinkamp & Hickler, 2015). Comparisons between species responses' to similar climatic extremes across geographical gradients are challenging because of local environmental variability, including weather and soil variability (Adams, Barnard, & Loomis, 2014; Clifford, Royer, Cobb, Breshears, & Ford, 2013; Olarieta, Bargués Tobella, Rodríguez-Ochoa, & Antúnez, 2017; Western, Grayson, & Blöschl, 2002), population variability due to genetic, demographical and management legacy (Cavin & Jump, 2017; Hampe & Petit, 2005; Valladares et al., 2014; Vilà-Cabrera, Martínez-Vilalta, Vayreda, & Retana, 2011) and species attributes (Greenwood et al., 2017; Martinez-Vilalta, Lloret, & Breshears, 2012)

It is often assumed that species perform better when they are closer to their niche optimum, rather than when they are near the edges of a niche (Abeli, Gentili, Mondoni, Orsenigo, & Rossi, 2014; Sexton, McIntyre, Angert, & Rice, 2009). However, populations close to the centre of a species's climatic niche could be also affected by extreme climatic events (Lloret & Kitzberger, 2018) while, conversely, populations living under less suitable conditions could be less vulnerable (Cavin & Jump, 2017; Lloret & Kitzberger, 2018). This pattern could appear as a consequence of high water-demanding organs, built during periods of high resource availability, of populations living close to a climatic niche optimum or of local adaptation or phenotypic plasticity in niche-edge populations (Rose, Leuschner, Köckemann, & Buschmann, 2009). However, these patterns could be modified by biotic interactions – i.e., competition, facilitation (Lloret & Granzow-de la Cerda, 2013) – or by increasing or decreasing vulnerability in the edge or core populations. More specifically, high stand density or high basal area has been reported as contributing to tree mortality under drought conditions (Bottero et al., 2017; Young et al., 2017).

Species distribution models (SDMs) are statistical models that relate species occurrences to environmental conditions, thus providing a species-specific index of habitat suitability, which can be specifically related to the climatic environment (species climatic suitability) (Serra-Diaz et al., 2013). SDMs have been used to predict populations' demographic performance and species' persistence (Thuiller et al., 2014). Furthermore, SDMs have also been applied to standardize the climatic conditions undergone by different populations of a given species or different co-occurring species during the same extreme climatic event, relative to the historical climate conditions that each populations or species have experience (Sapes et al. 2017, Lloret and Kitzberger 2018, Perez et al. 2018).

Here, we studied forest die-off during an extreme climatic event which occurred in France in 2003. From May to August 2003, vast areas of Western Europe experienced an extreme heat wave, concurrent with exceptionally low rainfall, and the functioning of forests was modified as a result (Ciais et al., 2005; Graf Pannatier et al., 2012; Pichler & Oberhuber, 2007). Thus, widespread forest die-off appeared in 2003 and their symptoms – i.e., loss of green canopy, leaf browning, growth reduction and mortality – persisted in the following years (Allen et al., 2010; Bréda, Huc, Granier, & Dreyer, 2006; Lloret et al., 2007). This loss of green coverage resulted in an anomaly in the Normalized Difference Vegetation Index (NDVI) (Zaitchik, Macalady, Bonneau, & Smith, 2006).

The main goal of this study was to assess how climatic suitability during an extreme climatic event relates to die-off processes at regional scale, and to fourteen different forest tree species. We used several estimates of species climatic suitability derived from SDM outputs: Historical Climatic Suitability (HCS), which provided the suitability during the historical climate series; Event Climatic Suitability (ECS), which provided the suitability during the heat wave; and Suitability Deviance (HCS-SD), which provided the historical climate variability during the reference period (Lloret & Kitzberger, 2018). We also considered plot forest structure (density and basal area) as a potential explanatory variable of die-off intensity (Klos et al., 2009; Linares, Camarero, & Carreira, 2010).

More specifically, we investigated (1) whether populations experiencing the hot-drought episode were highly affected when living close to their climatic limit of tolerance (negative effect of HCS on forest die-off) or when living close to the climatic optimum (positive effect of HCS on forest die-off); (2) the importance of extreme event magnitude on forest die-off (negative relationship between ECS and die-off); (3) whether populations were more affected in low climatic variability environments (negative effect of HCS-SD on forest die-off) or in high variability ones (positive effect of HCS-SD on forest die-off), thus demonstrating a climatic legacy effect in populations; (4) the interaction between climatic suitability variables in the elucidation of whether extreme episode suitability was increasing die-off close to the species' climatic optimum or close to their climatic limit of tolerance (interaction between ECS and HCS); and (5) whether past variability was reinforcing die-off in core or edge populations (interaction between

HCS and HCS-SD) or whether there was a connection between drought magnitude and climatic events legacy (interaction between ECS and HCS-SD). Finally, we also tested (6) the importance of forest structure on forest die-off, and whether forest structure modulates forest die-off in low or high climatic-suitable populations (interaction between forest structure and Climatic Suitability Indices).

Methods

Study system

We performed the study in mainland France (3° 6' E, 42° 30' N to 2° 32' E, 51° 05' N, 334,604 km^2). During 2003 precipitation was lower than average from May to September, especially in June and August (Rebetez, Mayer, & Dupont, 2006). In particular, August rainfall was 20% to 75% lower than the average for that month in the 1961-1990 period. Furthermore, temperatures in France were exceptionally high in 2003 (see Fig. S1 at supplementary material), which came to be considered the hottest summer since 1500 (Luterbacher, Dietrich, Xoplaki, Grosjean, & Wanner, 2004). Maximum air temperature was higher than the 1961-1990 average for May (by 1-3°C across the region) and August (by 4-6°C) (Rebetez et al., 2006).

Our study was based on semi-natural woodlands dominated by native species – unlike almost all European forests, which have been historically heavily managed and exploited (Farrell et al., 2000). We selected 6,400 plots from the French National Inventory (IFN) corresponding to the 2006 campaign. Since we aimed to analyze species-level patterns, we selected plots dominated by single species in order to minimize interactions between dominant species. We then selected those forest plots that satisfied the following requirements: (1) at least 40% of tree canopy cover; (2) location within a forest patch larger than 4 ha (200 meters wide); (3) dominant species that represented at least 67% of the total basal area. We then chose 14 species that were dominant in at least 40 plots and selected the respective plots (see Table 1). Finally, we extracted the information relating to the total basal area (BA) and tree density (N) from each selected IFN plot. The final number of selected plots was 2,943 (Fig. 1B).

Forest die-off maps

The Normalized Difference Vegetation Index (NDVI) (Tarpley, Schneider, & Money, 1984) was used to assess the vegetation response to the 2003 heatwave (Breshears et al., 2005; Lloret et al., 2007; Williams et al., 2013; Yuhas & Scuderi, 2009), since NDVI anomaly can be correlated to growth reduction (Kaufmann et al., 2008), loss of green coverage and warming-induced defoliation (Camarero, Franquesa, & Sangüesa-Barreda, 2015; Francisco Lloret et al., 2016) and eventual tree mortality (Breshears et al., 2005). All of these factors are symptoms of a die-off process (Jump et al., 2017).

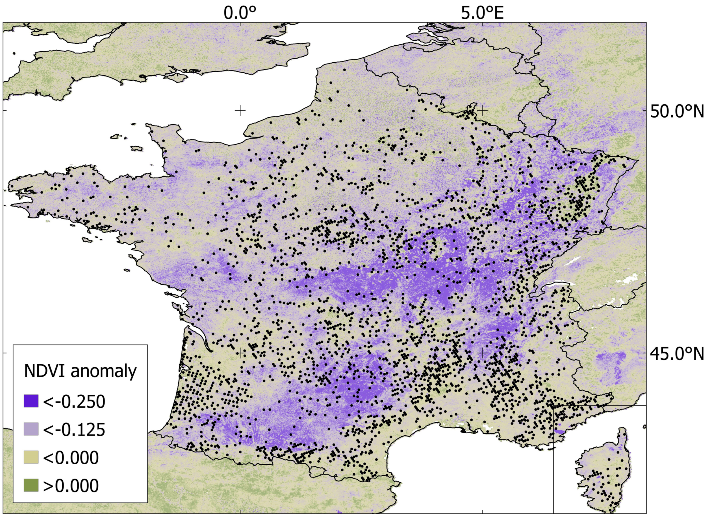

Figure 1: A, Map of the studied region (Metropolitan France) showing the August 2003 NDVI anomaly (in absolute values, ranged from -1 to 1). Values of NDVI are linearly scaled. B, Map of the studied region (Mainland France) showing the French Forest Inventory Plots of the fourteen studied species overlaid by NDVI loss.

NDVI images were extracted from the MODIS satellite after being calibrated and treated by the NASA/Goddard Space Flighter Center's Global Inventory Modelling and Mapping

Studies (GIMMS) (source: http://glam1.gsfc.nasa.gov). The NDVI values of this database ranged between 0 and 250, and they had a spatial resolution of 0.0025 degrees and a time resolution of eight days; negative values – probably due to rock, snow and water, for instance – were excluded. We linearly converted the NDVI pixels following MODIS specifications (source: https: //gimms.gsfc.nasa.gov/MODIS/README.txt), to a range of between 0 and 1. We used data from the Terra Modis products covering Metropolitan France from 2000 to 2003. We calculated the August NDVI mean for each pixel of the study area for the three years prior to the drought (2000, 2001 and 2002) and for 2003. In each pixel, we used the difference between the historical NDVI value and the 2003 NDVI value as a proxy for drought effects (Lloret et al., 2007) (Fig. 1A), here basically die-off intensity – loss of green coverage or mortality. NDVI can easily be affected by the timing of vegetation senescence, i.e., the yearly phenological cycle, and also by the specific composition of the plant cover (Soudani et al., 2012). Therefore, in order to avoid yearly NDVI dynamics, we excluded NDVI anomaly values for the autumn period, starting in September, after the hot drought episode, because in some deciduous tree populations leaf fall can begin in the early autumn months, potentially interfering with NDVI values. Thus, we used the anomaly of a single month in which the hot-drought episode ended (August), corresponding to the peak of the dry season, when herbaceous vegetation has probably decayed, causing minimal interference to the NDVI scores (Lloret et al., 2007). NDVI variability associated with species composition was minimized by considering pixels with a dominant forest species, virtually corresponding to monospecific stands, allowing for the analysis of species-specific responses. We used Terra Modis satellite imagery instead of other NDVI imagery sources with longer historical records because Terra Modis uses a resolution that correctly matches the studied forest patches in which the French inventory plots were located (0.0025 degrees at 46^{o} N longitude is equivalent to 200 m).

Species Distribution Modelling (SDM)

We used SDMs of each studied species to build species' climatic suitability indices. The EU-Forest occurrence dataset (Mauri, Strona, & San-Miguel-Ayanz, 2017) was used to build SDMs for each studied species. This dataset of occurrences is based on almost 250,000 plots of National Forest Inventories of the main countries of Europe. The use of the EU-Forest dataset allowed us to include data on absence in our models, in contrast with other data sources, such as the Global Biodiversity Information Facility (GBIF), which only provide data on presence.

We obtained climatic data from the CHELSA climate world database (Karger et al., 2017), version 1.2, with 1 km^2 raster resolution for every year in the period 1979-2003. The raster layers of monthly precipitation and mean, maximum and minimum temperatures of this period were used to calculated 19 yearly standard bioclimatic variable raster files (Table S2, supplementary material), using the dismo R package (Hijmans, Phillips, Leathwick, & Elith, 2011). To calibrate the model, we used the mean of the six least correlated bioclimatic variables in all the EU-Forest occurrences, for the 1979-2002 reference period (isothermality, temperature seasonality, mean temperature of wettest quarter, mean temperature of driest quarter, precipitation seasonality and precipitation of wettest quarter), after testing the collinearity between the nineteen explored bioclimatic variables by means the Variation Inflation Factor (VIF) (Marquaridt 1970).

Species distribution model algorithm used to calculate species' climatic suitability was Boosted Regression Tree (BRT), using the Gbm package 2.1.3 (Ridgeway, 2007). General Additive Models (GAM), GLM and BRT built with bioclimatic variables can have highly correlated outputs (Pérez Navarro et al., 2018), and among them BRT is recognized as the best in terms of accuracy and adjustment (Jane Elith & Graham, 2009).

Nevertheless, we ran GAM and BRT, which are the two algorithms providing the highest accuracy robustness when working with large presence-absence datasets (J. Elith, Leathwick, & Hastie, 2008). We finally selected BRT for its better performance, compared to GAM, in terms of the AUC (Area Under receiver operating characteristic Curve, Hanley and McNeil 1982) and correlation (See supplementary material, Table S1).

We built the species distribution model following recommendations from the literature: number of real absences equivalent to the number of species occurrences by randomly choosing from the total absences (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012; Pérez Navarro et al., 2018); tree complexity of 5 for those species with more than 250 occurrences and of 3 for those species with less than 250 occurrences. The learning rate of 0.005 was chosen because it made it possible to achieve at least 1,000 trees in each case (J. Elith et al., 2008).

The calibration of the model was repeated three times using k-fold cross-validation with three different training and test datasets. Model evaluation and final model output were based on the average of the three models (Pearson et al., 2006; Thuiller et al., 2004). The evaluation of the final models was based on the area under curve (AUC; Hanley and McNeil 1982) and deviance explained as R squared coefficient (see Table S1 in Supplementary material), using "caret R package" (Kuhn & others, 2008).

Each built SDM was projected to the average historical conditions (1979-2002) of each selected French Forest Inventory plot in order to calculate the HCS of each plot. SDMs were also projected onto each single year of the 1979-2002 period. We then calculated the standard deviations of these projections (HCS-SD) in order to estimate the variability of the species climatic suitability in each plot in the French Forest Inventory (Lloret & Kitzberger, 2018). We also projected each species' model on to the 2003 climatic conditions found on each plot to obtain the event climatic suitability (ECS), which shows the degree of unfavourability of climatic conditions a particular moment (Lloret & Kitzberger, 2018; Pérez Navarro et al., 2018).

Die-off modelling

First, we built a generalized mixed model (GLMM) with normal distribution to assess the general relationship between forest die-off and climatic suitability. We used the lme4 R package (Bates, Mächler, Bolker, & Walker, 2015), in which we included mean August NDVI loss as a dependent variable. The independent variables in the model were climatic suitability estimators (ECS, HCS, HCS-SD), the bivariate interactions between these bioclimatic variables and two climatic variables (Mean Annual Temperature (T) and Mean Annual Precipitation (P)) as fixed effects, and species as a random effect. We included these climatic variables to test whether populations distributed in warmer or wetter regions were more or less affected during the climatic event. Moreover, we included the interaction of T and P with HCS in order to analyse which edges of the climatic range were more affected during the extreme event (i.e., the wettest or the driest, or the warmest or the coldest edge). Each replicate was a French National Inventory plot. The final model was selected according to stepwise procedure based on the Akaike Information Criterion (AIC), using the MuMIn R package (Barton, 2018).

Second, for each species we used a Generalized Linear Model (GLM) with normal distribution to evaluate the relationship between forest die-off (estimated as a NDVI loss) and climatic suitability estimators (HCS, ECS, HCS-SD) and forest structure (BA, tree density). We made species-specific modelling to increase the sensitivity of the models, since the species could have different distributions patterns and the significant variables across models may be different. All possible bivariate interactions were also included in the models. Longitude and latitude coordinates were also incorporated to take into account geographical trends and to elucidate whether die-off vulnerability increases in a species's northern or southern distribution limits. The final models were selected according to stepwise procedure based on the Akaike Information Criterion (AIC), using the MuMIn R package (Barton, 2018). The significance of the drop in climatic suitability between historical conditions (HCS) and event climatic conditions (ECS) were tested by the Kruskal–Wallis test (Kruskal & Wallis, 1952). All the statistical analyses were carried out with the R version 3.4.0 (R Core Team 2017).

Table 1. Species description, including leaf seasonality, chorological distribution and number of French National Inventory plots used in the GLM.

Specie	Vernacular Name	Family	Leaf seasonality	Chorology	Plots
Abies alba	Silver fir	*Pinaceae*	Evergreen	Euro-Siberian	185
Betula pendula	Silver birch	*Betulaceae*	Deciduous	Euro-Siberian	44
Castanea sativa	Sweet chestnut	*Fagaceae*	Deciduous	Sub-Mediterranean	171
Fagus sylvatica	European beech	*Fagaceae*	Deciduous	Euro-Siberian	334
Fraxinus excelsior	European ash	*Oleaceae*	Deciduous	Euro-Siberian	63
Picea abies	Norway spruce	*Pinaceae*	Evergreen	Boreo-Alpine	201
Pinus halepensis	Aleppo pine	*Pinaceae*	Evergreen	Mediterranean	67
Pinus nigra	Austrian pine	*Pinaceae*	Evergreen	Sub-Mediterranean	51
Pinus pinaster	Maritime pine	*Pinaceae*	Evergreen	Sub-Mediterranean	274
Pinus sylvestris	Scots pine	*Pinaceae*	Evergreen	Euro-Siberian	287
Quercus ilex	Holm oak	*Fagaceae*	Evergreen	Mediterranean	95
Quercus petraea	Sessile oak	*Fagaceae*	Deciduous	Euro-Siberian	457
Quercus pubescens	Downy oak	*Fagaceae*	Marcescent	Sub-Mediterranean	291
Quercus robur	Common oak	*Fagaceae*	Deciduous	Euro-Siberian	423

Results

General analysis of forest die-off

The best fitted model, according to AIC, was a GLMM built with HCS-SD, mean annual temperature (T), mean annual precipitation (P), HCS, ECS and the following interactions: HCS:ECS, HCS:T and HCS:P. There was a negative relationship between both HCS-SD and mean annual temperature and forest die-off (Figure 2 left, Table 2). Meanwhile, HCS:ECS emerged as a significant negative interaction (Fig. 2).

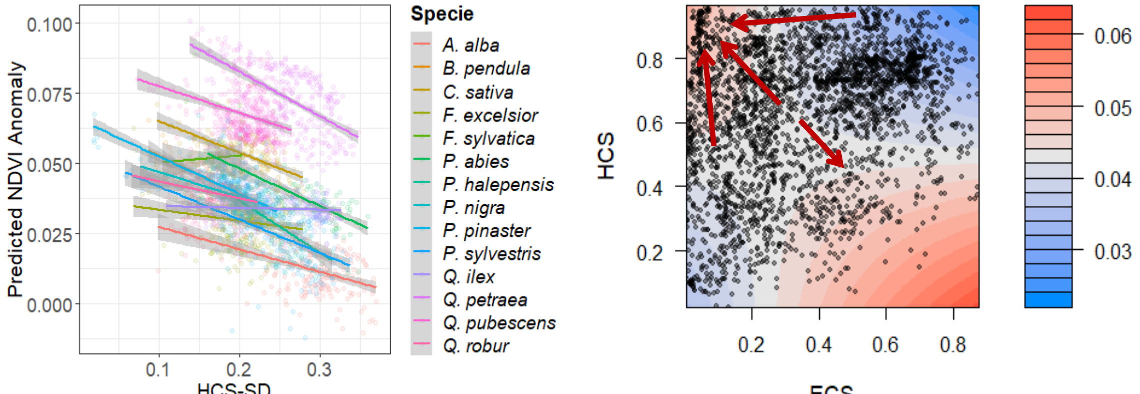

Figure 2. HCS-SD effect on NDVI loss according to GLMM considering all species (left). Die-off at different combination of HCS and ECS during the 2003 summer (reader colour means more die-off likelihood) (right). Dots indicate the situation of inventory plots in the bivariate space determined by ECS and HCS. Arrows are indicative of the direction of the HCS:ECS interaction; they approximately correspond to the higher slope with high density of plots.

Table 2. Results of GLMM considering all species, with NDVI loss (August 2003) as dependent variable and ECS, HCS-SD, HCS, T and P as explanatory variables.

r^2c = 0.09 N = 2,943	*Estimate*	*p-value*
Intercept	-0.0420	0.2429
HCS	0.0576	0.2815
ECS	0.0327	0.0748
HCS-SD	-0.1042	0.0016
HCS:ECS	-0.0665	0.0133
T	0.0076	0.0003
P	0.00001	0.5053
HCS:T	-0.0039	0.1883
HCS:P	0.000004	0.8768

Species-specific die-off analyses

At species level, we found significant correspondences between die-off (NDVI loss) and some of the climatic suitability indices and plot structure variables in twelve of the fourteen studied species. We failed to obtain any significant bioclimatic or structural predictor in the *Pinus sylvestris* and *Picea abies* models (Table 3).

	Abies alba		***Betula pendula***		***Fagus sylvatica***		***Quercus robur***	
	Estimate	*p*	Estimate	*p*	Estimate	*p*	Estimate	*p*
Intercept	0.0249	0.591	1.5966	<0.0001	0.2410	0.0013	0.6306	<0.0001
ECS	-0.2874	0.015	-4.7574	0.0241	-0.2990	0.0236	-0.2210	0.0119
HCS-SD	-0.0421	0.772	-9.8489	<0.0001	-0.1392	0.4734	0.1193	0.4297
N	1.31e-05	0.0865	-	-	1.18e-05	0.0258	-	-

ECS:HCS-SD	0.8548	0.029	30.7873	<0.0001	1.2040	0.0433	-	-
ECS:BA	-	-	0.0263	0.0243	0.0024	0.0373	-	-
BA	-	-	-0.0096	0.0241	-0.0008	0.0819	0.0004	0.1406
X	-	-	-	-	-0.0027	0.0403	0.0017	0.3634
Y	-	-	-	-	-0.0036	0.0193	-0.0119	<0.0001
HCS	-	-	-	-	-	-	-0.0666	0.1967
HCS:ECS	-	-	-	-	-	-	0.3350	0.0141
r^2	*0.07*		*0.38*		*0.10*		*0.08*	

Table 3. Results of final GLMs for the different forest species, considering NDVI loss (August 2003) as dependent variable and SDM outputs (ECS, HCS, HCS-SD), stem density (N), basal area (BA), UTM X and Y coordinates as explicative variables. Interactions between variables are also included.

HCS was positively related to NDVI loss – greater die-off – in plots dominated by *Pinus nigra*, *Pinus pinaster*, *Quercus ilex* and *Castanea sativa* (Table 3 extended). Lower ECS values were significantly related to greater die-off in plots dominated by *Abies alba, Betula pendula, Fagus sylvatica* and *Quercus robur* (Table 3). We found a positive interaction between HCS and ECS in plots dominated by *Q. robur* (Table 3), showing that the positive influence of HCS on die-off was greater in populations with high ECS (Fig. 3). In contrast, in plots dominated by *P. nigra*, a significant negative interaction between HCS and ECS was found (Table 3); it was determined by higher die-off with a combined effect of high HCS and low ECS (Fig. 3). In plots dominated by *P. pinaster, Pinus halepensis, Quercus pubescens* and *B. pendula,* lower HCS-SD was significantly related to greater die-off.

	Castanea sativa		***Pinus nigra***		***Quercus ilex***		***Pinus pinaster***		***Quercus pubescens***	
	Estimate	Pr (>t)	Estimate	Pr (>t)	Estimate	Pr (>t)	Estimate	Pr (>t)	Estimate	Pr (>t)
Intercept	-0.2636	0.0303	0.0014	0.9646	- 0.3441	0.0221	0.0693	0.0891	0.3200	0.0022
HCS-SD	1.5603	0.0120	-	-	1.8399	0.0047	-0.5447	0.0137	-0.9991	0.0347
HCS	0.5799	0.0015	0.1226	0.0497	0.4833	0.0216	0.1302	0.0102	-0.1926	0.1097
BA	0.0005	0.1354	-	-	-0.0005	0.0286	-0.0005	0.6951	-	-
N	-	-	3.06e-05	0.2403	-	-	-	-	-	-
ECS	-0.0599	0.0927	0.1378	0.1189	-	-	0.0341	0.0922	0.1496	0.1689
HCS:HCS-SD	-2.8319	0.0010	-	-	-2.4586	0.0054	-	-	-0.7149	0.0779
X	-	-	-	-	0.0034	0.0174	-	-	-	-
ECS:N	-	-	-7.89e-05	0.0928	-	-	-	-	-	-
ECS:HCS	-	-	-0.3909	0.0316	-	-	-	-	0.8679	0.1056
HCS:BA	-	-	-	-	-	-	- 0.0034	0.0198	-	-

HCS-SD:BA	-	-	-	-	-	-	0.0122	0.0724	-	-
***r*²**	0.12		0.24		0.23		0.09		0.14	

Table 3. Extended.

Conversely, in plots dominated by *Q. ilex* and *C. sativa*, higher HCS-SD was significantly related to greater die-off (Table 3). In these plots, HCS-SD also showed a significant negative interaction with HCS (Table 3), due in *Q. ilex* to greater die-off with low HCS and high HCS-SD values, and in *C. sativa* to more die-off in plots with low HCS-SD and high HCS (Fig. 3). Finally, there was a positive interaction between ECS and HCS-SD in *A. alba, B. pendula* and *F. sylvatica* (Table 3), with greater die-off in plots with a high variability of past climatic suitability, even in conditions of mild unsuitable conditions during the episode (high ECS); in the case of *B. pendula*, this vulnerability also occurs in plots with low climatic variability that experienced low values of ECS (Fig. 3).

Table 3. Extended.

	Pinus sylvestris		***Picea abies***		***Fraxinus excelsior***		***Quercus petraea***		***Pinus halpensis***	
	Estimate	*p*	Estimate	*p*	Estimate	*p*	Estimate	*p*	Estimate	*p*
Intercept	0.4019	0.0002	0.0310	<0.0001	0.0341	0.0104	0.5397	<0.0001	0.1611	0.0158
N	-	-	2.28e-06	0.6930	3.00e-06	0.0429	0.0005	0.0264	-	-
BA	-	-	-	-	-	-	1.28e-5	0.1096	-	-
HCS-SD	0.0834	0.2611	-	-	-	-	-	-	-0.5498	0.0378
X	-	-	-	-	-	-	0.0026	0.0538	-	-
Y	-	-	-0.0085	0.0003	-	-	-0.0107	<0.0001	-	-
HCS	-	-	-	-	-	-	-	-	-0.1397	0.1411
HCS:SD-HCS	-	-	-	-	-	-	-	-	0.6057	0.0768
***r*²**	0.05		0.06		0.07		0.08		0.07	

We observed a positive effect of tree density on the NDVI loss in plots dominated by *Fraxinus excelsior* and *Quercus petraea*. In contrast, in plots dominated by *B. pendula* and *Q. ilex*, basal area was negatively related to forest die-off (Table 3). In two of these species (*F. excelsior* and *Q. petraea*), only plot structure variables exhibited any significant effect on NDVI loss (Table 3).

We also found some significant interactions between structural parameters and bioclimatic variables. We found a positive interaction between ECS and basal area in plots dominated by *B. pendula* and *F. sylvatica* (Table 2). In these cases, the die-off was greater with the combination of a low basal area and low ECS (Fig. 3). In plots dominated by *P. pinaster* there was a negative interaction between HCS and BA, indicating a greater die-off under combined low HCS and a high basal area (Fig. 3).

Latitude and longitude (Y and X coordinates) were not significant in most of the species models. Otherwise, we observed a negative relationship between latitude and loss of NDVI in *F. sylvatica*, *Q. robur*, *Q. petraea*, *P. abies* and *P. halepensis* (Table 3), supporting a higher die-off in the southern limit of species distribution.

Discussion

The combination of climatic suitability derived from SDMs (HCS, ECS and HCS-SD) and mean annual temperature was able to partially explain regional die-off patterns across monospecific forests during the 2003 heatwave in Europe. This agrees with other studies that have used SDM to explain the effect of historical climatic conditions (Lloret and Kitzberger 2018, Perez Navarro et al. 2018), loss of climatic suitability (Lloret & Kitzberger, 2018; Sapes et al., 2017) or the past stability of climatic conditions (Lloret & Kitzberger, 2018) on forest die-off vulnerability at local and regional scales. Climatic Suitability during the extreme hot-drought (ECS) decreased in all cases with respect to historical climatic suitability (HCS), except for *P. sylvestris* (Table S1).

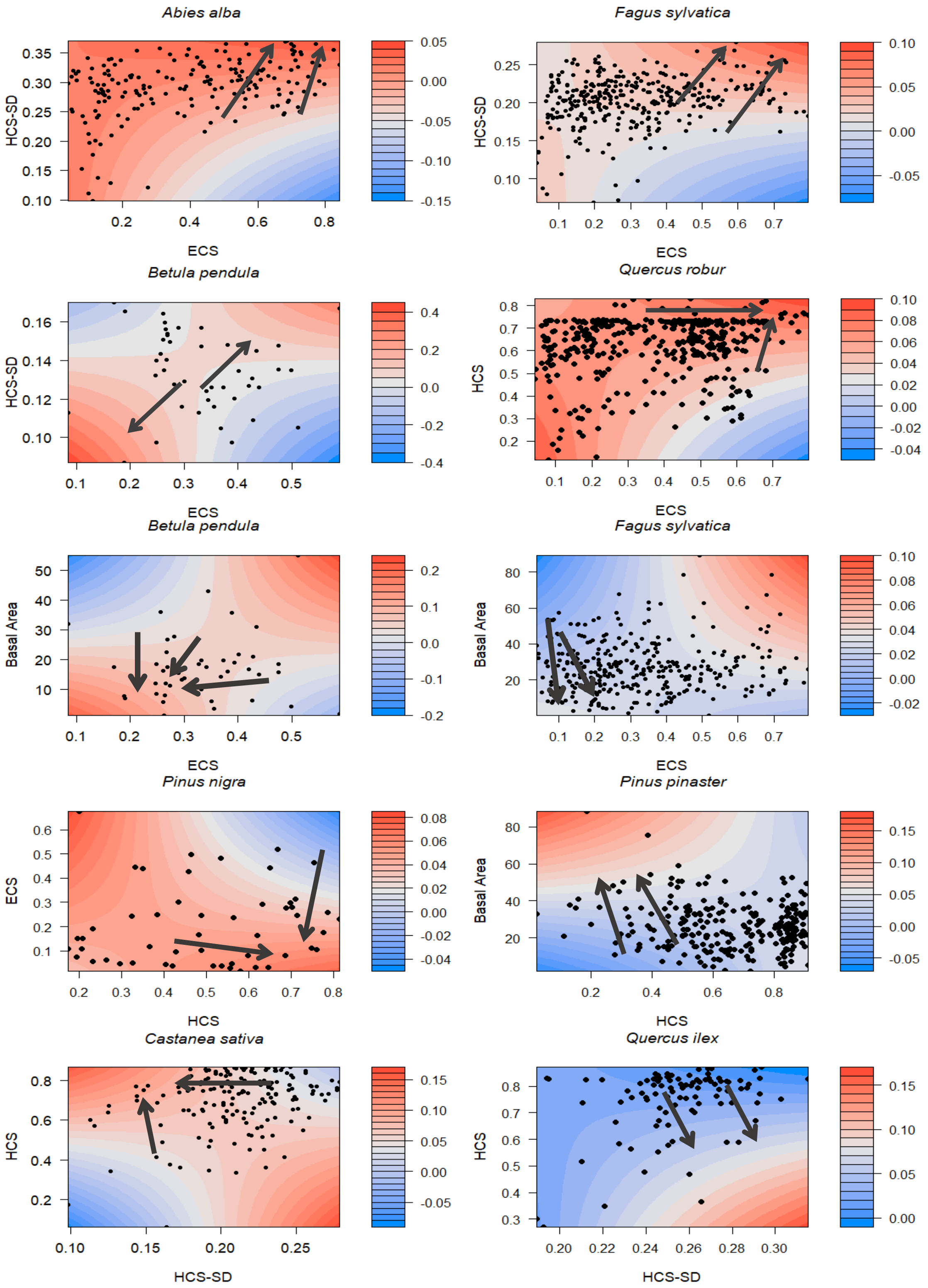

Figure 3. Interactions between explanatory variables (SDM outputs and basal area) obtained in GLMs of different species, illustrated by contour graphs of the 2003 summer loss. Redder surfaces indicate more NDVI loss and dots indicate the situation of French inventory plots in the variables space. Arrows are indicative of the direction of the interaction; they correspond to the higher slope with high density of plots. The graphs were obtained after fitting the GLM for each species (see Material and methods).

These results demonstrate that climatic variables associated with water deficit play an important role in forest die-off across a regional scale, as in other studies (e.g., Clifford et al. 2013, Lloret and Kitzberger 2018). They also support the hypothesis that SDM outputs could be used as a tool for standardizing the magnitude of a given extreme climatic event to explain vegetation responses across geographical gradients.

Historical climatic variability (HCS-SD) and the interaction of HCS and ECS proved to be significant for explaining forest die-off across species. Mean annual temperature also has a positive significant effect on forest die-off, showing that populations living under warmer conditions and species with warmer distributions could be more vulnerable to the episode. This warm-edge vulnerability is not directly related to the vulnerability of populations living near their limit of tolerance since no interaction was found between HCS and T. From this general viewpoint, the variability in historic climatic suitability emerged as a relevant variable to explain forest die-off, demonstrating that plots with more historic stable conditions showed more die-off in the face of a sudden pulse of variability, corresponding to extreme water deficit conditions. Interestingly, we also documented higher vulnerability to die-off in populations that experienced a greater magnitude of the episode when located in historically high suitable conditions, indicating that even populations living under regular suitable climatic conditions may be vulnerable to extreme pulses of climate variability, such as heat waves and droughts (Lloret & Kitzberger, 2018). So, acclimatization to past suitable conditions should increase vulnerability to extreme climatic episodes (Clark et al., 2016). Alternatively, the combinations of low HCS and high ECS (low magnitude of the episode) also tended to induce die-off, also highlighting the vulnerability of populations living at the edge of their climatic envelope when experiencing just a mild pulse of climatic adversity.

From these general trends, species-specific patterns emerged elsewhere. In four Euro-Siberian species, typical of wet, temperate to moderately cold climates *(A. alba, B. pendula, F. sylvatica* and *Q. robur)*, die-off was specially explained by low ECS values, revealing the vulnerability of species used to living in moist conditions when confronting episodic extreme hot and drought conditions. This result agrees with other studies that have reported sensitivity of these species to high levels of drought and temperature (Castagneri, Nola, Motta, & Carrer, 2014; Cavin & Jump, 2017; Kharuk, Ranson, Oskorbin, Im, & Dvinskaya, 2013; Linares & Camarero, 2012). Indeed, species with high water demand tend to be less drought-resistant, especially in moist and damper sites (Clark et al., 2016). This vulnerability could be related to ecological traits such as high-leaf area, low wood density (Greenwood et al., 2017) and poor hydraulic performance (P50) (William R. L. Anderegg et al., 2016).

Interestingly, Sub-Mediterranean species such as *P. pinaster*, *P. nigra*, *C. sativa* and the Mediterranean *Q. ilex* exhibited greater die-off in populations that have historically experienced better climatic conditions (higher HCS). In the case of *P. nigra*, this trend was exacerbated by the combination with higher stressing conditions during the event (low ECS). In *P. pinaster* populations, the trend was enhanced by low variability in historical climatic conditions (low HCS-SD), suggesting an acclimatization to suitable regular conditions. Several hypotheses can explain the vulnerability of populations living under constant conditions closer to a species's optimum climate: (1) populations located in mesic sites may develop high leaf area and high basal area due to acclimatization, which makes them especially vulnerable to a large drop in moisture availability (Clark et al., 2016; Jump et al., 2017); (2) populations located in climatically unsuitable areas usually live in sites where micro-local conditions such as soil characteristics and topography can buffer the effect of climatic anomalies at larger spatial scales (Lévesque, Rigling, Bugmann, Weber, & Brang, 2014); (3) populations from less suitable regions may have developed local adaptations enhancing resistance to more stressful climate (Rose et al., 2009).

Other species (*A. alba, B. pendula, F. sylvatica, P. halepensis, Q. petraea, Q. pubescens*) do not show any clear pattern of vulnerability in relation to the historical climatic suitability of the sites where their populations live. In fact, in these species, populations living near their tolerance limits or under very suitable conditions were equally prone to die-off during the extreme climatic event. Vulnerability to extreme episodes would probably be derived from processes operating at population level. In addition to local climatic conditions, historical legacies, such as management practices (Vilà-Cabrera et al., 2011), colonization history, genetic background (Valladares et al., 2014) and topographic and soil conditions (Galiano, Martínez-Vilalta, & Lloret, 2010; Lloret, Siscart, & Dalmases, 2004) have been reported as being important modulators of vulnerability to die-off.

We found a significant negative relationship between HCS-SD and green canopy loss across species at a regional scale (Table 2, Fig. 2). The mechanism involved in this vulnerability could be related to an acclimatization process under relatively stable conditions that provokes a great dependence on a regular water supply (Clark et al., 2016). This also implies that populations of those species living in highly variable climatic environments (high HCS-SD) are less vulnerable to die-off, maybe due to local adaptation to high climatic variability (Valladares et al., 2014). This pattern is visible in different species such as *B. pendula, P. halepensis*, *P. pinaster* and *Q. pubescens*. Furthermore, higher stable conditions (low HCS-SD) reinforce the vulnerability to die-off near the optimum climate or during the event, as seen in populations of *C. sativa* and *B. pendula* (Fig. 3).

In contrast, in populations of *Q. ilex*, die-off was enhanced by greater HCS-SD and low HCS, suggesting the existence of mechanisms of the so-called legacy effect involving cumulative damage, such as xylem embolism and carbon reserves depletions (Waldboth & Oberhuber, 2009). More specifically, the inability to recover carbon reserves after recurrent suitability changes can be higher in populations located in historically poor suitable conditions (Lloret et al., 2018). Vulnerability to die-off due to legacy effect also occurred in populations of *A. alba*, *F. sylvatica* and *B. pendula* that experienced mild drought during the episode (low ECS) (Fig. 3). These results support the hypothesis that previous extreme droughts could increase vulnerability to die-off, even in highly resilient species like *Q. ilex* (Lucía Galiano, Martínez-Vilalta, Sabaté, & Lloret, 2012; Lloret et al., 2004) or during non-extreme drought episodes. However, the lack of a positive relationship between historical climatic variability and die-off in many species suggests that vulnerability to drought due to this legacy effect probably persists for only a few years after a drought episode, since the recovery of carbon reserves and new tissues can be quite fast (Galiano et al., 2012).

In accordance with other studies (Bottero et al., 2017; L. Galiano et al., 2010; Jump et al., 2017; Vilà-Cabrera, Martínez-Vilalta, Galiano, & Retana, 2013), we also observed a positive significant correspondence between green canopy loss and plot density in species such as *F. excelsior* and *Q. petraea* (Table 3). This relationship is explained by greater competition for water in denser plots (Bottero et al., 2017). In the case of *P. pinaster*, a high basal area increased vulnerability in those plots that historically experienced poor suitable conditions (Fig. 3), i.e., those that were likely to be more water-limited (Clark et al., 2016; Young et al., 2017).

Conversely, basal area or plot density did not enhance forest die-off in other species. Furthermore, on *Q. ilex, P. pinaster* and *B. pendula* plots, die-off was greater on plots with a low basal area. In fact, a low basal area would represent less competition, but it may also indicate a site with a poor-quality habitat. So, sites that are less suitable due to low soil quality (e.g., rocky or thinner soils) could maintain a lower basal area (Meyer, North, Gray, & Zald, 2007) while being particularly vulnerable to episodic water deficit. Accordingly, the positive interaction between basal area and ECS observed on *B. pendula* and *F. sylvatica* plots would indicate that vulnerability to die-off from strong drought in these species was greater on plots located in poor suitable conditions. Finally, die-off intensity in *P. abies* and *P. sylvestris* across all the regional gradient was not explained by either bioclimatic or structural variables, although some local studies have shown the contribution of forest structure to drought-induced die-off in *P. sylvestris* (Galiano et al., 2010; Rigling et al., 2013; Vilà-Cabrera et al., 2013). Apart from species-specific responses to climate across the region, the absence of this relationship may reflect some limitations in SDMs when characterizing the suitability of a tree population since they generally disregard intra-specific genetic variability, phenotypic plasticity, biotic interactions, dispersal constraints or past management (Franklin et al., 2013). They also assume that species' response to bioclimatic variables is homogenous across all the species' range (Benito Garzón, Alía, Robson, & Zavala, 2011). *Pinus sylvestris*, with a wide range of distribution and high intra-specific genetic variability (Matías & Jump, 2012; Rehfeldt et al., 2002), could be poorly characterized with the use of SDM, especially if local adaptions and genetic plasticity are not considered (Benito Garzón et al., 2011). Meanwhile, the distribution of *P. abies* has been substantially modified by management practices (Hansen & Spiecker, 2005) and their SDMs could be skewed by, for instance, artificial plantations that could be installed in unsuitable locations.

Nevertheless, this study shows that SDM outputs interpreted as climatic suitability indices are related to climate-induced forest die-off following certain extreme climatic events across regional scales. This approach may not be so effective to explain patterns of tree growth over longer periods of time as climatic variability may be buffered over the lifespan of long-living species (van der Maaten et al., 2017)). More specifically, our results show that ECS is a useful index for standardizing the magnitude of extreme climatic events and enabling comparisons across landscapes for distinct forest species. The use of SDMs also makes it possible to evaluate interactions between past and present climatic conditions and thus assess the existence of reinforcing effects and the vulnerability of niche-core and niche-edge populations. We also demonstrated that, although vulnerability to die-off is species-specific, some trends related to species' chorology can be found (i.e., Euro-Siberian vs. Mediterranean and Sub-Mediterranean species). However, our study focused on monospecific populations, so further research applying this methodology to mixed forests is required to scale up the use of climatic suitability indices to community level.

Acknowledgements

We thank the CHELSA climate database for making their data freely available online. We also thank the Institut Géographique National (IGN) for making the forest inventory data freely available. This study was funded by the Spanish Ministry of Education through a doctoral grant nº FPU15/04593, by the Spanish Ministry of Economy and Competitiveness through the BIOCLIM project nº CGL2015-67419-R, and by an AGAUR 2017 SGR 1001 grant (Generalitat de Catalunya). We also thank two anonymous reviewers for their useful comments and improvements in the final version of this paper.

References

Abeli, T., Gentili, R., Mondoni, A., Orsenigo, S., & Rossi, G. (2014). Effects of marginality on plant population performance. *Journal of Biogeography*, *41*(2), 239–249. https://doi.org/10.1111/jbi.12215

Adams, H. R., Barnard, H. R., & Loomis, A. K. (2014). Topography alters tree growth-climate relationships in a semi-arid forested catchment. *Ecosphere*, *5*(11), 1–16. https://doi.org/10.1890/ES14-00296.1

Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, *6*(8), 1–55. https://doi.org/10.1890/ES15-00203.1

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., … Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, *259*(4), 660–684. https://doi.org/10.1016/j.foreco.2009.09.001

Anderegg, W. R. L., Smith, D. D., Berry, J. A., Anderegg, L. D. L., Field, C. B., & Sperry, J. S. (2011). The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *Proceedings of the National Academy of Sciences*, *109*(1), 233–237. https://doi.org/10.1073/pnas.1107891109

Anderegg, William R. L., Klein, T., Bartlett, M., Sack, L., Pellegrini, A. F. A., Choat, B., & Jansen, S. (2016). Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proceedings of the National Academy of Sciences*, *113*(18), 5024–5029. https://doi.org/10.1073/pnas.1525678113

Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: How, where and how many? *Methods in Ecology and Evolution*, *3*(2), 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x

Barton, K. (2018). MuMIn: Multi-Model Inference. Retrieved from https://cran.r-project.org/package=MuMIn

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using {lme4}. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Benito Garzón, M., Alía, R., Robson, T. M., & Zavala, M. A. (2011). Intra-specific variability and plasticity influence potential tree species distributions under climate change. *Global Ecology and Biogeography*, *20*(5), 766–778. https://doi.org/10.1111/j.1466-8238.2010.00646.x

Bigler, C., Gavin, D. G., Gunning, C., & Veblen, T. T. (2007). Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains. *Oikos*, *116*(12), 1983–1994. https://doi.org/10.1111/j.2007.0030-1299.16034.x

Bottero, A., D'Amato, A. W., Palik, B. J., Bradford, J. B., Fraver, S., Battaglia, M. A., & Asherin, L. A. (2017). Density-dependent vulnerability of forest ecosystems to drought. *Journal of Applied Ecology*, *54*(6), 1605–1614. https://doi.org/10.1111/1365-2664.12847

Bréda, N., Huc, R., Granier, A., & Dreyer, E. (2006). Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, *63*(6), 625–644. https://doi.org/10.1051/forest:2006042

Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Balice, R. G., … Meyer, C. W. (2005). Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences*, *102*(42), 15144–15148. https://doi.org/10.1073/pnas.0505734102

Camarero, J. J., Franquesa, M., & Sangüesa-Barreda, G. (2015). Timing of drought triggers distinct growth responses in holm oak: Implications to predict warming-induced forest defoliation and growth decline. *Forests*, *6*(5), 1576–1597. https://doi.org/10.3390/f6051576

Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sanchez, G., & Penuelas, J. (2011). Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Sciences*, *108*(4), 1474–1478. https://doi.org/10.1073/pnas.1010070108

Castagneri, D., Nola, P., Motta, R., & Carrer, M. (2014). Summer climate variability over the last 250years differently affected tree species radial growth in a mesic Fagus-Abies-Picea old-growth forest. *Forest Ecology and Management*, *320*, 21–29. https://doi.org/10.1016/j.foreco.2014.02.023

Cavin, L., & Jump, A. S. (2017). Highest drought sensitivity and lowest resistance to growth suppression are found in the range core of the tree Fagus sylvatica L. not the equatorial range edge. *Global Change Biology*, *23*(1), 362–379. https://doi.org/10.1111/gcb.13366

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., … Valentini, R. (2005). Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, *437*(7058), 529–533. https://doi.org/10.1038/nature03972

Clark, J. S., Zimmermann, N. E., Schwartz, M. W., Matthews, S., Jackson, S. T., Allen, C. D., … Davis, F. W. (2016). The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. *Global Change Biology*, *22*(7), 2329–2352. https://doi.org/10.1111/gcb.13160

Clifford, M. J., Royer, P. D., Cobb, N. S., Breshears, D. D., & Ford, P. L. (2013). Precipitation thresholds and drought-induced tree die-off: Insights from patterns of Pinus edulis mortality along an environmental stress gradient. *New Phytologist*, *200*(2), 413–421. https://doi.org/10.1111/nph.12362

Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, *77*(4), 802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x

Elith, Jane, & Graham, C. H. (2009). Do they? How do they? WHY do they differ? on finding reasons for differing performances of species distribution models. *Ecography*, *32*(1), 66–77. https://doi.org/10.1111/j.1600-0587.2008.05505.x

Faber-Langendoen, D., & Tester, J. R. (2006). Oak Mortality in Sand Savannas Following Drought in East-Central Minnesota. *Bulletin of the Torrey Botanical Club*, *120*(3), 248. https://doi.org/10.2307/2996989

Farrell, E. P., Führer, E., Ryan, D., Andersson, F., Hüttl, R., & Piussi, P. (2000). European forest ecosystems: Building the future on the legacy of the past. *Forest Ecology and Management*, *132*(1), 5–20. https://doi.org/10.1016/S0378-1127(00)00375-3

Franklin, J., Davis, F. W., Ikegami, M., Syphard, A. D., Flint, L. E., Flint, A. L., & Hannah, L. (2013). Modeling plant species distributions under future climates: How fine scale do climate projections need to be? *Global Change Biology*, *19*(2), 473–483. https://doi.org/10.1111/gcb.12051

Galiano, L., Martínez-Vilalta, J., & Lloret, F. (2010). Drought-Induced Multifactor Decline of Scots Pine in the Pyrenees and Potential Vegetation Change by the Expansion of Co-occurring Oak Species. *Ecosystems*, *13*(7), 978–991. https://doi.org/10.1007/s10021-010-9368-8

Galiano, Lucía, Martínez-Vilalta, J., Sabaté, S., & Lloret, F. (2012). Determinants of drought effects on crown condition and their relationship with depletion of carbon reserves in a Mediterranean holm oak forest. *Tree Physiology*, *32*(4), 478–489. https://doi.org/10.1093/treephys/tps025

Graf Pannatier, E., Dobbertin, M., Heim, A., Schmitt, M., Thimonier, A., Waldner, P., & Frey, B. (2012). Response of carbon fluxes to the 2003 heat wave and drought in three mature forests in Switzerland. *Biogeochemistry*, *107*(1–3), 295–317. https://doi.org/10.1007/s10533-010-9554-y

Greenwood, S., Ruiz-Benito, P., Martínez-Vilalta, J., Lloret, F., Kitzberger, T., Allen, C. D., … Jump, A. S. (2017). Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology Letters*, *20*(4), 539–553. https://doi.org/10.1111/ele.12748

Hampe, A., & Petit, R. J. (2005). Conserving biodiversity under climate change: The rear edge matters. *Ecology Letters*, *8*(5), 461–467. https://doi.org/10.1111/j.1461-0248.2005.00739.x

Hanley, A. J., & McNeil, J. B. (1982). The Meaning and Use of the Area under a Receiver Operating Characteristic (ROC) Curve. *Radiology*, *143*, 29–36. https://doi.org/10.1148/radiology.143.1.7063747

Hansen, J., & Spiecker, H. (2005). Conversion of Norway spruce (Picea abies [L.] Karst.) forests in Europe. *Restoration of Boreal and Temperate Forests*, 339–347.

Hereş, A. M., Martínez-Vilalta, J., & López, B. C. (2012). Growth patterns in relation to drought-induced mortality at two Scots pine (Pinus sylvestris L.) sites in NE Iberian Peninsula. *Trees - Structure and Function*. https://doi.org/10.1007/s00468-011-0628-9

Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2011). Package "dismo". Species distribution modeling. R package version 0.7-17.

IPCC. (2013). *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press. https://doi.org/10.1017/CBO9781107415324

Jump, A. S., Ruiz-Benito, P., Greenwood, S., Allen, C. D., Kitzberger, T., Fensham, R., … Lloret, F. (2017). Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback. *Global Change Biology*, *23*(9), 3742–3757. https://doi.org/10.1111/gcb.13636

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., … Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*, 1–20. https://doi.org/10.1038/sdata.2017.122

Kaufmann, R. K., D'Arrigo, R. D., Paletta, L. F., Tian, H. Q., Jolly, W. M., & Myneni, R. B. (2008). Identifying climatic controls on ring width: The timing of correlations between tree rings and NDVI. *Earth Interactions*, *12*(14), 1–14. https://doi.org/10.1175/2008EI263.1

Kharuk, V. I., Ranson, K. J., Oskorbin, P. A., Im, S. T., & Dvinskaya, M. L. (2013). Forest Ecology and Management Climate induced birch mortality in Trans-Baikal lake region , Siberia. *Forest Ecology and Management*, *289*, 385–392. https://doi.org/10.1016/j.foreco.2012.10.024

Klos, R. J., Wang, G. G., Bauerle, W. L., Rieck, J. R., Applications, E., Klos, J., & James, R. (2009). Drought Impact on Forest Growth and Mortality in the Southeast USA : An Analysis Using Forest Health and Monitoring Data Published by : Ecological Society of America content in a trusted digital archive . We use information technology and tools to increas, *19*(3), 699–708.

Kruskal, W. H., & Wallis, W. A. (1952). Use of ranks in one-criterion variance analysis stable, *47*(260), 583–621.

Kuhn, M., & others. (2008). Building predictive models in R using the caret package. *Journal of Statistical Software*, *28*(5), 1–26.

Lévesque, M., Rigling, A., Bugmann, H., Weber, P., & Brang, P. (2014). Growth response of five co-occurring conifers to drought across a wide climatic gradient in Central Europe. *Agricultural and Forest Meteorology*, *197*, 1–12. https://doi.org/10.1016/j.agrformet.2014.06.001

Linares, J. C., & Camarero, J. J. (2012). Silver Fir Defoliation Likelihood Is Related to Negative Growth Trends and High Warming Sensitivity at Their Southernmost Distribution Limit. *ISRN Forestry*, *2012*, 1–8. https://doi.org/10.5402/2012/437690

Linares, J. C., Camarero, J. J., & Carreira, J. A. (2010). Competition modulates the adaptation capacity of forests to climatic stress: Insights from recent growth decline and death in relict stands of the Mediterranean fir Abies pinsapo. *Journal of Ecology*, *98*(3), 592–603. https://doi.org/10.1111/j.1365-2745.2010.01645.x

Lloret, F., Lobo, A., Estevan, H., Maisongrande, P., Vayreda, J., & Terradas, J. (2007). Woody plant richness and NDVI response to drought events in Catalonian (northeastern Spain) forests. *Ecology*, *88*(9), 2270–2279. https://doi.org/10.1890/06-1195.1

Lloret, Francisco, de la Riva, E. G., Pérez-Ramos, I. M., Marañón, T., Saura-Mas, S., Díaz-Delgado, R., & Villar, R. (2016). Climatic events inducing die-off in Mediterranean shrublands: are species' responses related to their functional traits? *Oecologia*, *180*(4), 961–973. https://doi.org/10.1007/s00442-016-3550-4

Lloret, Francisco, & Granzow-de la Cerda, I. (2013). Plant competition and facilitation after extreme drought episodes in Mediterranean shrubland: Does damage to vegetation cover trigger replacement by juniper woodland? *Journal of Vegetation Science*, *24*(6), 1020–1032. https://doi.org/10.1111/jvs.12030

Lloret, Francisco, & Kitzberger, T. (2018). Historical and event-based bioclimatic suitability predicts regional forest vulnerability to compound effects of severe drought and bark beetle infestation. *Global Change Biology*, (August 2017), 1952–1964. https://doi.org/10.1111/gcb.14039

Lloret, Francisco, Sapes, G., Rosas, T., Galiano, L., Saura-Mas, S., Sala, A., & Martínez-Vilalta, J. (2018). Non-structural carbohydrate dynamics associated with drought-induced die-off in woody species of a shrubland community. *Annals of Botany*, *121*(7), 1383–1396. https://doi.org/10.1093/aob/mcy039

Lloret, Francisco, Siscart, D., & Dalmases, C. (2004). Canopy recovery after drought dieback in holm-oak Mediterranean forests of Catalonia (NE Spain). *Global Change Biology*, *10*(12), 2092–2099. https://doi.org/10.1111/j.1365-2486.2004.00870.x

Luterbacher, J., Dietrich, D., Xoplaki, E., Grosjean, M., & Wanner, H. (2004). European Seasonal and Annual Temperature Variability, Trends, and Extremes since 1500. *Science*, *303*(5663), 1499–1503. https://doi.org/10.1126/science.1093877

Marquaridt, D. W. (1970). Generalized inverses, ridge regression, biased linear estimation, and nonlinear estimation. *Technometrics*, *12*(3), 591–612.

Martinez-Vilalta, J., Lloret, F., & Breshears, D. D. (2012). Drought-induced forest decline: causes, scope and implications. *Biology Letters*, *8*(5), 689–691. https://doi.org/10.1098/rsbl.2011.1059

Matías, L., & Jump, A. S. (2012). Interactions between growth, demography and biotic interactions in determining species range limits in a warming world: The case of Pinus sylvestris. *Forest Ecology and Management*, *282*, 10–22. https://doi.org/10.1016/j.foreco.2012.06.053

Mauri, A., Strona, G., & San-Miguel-Ayanz, J. (2017). EU-Forest, a high-resolution tree occurrence dataset for Europe. *Scientific Data*, *4*, 1–8. https://doi.org/10.1038/sdata.2016.123

Meyer, M. D., North, M. P., Gray, A. N., & Zald, H. S. J. (2007). Influence of soil thickness on stand characteristics in a Sierra Nevada mixed-conifer forest. *Plant and Soil*, *294*(1–2), 113–123. https://doi.org/10.1007/s11104-007-9235-3

Olarieta, J. R., Bargués Tobella, A., Rodríguez-Ochoa, R., & Antúnez, M. (2017). Soil control over the distribution of Mediterranean oak forests in the Montsec mountains (northeastern Spain). *Geoderma*, *291*, 11–20. https://doi.org/10.1016/j.geoderma.2016.12.019

Pearson, R. G., Thuiller, W., Araújo, M. B., Martinez-Meyer, E., Brotons, L., McClean, C., … Lees, D. C. (2006). Model-based uncertainty in species range prediction. *Journal of Biogeography*, *33*(10), 1704–1711. https://doi.org/10.1111/j.1365-2699.2006.01460.x

Pérez Navarro, M. Á., Sapes, G., Batllori, E., Serra-Diaz, J. M., Esteve, M. A., & Lloret, F. (2018). Climatic Suitability Derived from Species Distribution Models Captures Community Responses to an Extreme Drought Episode. *Ecosystems*, *22*(1), 77–90. https://doi.org/10.1007/s10021-018-0254-0

Pichler, P., & Oberhuber, W. (2007). Radial growth response of coniferous forest trees in an inner Alpine environment to heat-wave in 2003. *Forest Ecology and Management*, *242*(2–3), 688–699. https://doi.org/10.1016/j.foreco.2007.02.007

Rebetez, M., Mayer, H., & Dupont, O. (2006). Heat and drought 2003 in Europe: a climate synthesis. *Annals of Forest …*, *63*, 569–577. https://doi.org/10.1051/forest

Rehfeldt, G. E., Tchebakova, N. M., Parfenova, Y. I., Milyutin, L. I., Kuzmina, N. A., & Wykoff, W. R. (2002). Intraspecific responses to climate in Pinus sylvestris. *Global Change Biology*, *8*(9), 912–929. https://doi.org/10.1046/j.1365-2486.2002.00516.x

Ridgeway, G. (2007). Generalized Boosted Models: A guide to the gbm package. *Compute*, *1*(4), 1–12. https://doi.org/10.1111/j.1467-9752.1996.tb00390.x

Rigling, A., Bigler, C., Eilmann, B., Feldmeyer-Christe, E., Gimmi, U., Ginzler, C., … Dobbertin, M. (2013). Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. *Global Change Biology*, *19*(1), 229–240. https://doi.org/10.1111/gcb.12038

Rose, L., Leuschner, C., Köckemann, B., & Buschmann, H. (2009). Are marginal beech (Fagus sylvatica L.) provenances a source for drought tolerant ecotypes? *European Journal of Forest Research*, *128*(4), 335–343. https://doi.org/10.1007/s10342-009-0268-4

Sapes, G., Serra-Diaz, J. M., & Lloret, F. (2017). Species climatic niche explains drought-induced die-off in a Mediterranean woody community. *Ecosphere*, *8*(5). https://doi.org/10.1002/ecs2.1833

Sarris, D., Christodoulakis, D., & Körner, C. (2007). Recent decline in precipitation and tree growth in the eastern Mediterranean. *Global Change Biology*, *13*(6), 1187–1200. https://doi.org/10.1111/j.1365-2486.2007.01348.x

Serra-Diaz, J. M., Keenan, T. F., Ninyerola, M., Sabaté, S., Gracia, C., & Lloret, F. (2013). Geographical patterns of congruence and incongruence between correlative species distribution models and a process-based ecophysiological growth model. *Journal of Biogeography*, *40*(10), 1928–1938. https://doi.org/10.1111/jbi.12142

Sexton, J. P., McIntyre, P. J., Angert, A. L., & Rice, K. J. (2009). Evolution and Ecology of Species Range Limits. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 415–436. https://doi.org/10.1146/annurev.ecolsys.110308.120317

Soudani, K., Hmimina, G., Delpierre, N., Pontailler, J. Y., Aubinet, M., Bonal, D., … Dufrêne, E. (2012). Ground-based Network of NDVI measurements for tracking temporal dynamics of canopy structure and vegetation phenology in different biomes. *Remote Sensing of Environment*, *123*, 234–245. https://doi.org/10.1016/j.rse.2012.03.012

Steinkamp, J., & Hickler, T. (2015). Is drought-induced forest dieback globally increasing? *Journal of Ecology*, *103*(1), 31–43. https://doi.org/10.1111/1365-2745.12335

Tarpley, J. D., Schneider, S. R., & Money, R. L. (1984). Global Vegetation Indices from the NOAA-7 Meteorological Satellite. *Journal of Climate and Applied Meterology*. https://doi.org/10.1175/1520-0450(1984)023<0491:GVIFTN>2.0.CO;2

Thuiller, W., Araújo, M. B., Pearson, R. G., Whittaker, R. J., Brotons, L., & Lavorel, S. (2004). Uncertainty in predictions of extinction risk. *Nature*, *430*(6995), 34–34. https://doi.org/10.1038/nature02716

Thuiller, W., Münkemüller, T., Schiffers, K. H., Georges, D., Dullinger, S., Eckhart, V. M., … Schurr, F. M. (2014). Does probability of occurrence relate to population dynamics? *Ecography*, *37*(12), 1155–1166. https://doi.org/10.1111/ecog.00836

Valladares, F., Matesanz, S., Guilhaumon, F., Araújo, M. B., Balaguer, L., Benito-Garzón, M., … Zavala, M. A. (2014). The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters*, *17*(11), 1351–1364. https://doi.org/10.1111/ele.12348

van der Maaten, E., Hamann, A., van der Maaten-Theunissen, M., Bergsma, A., Hengeveld, G., van Lammeren, R., … Sterck, F. (2017). Species distribution models predict temporal but not spatial variation in forest growth. *Ecology and Evolution*, *7*(8), 2585–2594. https://doi.org/10.1002/ece3.2696

van Mantgem, P. J., Stephenson, N. L., Byrne, J. C., Daniels, L. D., Franklin, J. F., Fule, P. Z., … Veblen, T. T. (2009). Widespread Increase of Tree Mortality Rates in the Western United States. *Science*, *323*(5913), 521–524. https://doi.org/10.1126/science.1165000

Vilà-Cabrera, A., Martínez-Vilalta, J., Galiano, L., & Retana, J. (2013). Patterns of Forest Decline and Regeneration Across Scots Pine Populations. *Ecosystems*, *16*(2), 323–335. https://doi.org/10.1007/s10021-012-9615-2

Vilà-Cabrera, A., Martínez-Vilalta, J., Vayreda, J., & Retana, J. (2011). Structural and climatic determinants of demographic rates of Scots pine forests across the Iberian Peninsula Author (s): Albert Vilà-Cabrera , Jordi Martínez-Vilalta , Jordi Vayreda and Javier Retana Source : Ecological Applications , Vol . 21 , No . 4. *Ecological Applications*, *21*(4), 1162–1172. https://doi.org/10.1890/10-0647.1

Waldboth, M., & Oberhuber, W. (2009). Synergistic effect of drought and chestnut blight (Cryphonectria parasitica) on growth decline of European chestnut (Castanea sativa). *Forest Pathology*, *39*(1), 43–55. https://doi.org/10.1111/j.1439-0329.2008.00562.x

Western, A. W., Grayson, R. B., & Blöschl, G. (2002). Scaling of Soil Moisture: A Hydrologic Perspective. *Annual Review of Earth and Planetary Sciences*, *30*(1), 149–180. https://doi.org/10.1146/annurev.earth.30.091201.140434

Williams, A. P., Allen, C. D., Macalady, A. K., Griffin, D., Woodhouse, C. A., Meko, D. M., … Mcdowell, N. G. (2013). Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*, *3*(3), 292–297. https://doi.org/10.1038/nclimate1693

Young, D. J. N., Stevens, J. T., Earles, J. M., Moore, J., Ellis, A., Jirka, A. L., & Latimer, A. M. (2017). Long-term climate and competition explain forest mortality patterns under extreme drought. *Ecology Letters*, *20*(1), 78–86. https://doi.org/10.1111/ele.12711

Yuhas, A. N., & Scuderi, L. A. (2009). MODIS-derived NDVI characterisation of drought-induced evergreen dieoff in Western North America. *Geographical Research*, *47*(1), 34–45. https://doi.org/10.1111/j.1745-5871.2008.00557.x

Zaitchik, B. F., Macalady, A. K., Bonneau, L. R., & Smith, R. B. (2006). Europe's 2003 heat wave: A satellite view of impacts and land - Atmosphere feedbacks. *International Journal of Climatology*, *26*(6), 743–769. https://doi.org/10.1002/joc.1280