Widespread crown condition decline, food web disruption and amplified tree mortality with increased climate-change-type drought

Supporting Information

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Supporting Information. Materials and Methods

Data. To study defoliation responses in the Iberian Peninsula and Europe we gathered data from ICP-Forests Level 1 network for 1987-2008 (1). European Level 1 network covers most of European forested areas with 6000 monitoring plots. In each Level 1 plot, 24 trees were annually sampled according to standardized procedures (1). Selected trees were predominant, dominant and co-dominant individuals with a minimum height of 60 cm and without significant mechanical damage (1). Annually, a visual evaluation of the defoliation and discoloration of each tree crown was performed. Defoliation was defined as the percentage of needle/leaf loss in the assessable crown as compared to a reference tree, using a sliding scale of 5%. To quantify defoliation, local reference trees were defined as the best tree with full foliage that could grow at this particular site (1). Each sampled tree was visually examined in the field and factors associated with the observed defoliation (vertebrate herbivory, insect herbivory, fungal damage, drought impacts, management impacts and fire damage) were recorded using a code of binary variables (0-damage type absence, 1-damage type presence; Table S1). Additionally, plot information on soil type and humus layer depth was recorded by means of ordinal variables (1). Similarly, tree diameter and density per plot were estimated. Tree density was estimated as the averaged spatial distance of the 24 sampled trees in each plot (1). A list of the tree species analyzed is provided in Table S2.

Mortality data were gathered from the Second and Third Spanish National Forest Inventory (IFN2 and 3), which respectively comprise an extensive network of 51.958 and 81.179 plots of 25 m of radius distributed across all types of forests in Spain. IFN2 field sampling plots were surveyed between 1989 and 1996. IFN3 plots were surveyed between 1997 and 2007. For each plot and species, three mortality measures were quantified: a binomial variable recording mortality presence or absence in a plot, the number of dead trees per hectare, and the percentage of dead trees relative to the total number of trees of the same species. In each IFN plot we also assessed the density of trees (number of trees per hectare with diameter > 7.5 cm) and the mean diameter at breast height in each plot. These variables were calculated both by grouping all species and for each species.

Meteorological data for 1951-2006 in Spain were obtained from the Spanish Meteorological Agency (2, 3). We gathered mean air temperature, minimum air temperature, mean maximum air temperature and rainfall data for each month. The number of meteorological stations increased progressively with time during 1951-2006, ranging from 212 to 1675 stations for temperature variables, and from 620 to 4515 stations for rainfall. Elevation data were obtained from a digital elevation model of 200 m of spatial resolution. Solar global radiation grids were derived from a physical computational model based on relief and the position of the Sun (4).

Climatic maps. Interpolated climatic maps were derived applying a mixed spatial interpolation method that combines sequentially two interpolation techniques (2, 3) (Fig. S1). Firstly the method applies a global statistical interpolation (multiple regression) using geographical variables, and subsequently calculates a local interpolation (inverse distance weighted) that uses the residuals of the regression fitting to generate a local anomalies corrector (2, 3). Altitude, latitude, distance to the coast, solar global radiation and terrain curvature were introduced in the regression models (3, 4). For each year, we randomly excluded 40% of the stations in order to cross-validate the model fit. To test the fitting we assessed the RMS (root mean square error) obtained for each map (3, 4). The mean RMS for monthly temperature maps (mean, maximum and minimum) was 1.27, 1.72 and 1.73 °C respectively, while the mean RMS for monthly rainfall maps was 19 mm.

From 1951 to 2006, we obtained a set of monthly climatic maps for mean air temperature, mean maximum air temperature and rainfall with 200 m of spatial resolution. Monthly rainfall maps were accumulated to obtain annual rainfall maps. Likewise, annual temperature maps were averaged from monthly temperature maps. Using rainfall and temperature data, we calculated the Emberger water deficit index (5) and mapped their distribution. Emberger water deficit was calculated simply changing the sign of the Pluviometric Quotient of Emberger (5). Emberger index is considered a useful and suitable index because it accounts for irregular hydrothermic conditions in the Mediterranean basin (5, 6). We used MiraMon GIS software for all these calculations (7).

Crown defoliation maps. To describe the spatiotemporal variation of crown defoliation in the Iberian Peninsula and Europe we built crown defoliation maps interpolating data from the Spanish and the European ICP Forests inventories (Fig. S3). The geographical range occupied by each tree species in Spain was derived from the Spanish National Forest Inventory (IFN), which has greater spatial resolution than the ICP-Forests Inventory. Similarly, European ICP-Forests datasets were used to explore latitudinal gradients in averaged defoliation for all species combined. In this case, we used Corine Land Cover 2000 map to define the spatial range of the forested areas in Europe. Crown defoliation maps were interpolated using the same methodologies as in climate data (see previous section). The variables included in the multiple regression models were altitude, latitude, distance to the coast, solar global radiation, terrain curvature, Emberger water deficit index and annual rainfall. The spatial resolution was 200 m and the temporal resolution ranged from 1987 to 2008. Using the same methodology, maps of the percentage of trees affected by different damage types were obtained for each species and year (Figs. S3 and S5).

Hypothesis testing.

Crown defoliation. To assess which ecological and climatic factors were consistently associated with crown defoliation trends we applied a model selection approach (8). The statistical analysis was restricted to the 1987-2006 period. The response variable analyzed was the observed percentage of crown defoliation for each sampled tree. To perform the models, we crossed defoliation data with climatic data extracted from interpolated maps for each plot and year (temperature, rainfall and Emberger water deficit). In addition, we introduced in the models plot-specific measures of soil type, humus layer depth, altitude and solar global radiation and field measures of the impact of vertebrate grazing, insect herbivory, fungal damage, drought damage, management and fire (binomial variables recorded for each tree and year) (Table S1).

Many studies report lagged and cumulative effects of climatic factors on drought-induced physiological responses (e.g. defoliation, growth, mortality) during time-periods ranging from several weeks to few years (9-11). Furthermore, some empirical studies suggest that relative climatic variables (i.e. measures of the relative difference between a local climatic record and the long-term average in this locality) might in some cases perform as better predictor variables (12-13), presumably because trees are acclimated or adapted to specific local conditions. To screen the relative importance of cumulated and lagged climatic effects, we correlated defoliation with climatic lagged variables (with a lag of 1, 2 and 3 years) and with cumulated climatic variables (averaging for 1, 2 and 3 years). These correlations were calculated for maximum, minimum and mean annual and summer temperatures, annual rainfall, cumulated winter-summer rainfall (January-August) and Emberger water deficit. To account for local responses associated with deviations from long-term local climatic conditions, we calculated a relative Emberger index (REMB), defined as the relative difference of the Emberger index (for year i and census plot j) respect to the long-term mean value of the Emberger index in each plot (57 years mean, 1951-2006):

$$REMB_{i,j} = \frac{emb_{i,j} - mean(emb)_{1951-2006,j}}{mean(emb)_{1951-2006,j}}$$

Mean and lagged REMB values for 1, 2 and 3 years were also correlated with crown defoliation. After analyzing all these variables and correlates, we observed that averaged two-year mean summer temperature (June-July-August), and averaged two-year REMB (REMBi,2) presented the highest correlations with crown defoliation. Consequently, these climatic variables were finally selected and introduced in the models as independent variables.

Step function in R package (14) was used to rank the independent variables for each model (according to AIC criteria). We contrasted a battery of modeling approaches (Ordinary Least Squares (OLS), Generalized Linear Models (GLM), Spatial simultaneous autoregressive models (SAR), Generalized Estimating Equations (GEE) and Generalized

Linear Mixed Models (GLMM)) using R package (14-15). GlmmPQL and lme4 packages in R were applied for the GLMM models, using respectively penalized likelihood (PQL) and Laplace parameter estimation techniques. In GLMM models, plot was introduced as a random factor. Quasipoisson and quasibinomial distributions (for count and proportion data respectively) were applied when significant overdispersion was detected. The degree of spatial autocorrelation in the residuals of the models was assessed both using Moran's I correlograms and plotting spatial maps of the distribution of residuals, following Dormann et al. (15). To account for the effects of temporal autocorrelation, GLMM and GEE models with a first order autocorrelative term were applied using corAR1 function in R package (15-16). Significant spatial and temporal autocorrelation was detected, suggesting the need for accounting for these effects. Cross comparisons of the modeling approaches (with or without spatial or temporal autocorrelation corrections) asserted that the results were robust to the autocorrelative effects (Table S4).

Several empirical studies assert that interactions between the predictor variables examined are likely to occur and may play an important role. For instance, climatic factors (water deficit, temperature, rainfall) can influence insect- and fungus-plant defoliation interactions via effects on the pathogen, the host or both (17). Similarly, many studies assert that rising drought impacts also increase the recurrence and severity of fires (18, 19), enhance vertebrate herbivory on trees (20) and interact with insect herbivory (21). To quantitatively assess the importance of these interactions, a supplementary modeling approach was performed accounting for these interactions (Table S5).

Species-specific divergent responses to drought have been observed in previous studies (22-23). To assess how species differentially responded to temperature and drought impacts in dry and humid localities we divided the dataset in rainfall quantiles and performed an independent modeling analysis in each quartile. The datasets of species with larger number of plots available (N>15 plots) were divided in four quartiles. For species with smaller number of plots (10-15 plots) the dataset was divided in two quantiles. The datasets of species with less than 10 plots were not subdivided (Supplementary Table 2). In each quantile, we performed a GLMM-AR1 model with REMBi,2 and averaged two year summer temperature as independent variables.

Tree mortality. Tree mortality responses were modeled applying generalized linear models with a binomial error distribution, and using mortality presence at the plot level per each species as the response variable. Supplementary analyses were performed using the percentage and the number of dead trees per hectare. Consecutive IFN field surveys were separated by a time lag of ten years, and the date (year) of sampling was variable depending on the plot. Therefore, mortality events in each plot survey cumulatively occurred during the10 year-period separating two consecutive IFN field surveys. Consequently, to assess the effects of climatic variables on mortality during this time period, we calculated for each plot a ten-year average of the climatic variables (Emberger water deficit, temperature and rainfall), using the date of survey to define the 10-year climatic temporal sequence considered. Finally, Emberger water deficit, temperature, plot tree density, and mean plot tree diameter were introduced in the generalized linear models as independent predictor variables. Exploratory graphical analyses showed that mortality and water deficit presented a hump-shaped relationship in many of the species, and therefore a quadratic term for water deficit was introduced in the model selection procedure, to fully account for these non-linear relationships. Mortality analyses were first performed for all the dataset (IFN2 & IFN3 grouped). Subsequently, we repeated the analyses for each survey (i.e. IFN2 [1989-1996] and IFN3 [1997-2007]), restricting the analysis to the plots that were surveyed in both inventories (42.230 plots).

Supporting Information. Tables

Table S1

Damage type	**Description**
Vertebrate herbivory	Cervidae, Suidae, Rodentia, birds, domestic animals and other vertebrates.
Insect herbivory	Defoliating insects. Stem, branch, twig, bud and fruit borer insects. Sucking insects, mining insects and gall-makers.
Fungi	Needle cast and needle-rust fungi, stem and shoot rusts, dieback and canker fungi, root rot and decay fungi, leaf spot fungi, anthracnose, powdery mildew. Virus damages were also included.
Drought and abiotic stress	Drought damage. Also includes secondary stresses derived from frost, hail, snow and wind impacts.
Management	Forest and land management.
Fire	Fire damage

Table S2. A summary of the crown defoliation analyses and maps performed for each species. GLMM-AR1: Generalized Linear Mixed model with a first order autocorrelative term (corAR1 function); $REMB_{i2}$: Two-year averaged relative Emberger water deficit; Temp: averaged two year mean summer temperature.

Species	*Crown Defoliation and Damage type Maps*	*GLMM-AR1 Model (All predictors)*	*GLMM-AR1 (REMB, Temp) Four Quartiles*	*GLMM-AR1 (REMB, Temp) Two Quantiles*	*GLMM-AR1 (REMB, Temp) Without Subgroups*	*Number of Plots*
Abies alba	√					2
Acer campestre	√					4
Betula pendula	√	√			√	7
Castanea sativa	√	√	√			18
Eucalyptus sp.	√	√	√			23
Fagus sylvatica	√	√		√		15
Juniperus oxycedrus	√	√	√			19
Juniperus thurifera	√	√	√			20
Olea europaea	√	√			√	5
Pinus halepensis	√	√	√			68
Pinus nigra	√	√	√			59
Pinus pinaster	√	√	√			56
Pinus pinea	√	√	√			19
Pinus radiata	√	√			√	6
Pinus sylvestris	√	√	√			67
Pinus uncinata	√	√	√		√	9
Quercus faginea	√	√	√			37
Quercus ilex	√	√	√			137
Quercus petraea	√	√	√		√	6
Quercus pubescens	√	√		√		13
Quercus pyrenaica	√	√	√			35
Quercus robur	√	√	√			24
Quercus suber	√	√	√			25

Table S3. Independent variables examined in the defoliation modeling analyses.

Factors Tested	Independent variables	Data source
Drought damage	Damage type binary variable	ICP Forests Inventory
Landscape water deficit	Averaged two-year relative Emberger index ($REMB_{I2}$)	Spanish National Institute of Meteorology
Insect damage	Damage type binary variable	ICP Forests Inventory
Fungal damage	Damage type binary variable	ICP Forests Inventory
Fire	Damage type binary variable	ICP Forests Inventory
Forest management	Damage type binary variable	ICP Forests Inventory
Vertebrate herbivory	Damage type binary variable	ICP Forests Inventory
Soil quality	Humus layer depth	ICP Forests Inventory
Soil type	FAO soil type	ICP Forests Inventory
Topography	Altitude Solar radiation	Pons and Ninyerola 2008 (S5)
Temperature	Averaged two-year mean summer temperature	Spanish National Institute of Meteorology
Tree density	Tree density	ICP Forests Inventory
Tree diameter	Mean tree diameter	ICP Forests Inventory

Table S4. Effect tests for GLMM-AR1 crown defoliation models and for Generalized Linear Models of mortality. The sign (+/-) and significance (color code) of the test estimates is shown. For illustrative purposes, a different color code has been used to highlight the relative explanatory power of each significant factor. Red=first and second predictors ($p<0.0001$); orange= third and fourth predictors ($p<0.05$); yellow= all other significant predictors ($p<0.05$). GLMM-AR1: Generalized Linear Mixed model with a first order autocorrelative term. To fully account for the observed hump-shaped relationships between mortality and water deficit, a quadratic term was included in the models (Water deficit^2). * Species with insufficient or no available mortality data.

	Qurcus petraea	*Quercus robur*	*Quercus ilex*	*Quercus suber*	*Quercus faginea*	*Quercus pyrenaica*	*Quercus pubescens*	*Olea europaea*	*Fagus sylvatica*	*Castaena sativa*	*Betula pendula*	*Pinus uncinata*	*Pinus pinea*	*Pinus pinaster*	*Pinus nigra*	*Pinus halepensis*	*Pinus sylvestris*	*Pinus radiata*	*Eucalyptus sp.*	*Juniperus thurifera*	*Juniperus oxycedrus*
	DEFOLIATION																				
Drought damage		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Water deficit		+	+	+	+	+		+		-	-	-	+	+	+	+	+	+		+	+
Fire			+	+	+		+	+	+			-	+	+	+	+	+		+	-	+
Insect	+	+	-	-	+	+		+	+		+			+	+	+	+	+	+	+	
Temperature			+	+	+	+				+			-	+	+	+	+	+	+	-	
Solar radiation	-	+		+	+										+			-		+	

Fungi	-		+	+				+	+	+		-	+	+	+	+	+		+		+
Management			-	-				-					+	-		-				-	
Diameter			-				-					+		-	-	+		+	+	+	
Density		+		+	+		-			-				-		+	-	+	+	+	
Altitude	-			+		-					+	-	-	-	+	-	-		+		+
Humus	-	+	-		-								-			+		+		-	-
Soil		+				-				-		-			-	+	-				-
Herbivory								-					+								
	MORTALITY																				
Tree density	+		+	+	+	+		*	+	+	*	+	+	+	+	+	+	+	*	*	*
Tree diameter			-	+				*			*	+	+	+	+	+	+	+	*	*	*
Water Deficit^2	+		+	+		+	+	*			*	+		+		+	+		*	*	*
Water Deficit	-		-	-	-	-	-	*			*	-		-		-	-		*	*	*
Temperature			+	+	+			*	-	+	*	+	+	+	+	+	+	+	*	*	*

Table S5. A comparison of the estimates of the different modeling approaches applied for *Quercus ilex* defoliation. The sign (+/-) and significance (* p<0.05, ** p<0.01, *** p<0.001) of the test estimates are contrasted. Note that the sign and significance of main predictor variables (Drought, Fire, Landscape water deficit, Insect damage and Tree diameter) is robustly maintained across all modeling approaches.

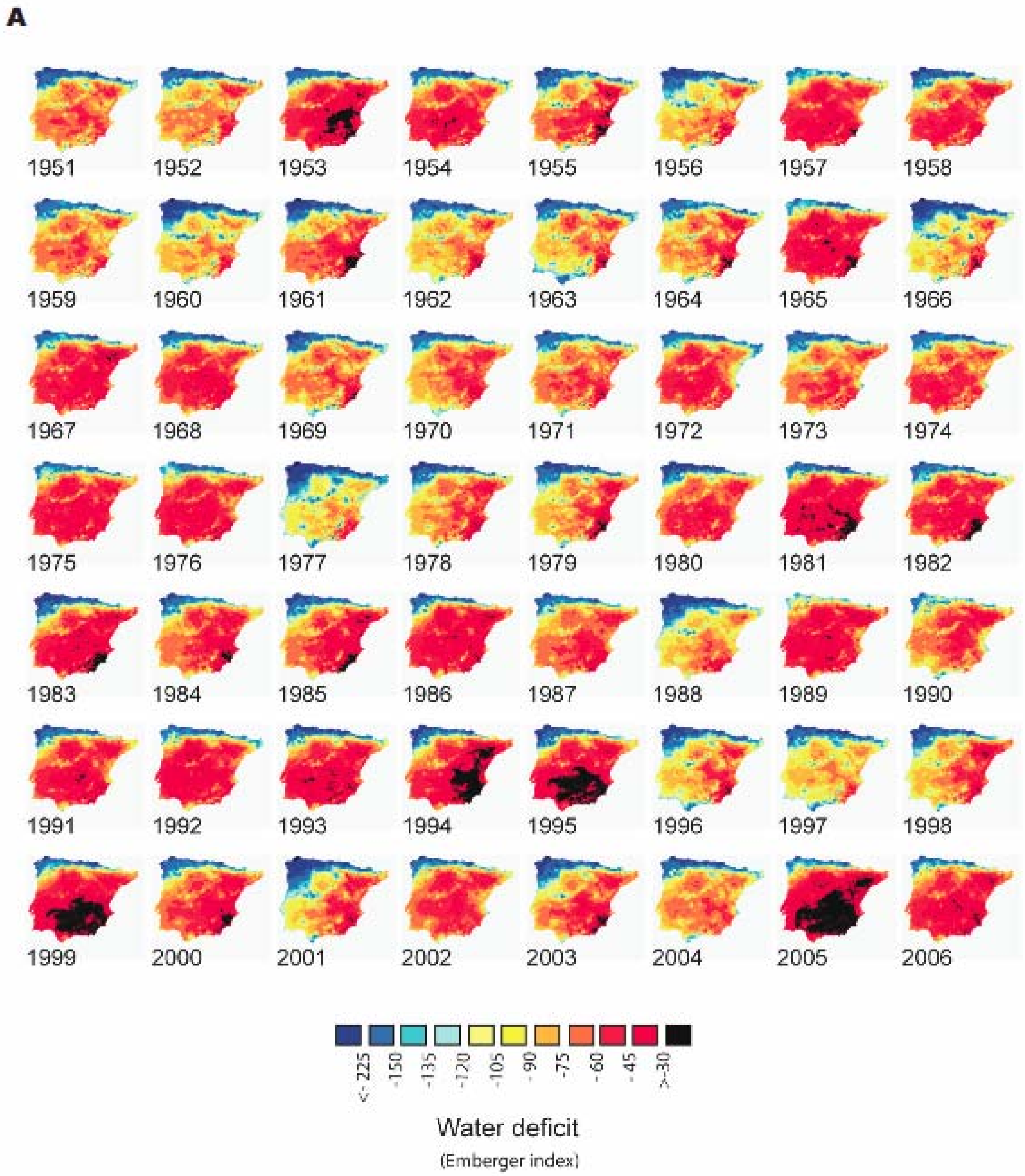
Species	Independent Variables	OLS	GLM	GLMM pql	GLMM Laplace	Spatial SAR	GEE AR1	GLMM AR1
Quercus ilex	Drought damage	+***	+***	+***	+***	+***	+***	+***
	Water deficit	+***	+*	+***	+*	+***	+***	+***
	Fire	+***	+***	+***	+***	+***	+***	+***
	Insect	-***	-***	-***	-***	-***	-***	-***
	Temperature	+***	+**	+***	+**	+*	+***	+***
	Radiation	+*						
	Fungi	+***	+*	+*	+*		+***	+***
	Management	-***	-***	-***	-***		-***	-***
	Diameter	-***	-***	-***	-***	-*	-***	-***
	Density	+*		+*				
	Altitude	-***				-*	-***	
	Herbivory	+**		+***			+**	
	Humus	-***	-*	-***	-*		-***	-***
	Soil	+**					+**	

Table S6. Test effects for the GLMM-AR1 crown defoliation models with interactions. The sign (+/-) and significance of the test estimates are shown. Yellow color indicates significant effects with $p<0.05$. Estimates for single predictors were also included in the model.

	Quercus petraea	Quercus robur	Quercus ilex	Quercus suber	Quercus faginea	Quercus pyrenaica	Quercus pubescens	Olea europaea	Fagus sylvatica	Castaena sativa	Betula pendula	Pinus uncinata	Pinus pinea	Pinus pinaster	Pinus nigra	Pinus halepensis	Pinus sylvestris	Pinus radiata	Eucalyptus sp.	Juniperus thurifera	Juniperus oxycedrus
WD*Herb			-	-																+	
WD*Insect	+	-	+		-				+	-	-		-	-	+	-		-	+	-	
WD*Fungi			-	+	-		-	-			+			-	-	-	+	-	+		-
WD*Mg		-	+	+		+					+		-	+			-				
WD*Fire			-	+	-	+	+		+				+	-	+	-	+		-		
WD*Diam	+			-	-	-	-		+		+		-		-	-	-		-		
WD*Dens	+	+						+	+				-	+	+	-		+			-
WD*Humus		+	-	+		-	+				+				+	-		-	+		
WD*Soil		-	+						+		+	+		+	+	+				-	
Insect*temp		+	+		-	-	-			-	+	-			-		-			-	-
Insect*Diam	-		+	-		-	+		+		+				-		-	+			
Insect*Dens	-	+		-			+		+	+	+		+		+	-	-	-		+	+
Fungi*temp		-	+	-		+				-		-	+		-				-	-	
Fungi*Diam	+		+		-				-							+	+				
Fungi*Dens	+				-	-	-		-		-	+			+		-				

Supporting Information. Figures

Figure S1. Annual variation in Emberger water deficit index (*A*); annual rainfall (*B*); and annual temperature (*C*) during 1951-2006 in the Iberian Peninsula.



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Water deficit
(Emberger index)

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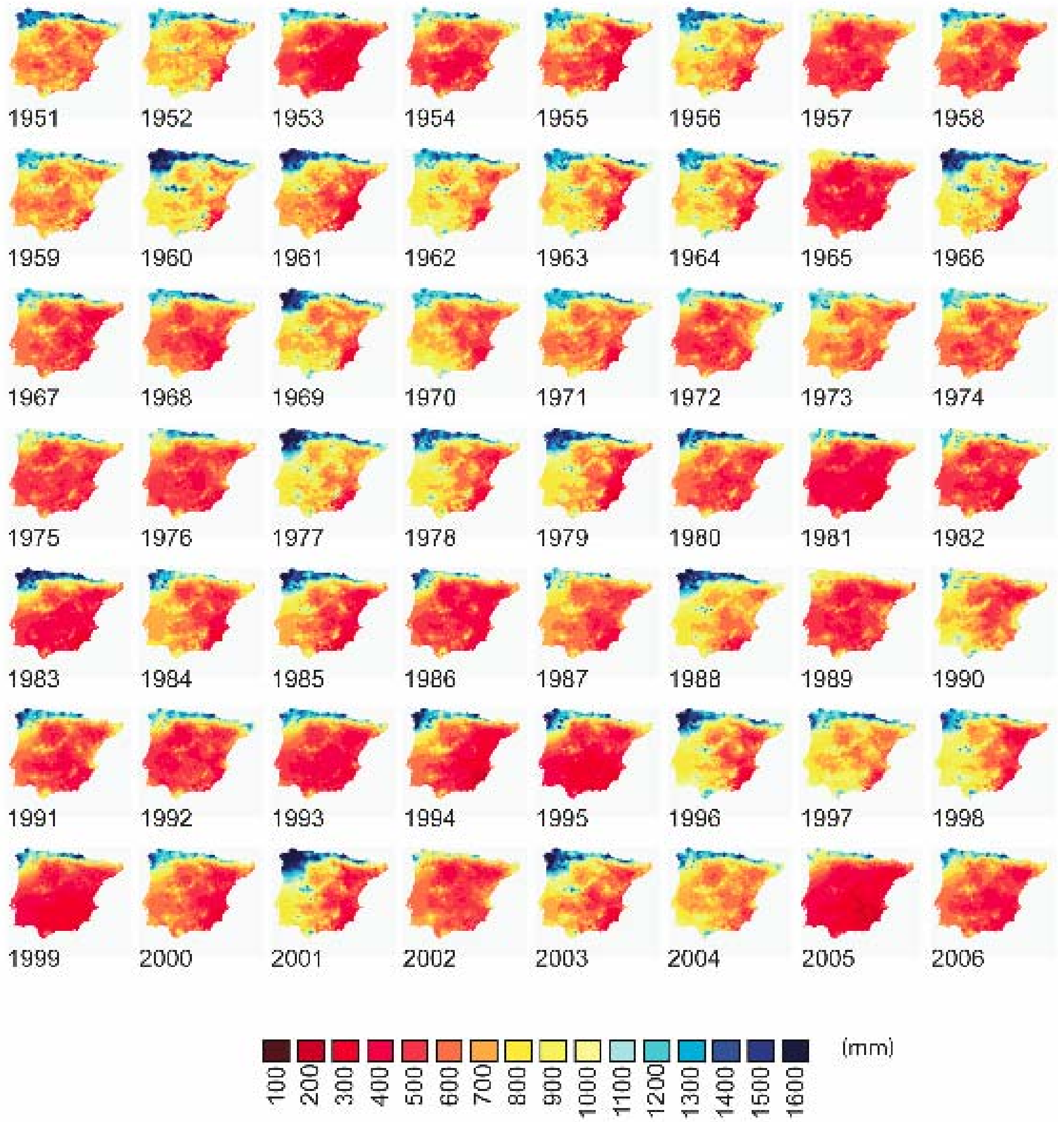
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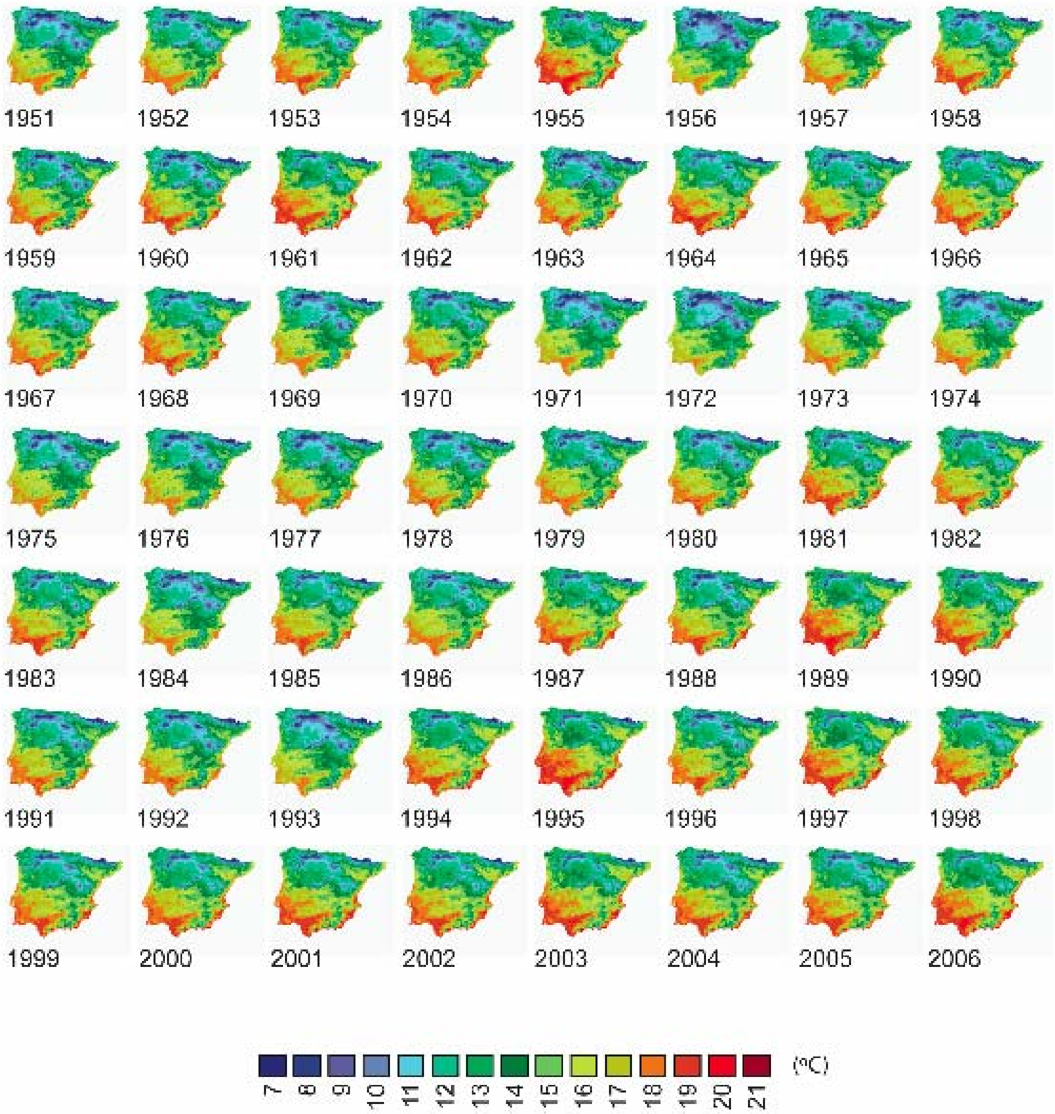
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Figure S2. Linear regression fits (black lines) and kernel smoothing functions (color lines) for one-year smoothed monthly temperature and monthly rainfall data in the sampled plots. The temporal increase of temperature and the decrease in rainfall for 1951-2006 were statistically significant ($p<0.0001$). Time series analyses (24) indicated a significant trend of increased temperature and reduced rainfall (Rainfall trend estimate (annual decrease of monthly rainfall): -0.13±0.02; t=-6.32; $p<0.0001$; Temperature trend estimate (annual increase of monthly temperature): 0.017±0.001; t=15.13; $p<0.0001$).

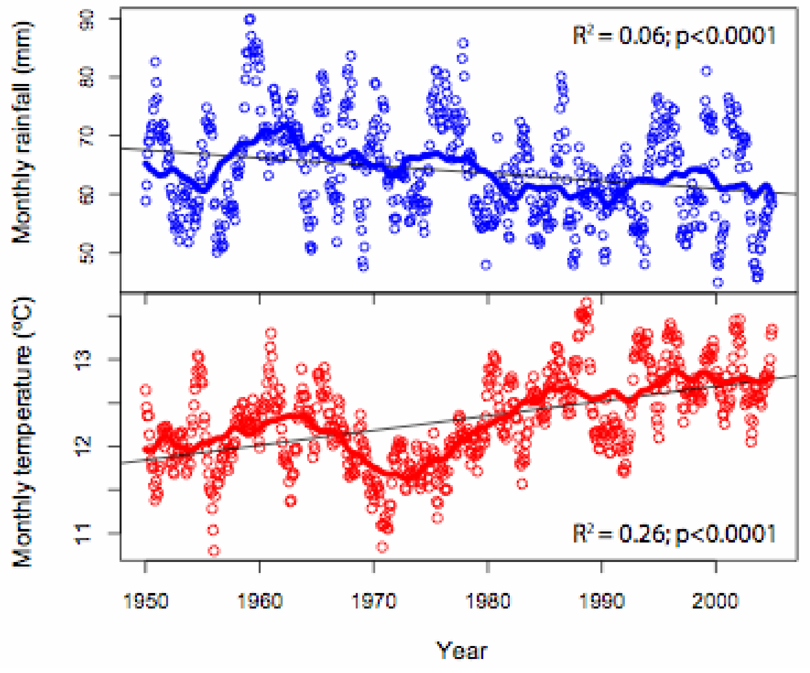
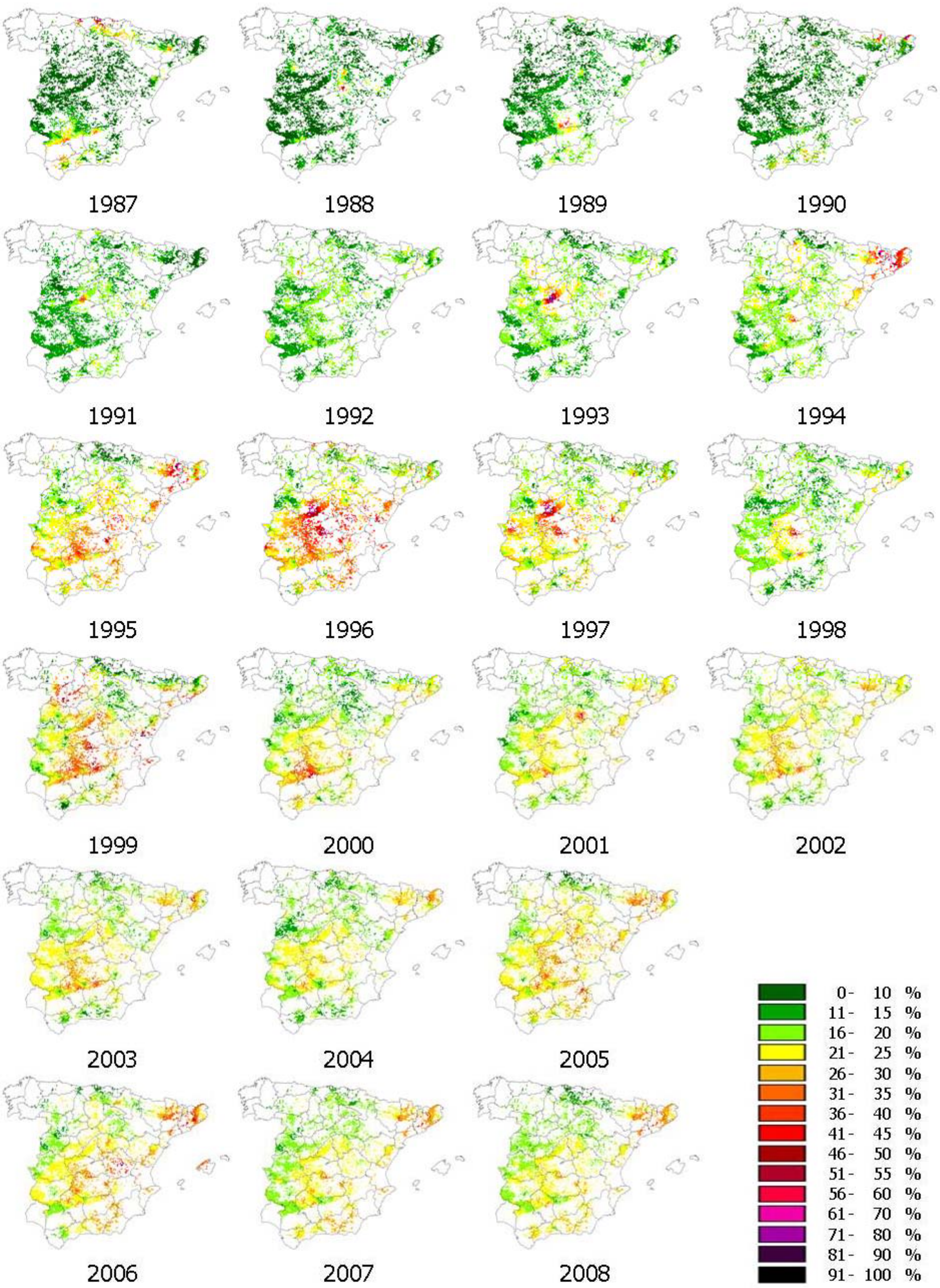
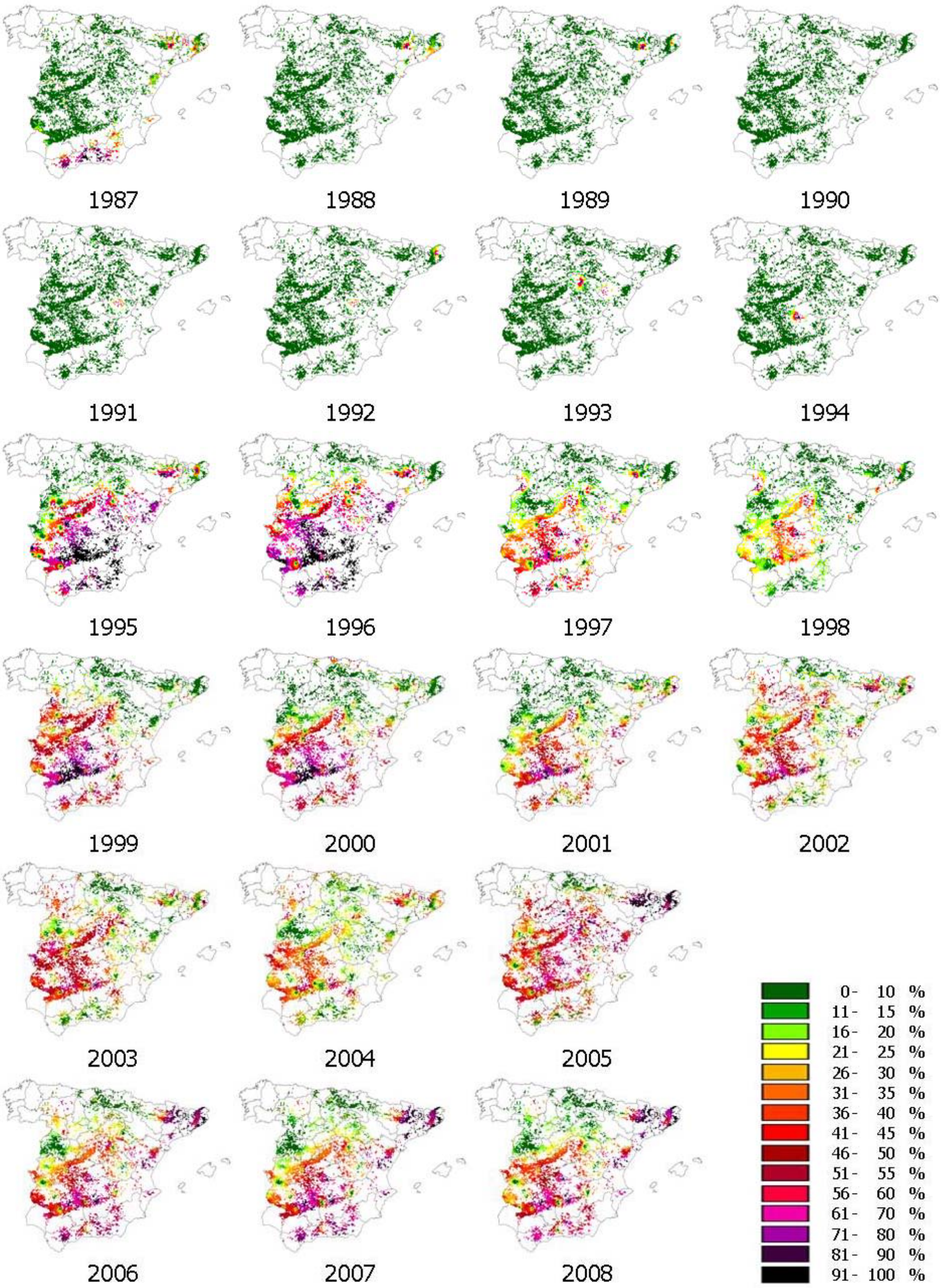


Figure S3. Maps of the percentage of crown defoliation and drought impacts (percentage of trees affected by drought per plot) for each tree species. *Quercus ilex* and *Pinus halepensis* maps are shown as illustrative examples.

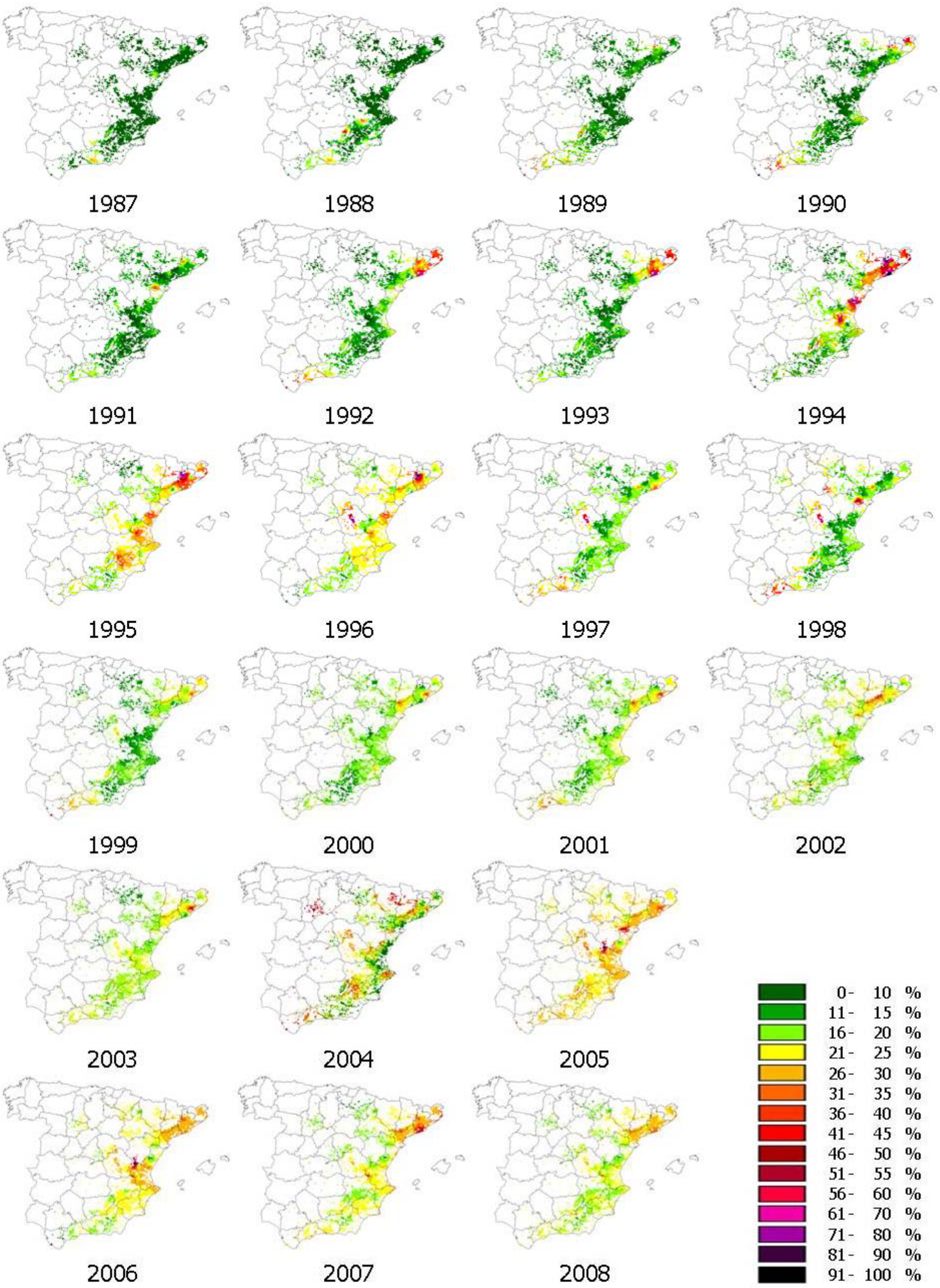
Quercus ilex **- Defoliation (%)**



***Quercus ilex* -** Drought (% damaged trees)



Pinus halepensis **- Defoliation (%)**



***Pinus halepensis* -** Drought (% damaged trees)

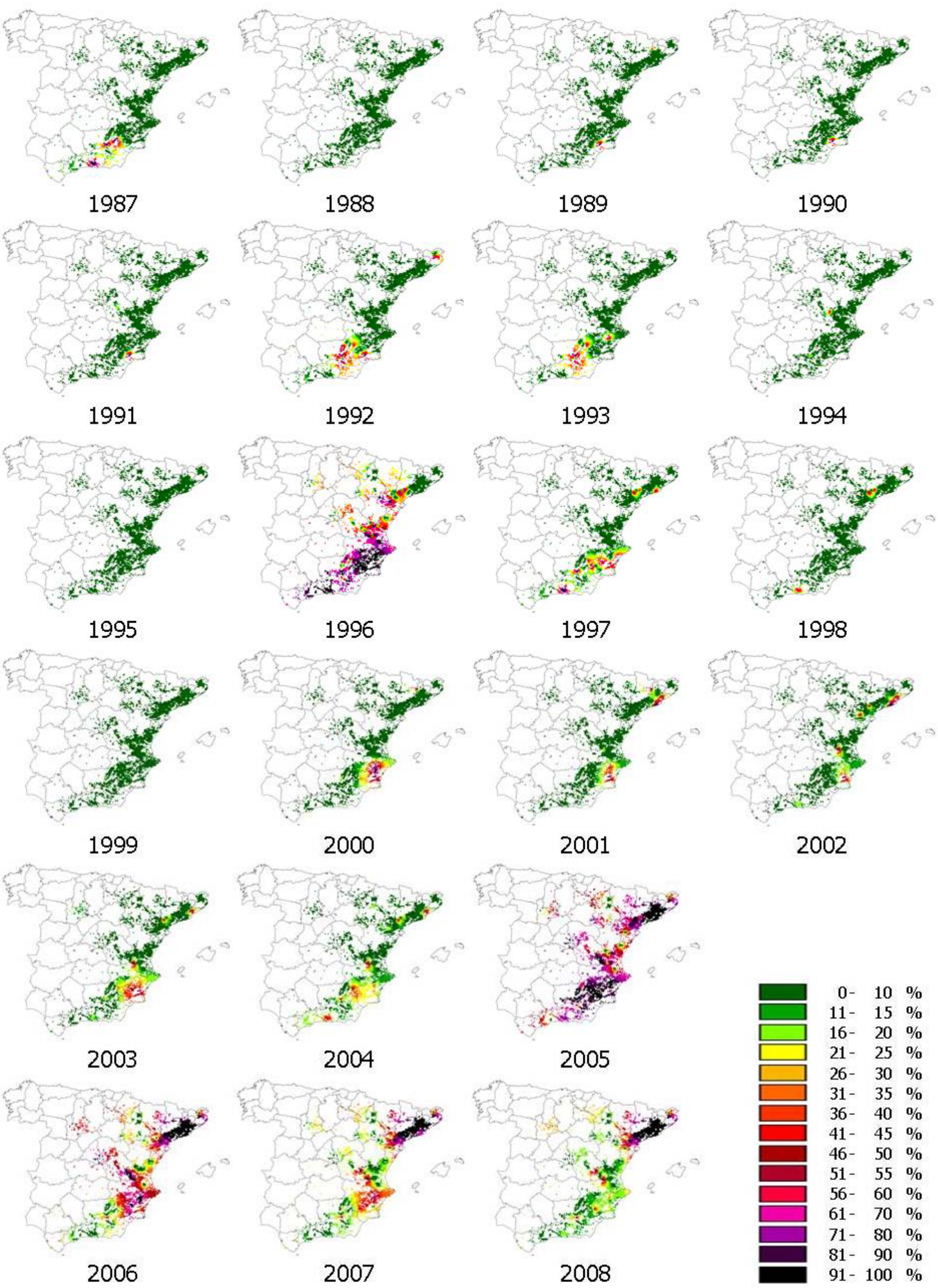


Figure S4. Observed variation in beta coefficients of GLMM-AR1 models in each rainfall quartile for tree species with large sample size (N plots ≥ 25) (Model: Crown Defoliation = b_1 $REMB_{i2}$ + b_2 Temperature). Red dots: Averaged two-year relative Emberger water deficit ($REMB_{i2}$) beta coefficients; Green dots: averaged two-year summer temperature beta coefficients. Filled dots: significant coefficients. Empty dots: non-significant coefficients.

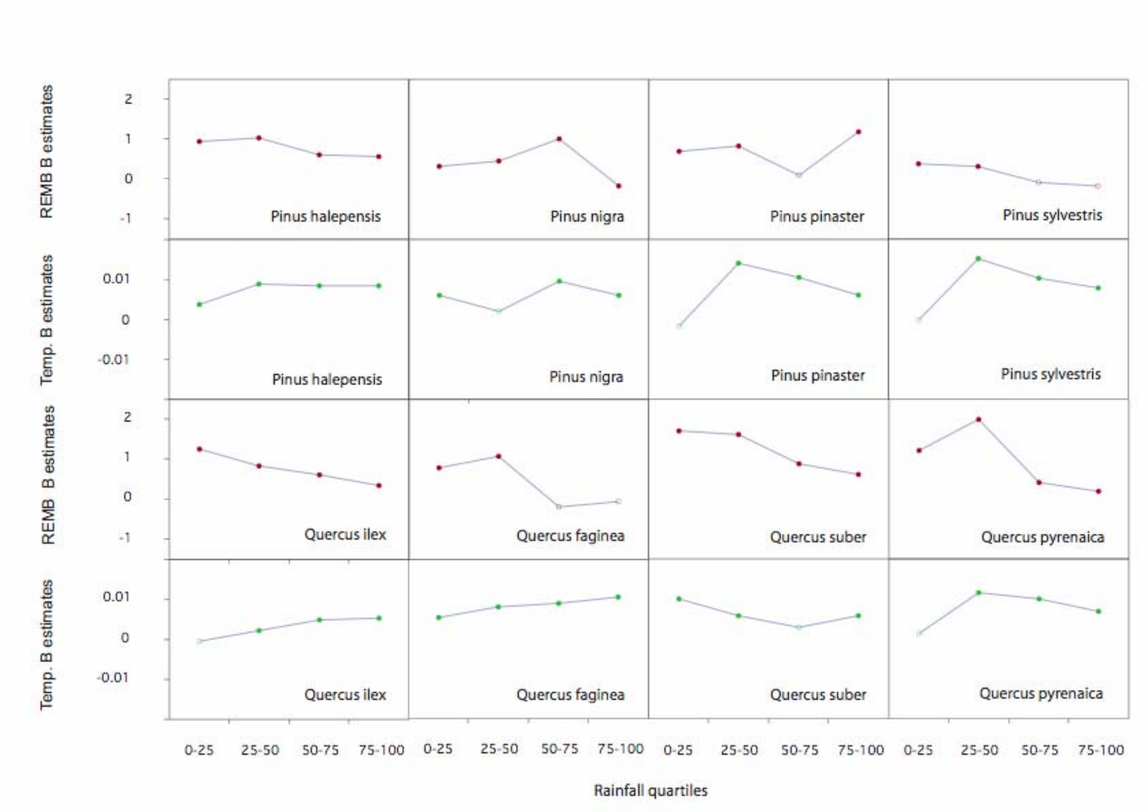


Figure S5. Observed mortality rates in the Second and Third Spanish National Forest Inventory Surveys. (*A*) IFN2 inventory (1989-1996); (*B*) IFN3 Inventory (1997-2007).

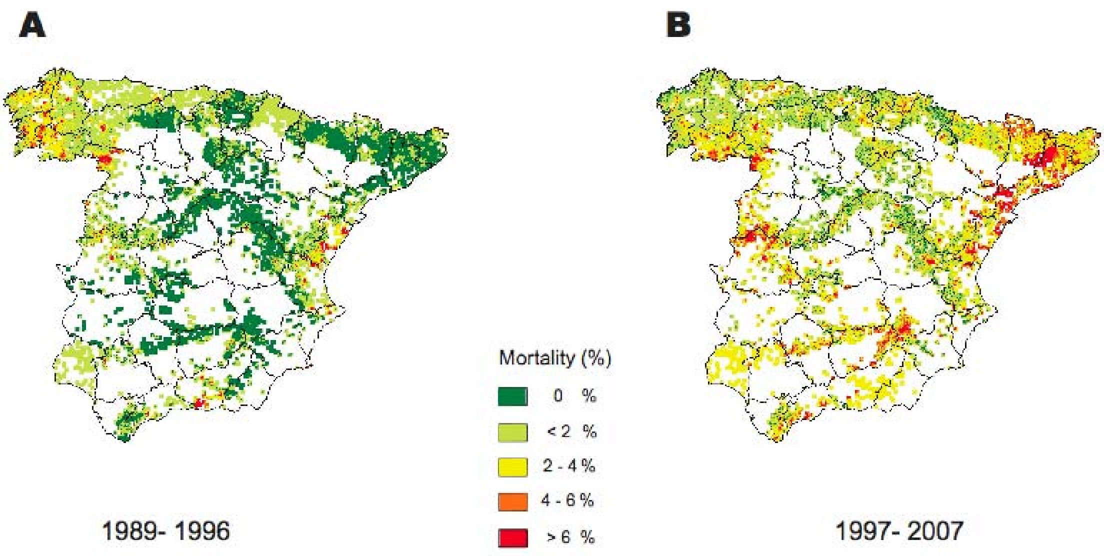


Figure S6. Observed changes in the mortality rates between the second and third Spanish National Forest Inventories (IFN2 and IFN3). Mortality rates significantly increased in all species with the exception of *Pinus radiata (F* test, ***p<0.001).

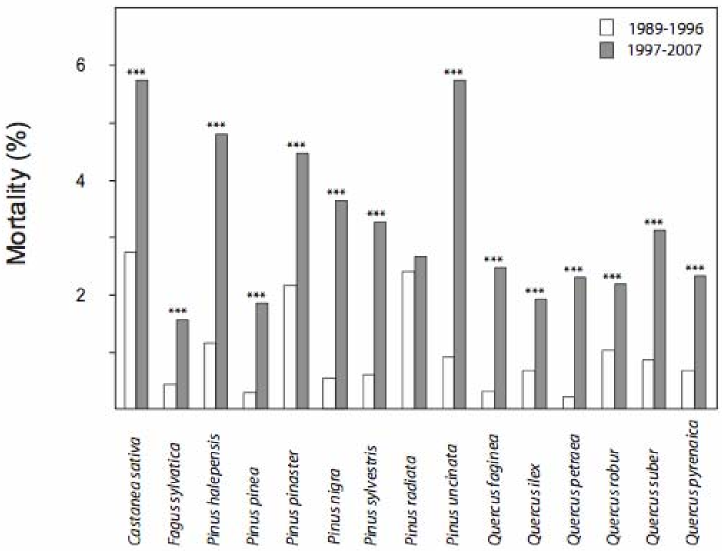


Figure S7. A comparison of tree density and temperature effects on mortality between the Second Spanish Forest National Inventory (1989-1996, IFN2) and the Third Spanish Forest National Inventory (1997-2007; IFN3). We compared 42.230 plots that were surveyed in both inventories, with a time lag of 10 years between the two consecutive surveys. Mortality was modeled as a function of temperature, water deficit, tree density and tree diameter using Generalized Linear Models per each species and rainfall quartile. (*A*) Changes in plot tree density beta coefficient values with increased rainfall for mortality models for IFN2; (*B*) Changes in temperature beta coefficient values with increased rainfall for mortality models for IFN2; (*C*) Changes in plot tree density beta coefficient values with increased rainfall for mortality models for IFN3; (*D*) changes in temperature beta coefficient values with increased rainfall for mortality models for IFN3. Red dots: 0-25 quantiles; Orange dots: 25-50 quantiles; Yellow dots: 0-50 quantiles; Green dots: 50-75 quantiles; Dark blue dots: 75-100 quantiles.

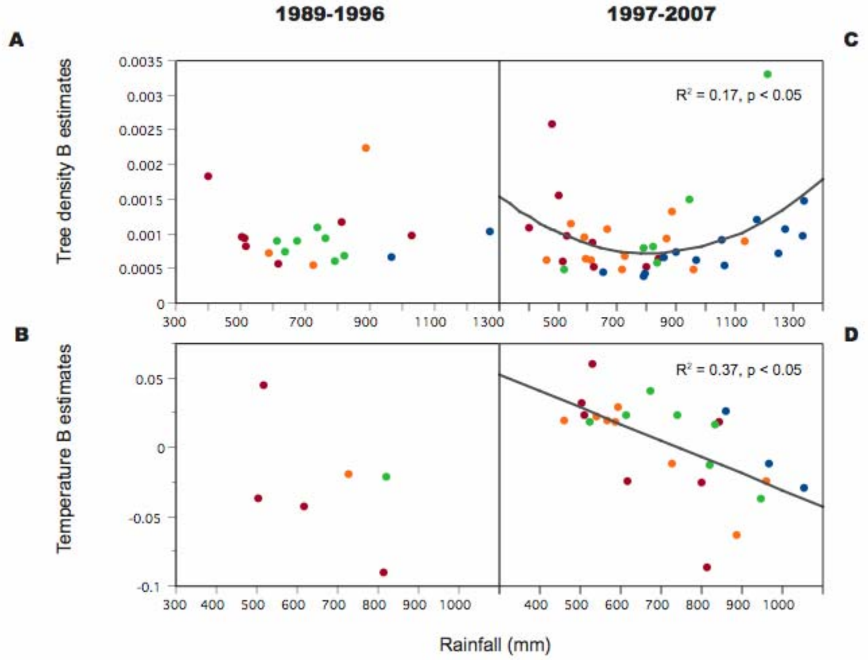
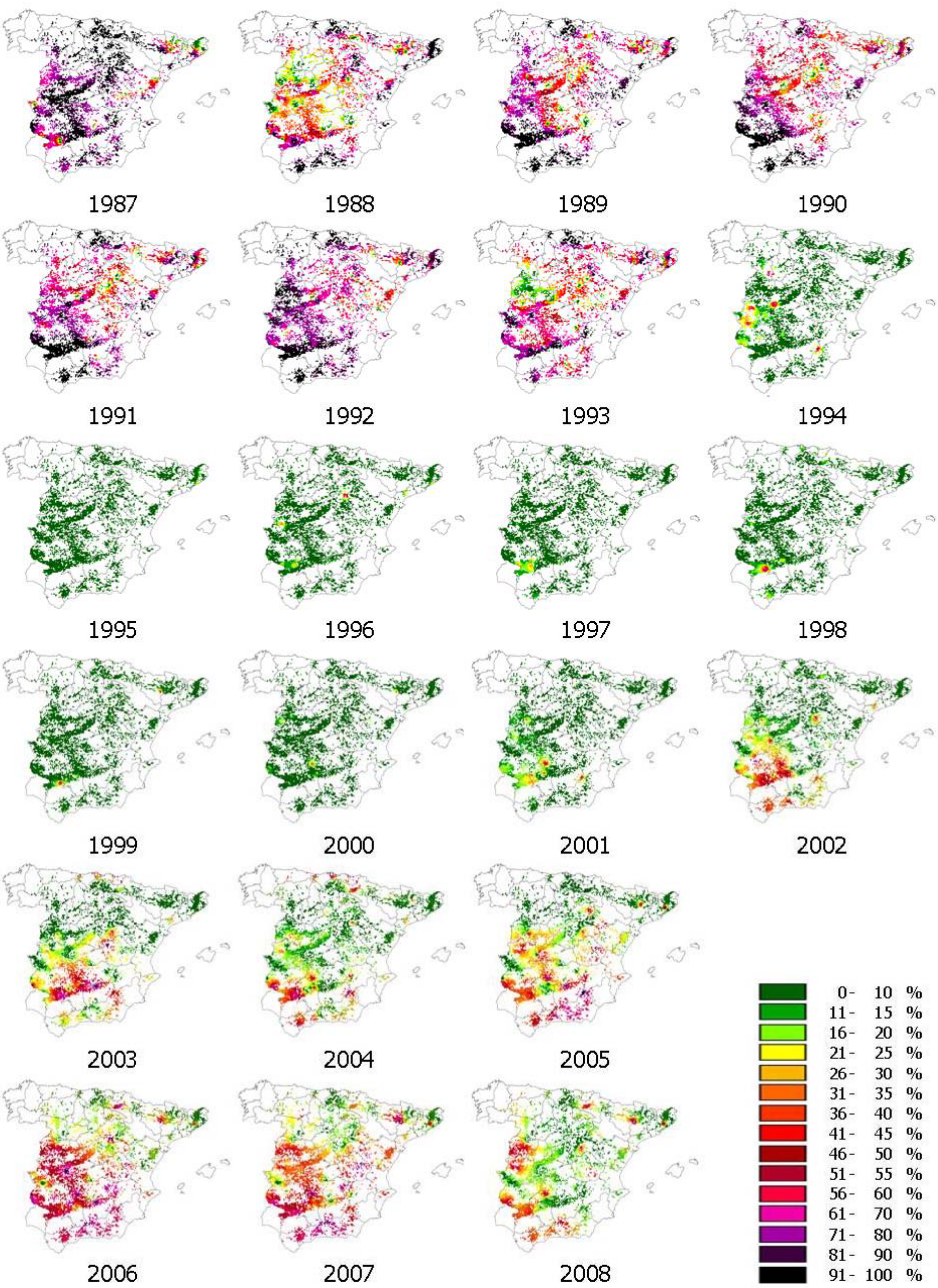
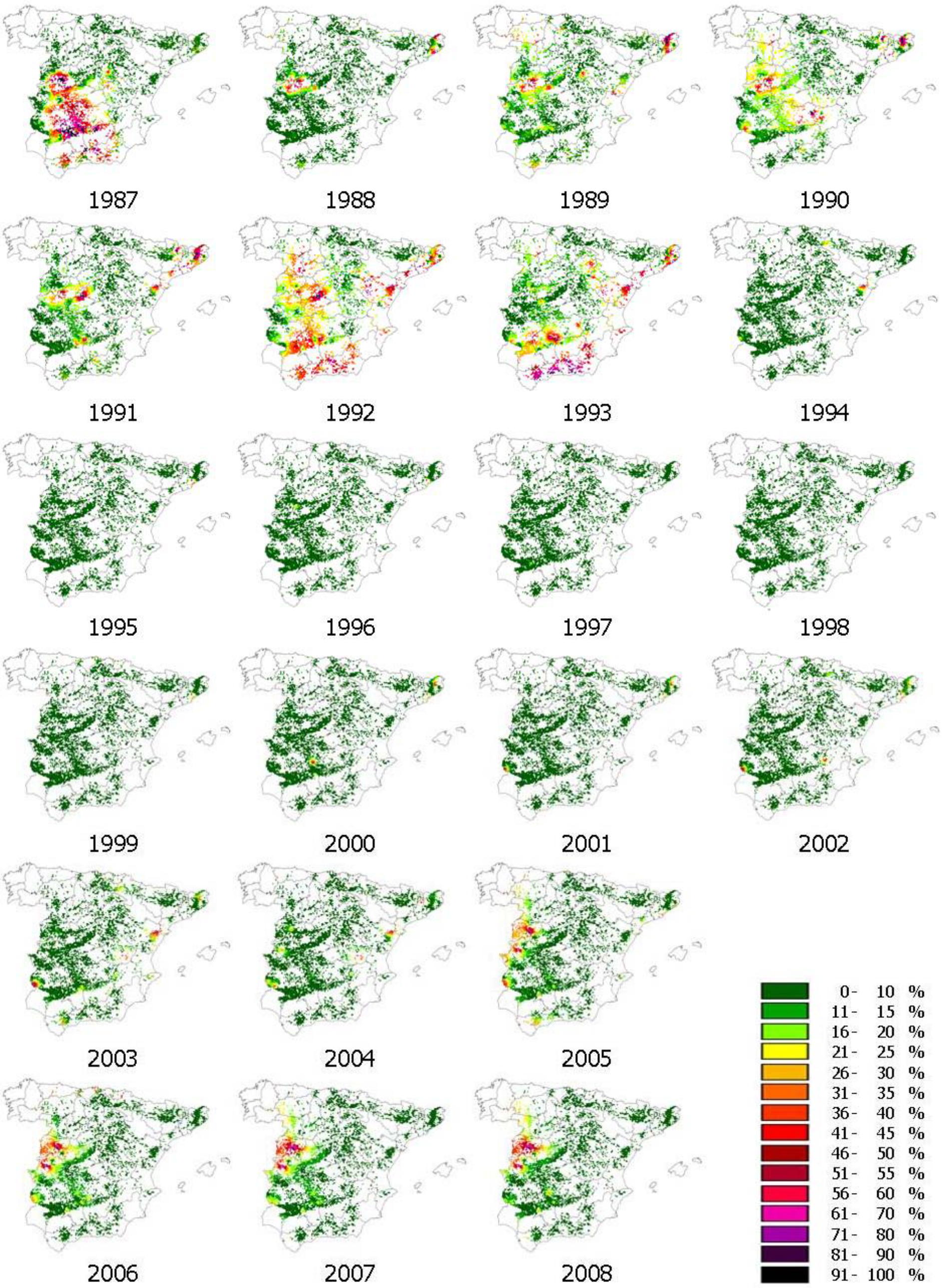

1989-1996
1997-2007
A
B
C
D
Tree density B estimates
Temperature B estimates
R² = 0.17, p < 0.05
R² = 0.37, p < 0.05
Rainfall (mm)

Figure S8. Maps of the percentage of trees affected by insect and fungal damages for each tree species. *Quercus ilex* and *Pinus halepensis* maps are shown as illustrative examples.

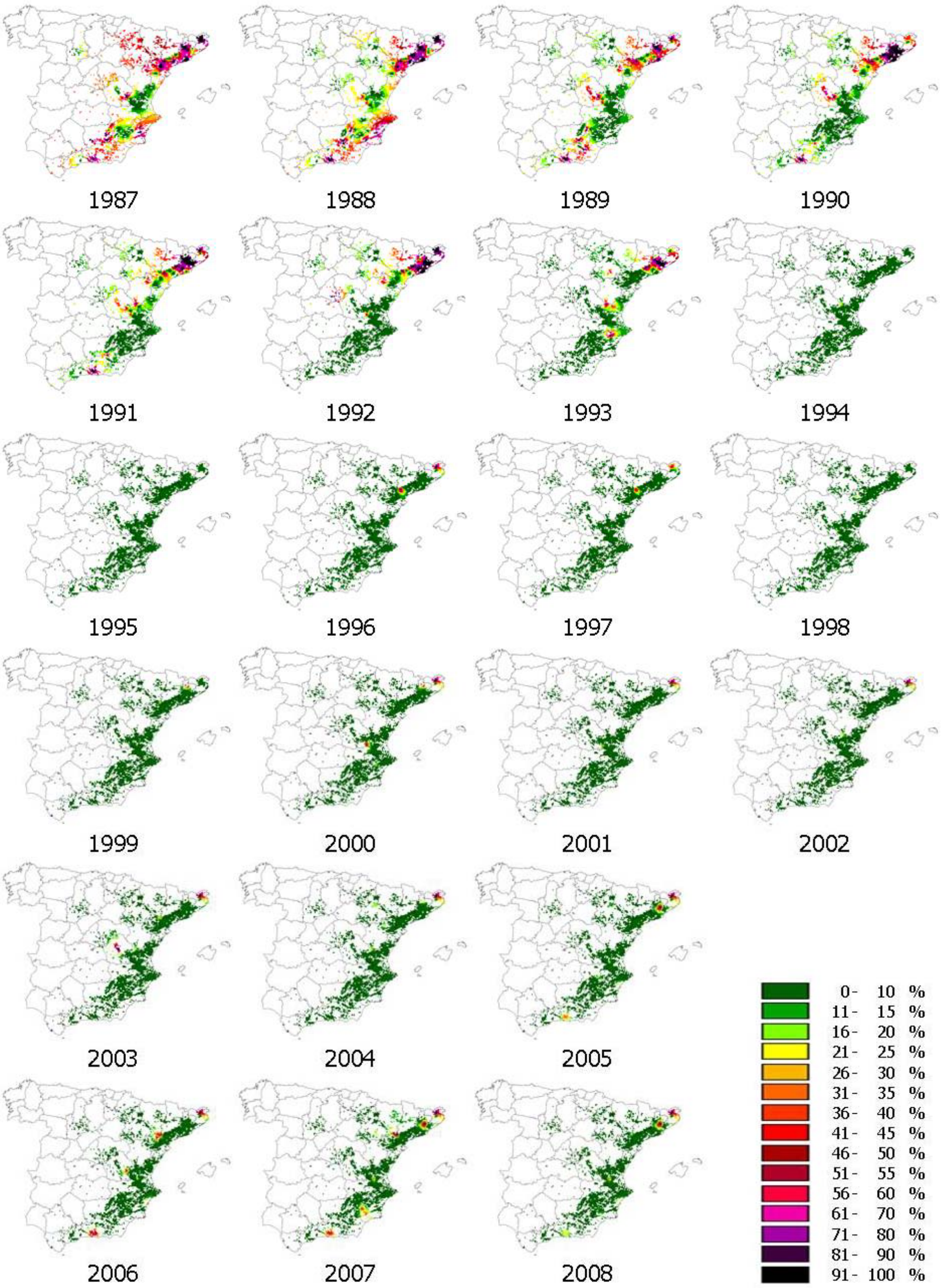
***Quercus Ilex* -** Insect herbivory (% damaged trees)



***Quercus ilex* -** Fungi (% damaged trees)



***Pinus halepensis* -** Insect herbivory (% damaged trees)



***Pinus halepensis* -** Fungi (% damaged trees)

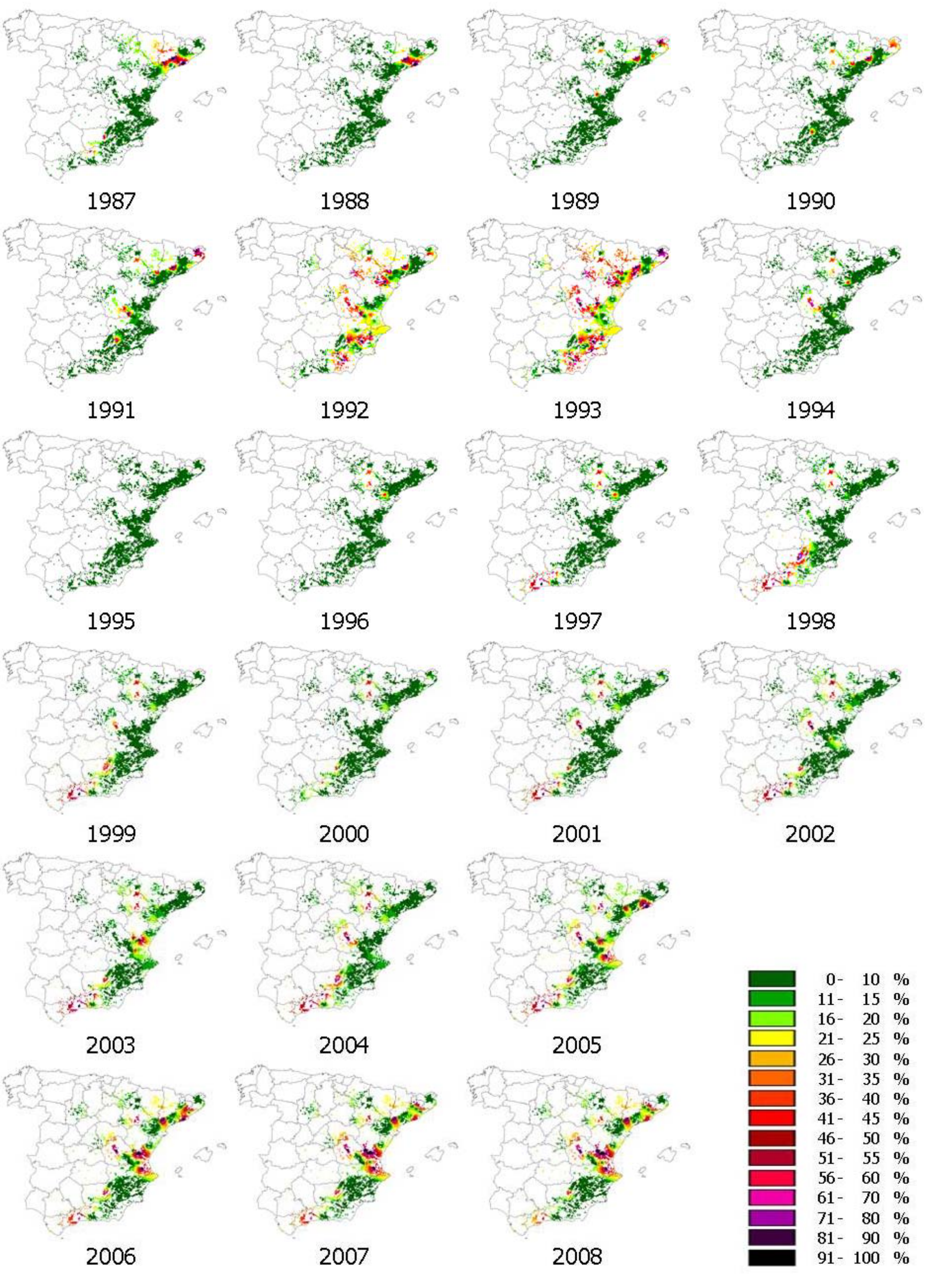
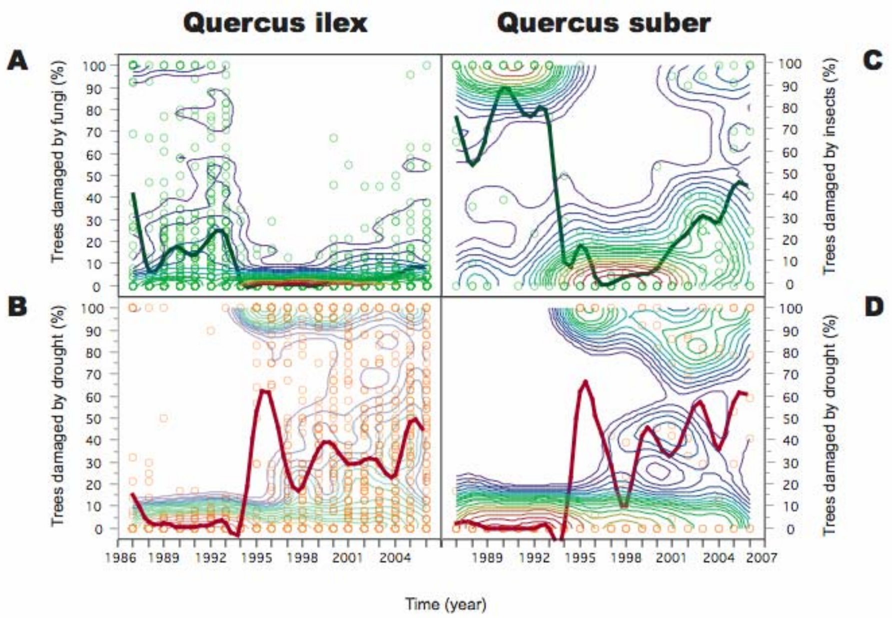


Figure S9. Shifts in fungal damage and insect damage dynamics associated to drought impacts in *Quercus ilex* and *Quercus suber*; (*A*) Temporal trends in the percentage of *Quercus ilex* trees affected by fungal defoliation in the Iberian Peninsula; (*B*) Temporal trends in the percentage of *Quercus ilex* trees affected by drought; (*C*) Temporal trends in the percentage of *Quercus suber* trees affected by insects; (*D*) Temporal trends in the percentage of *Quercus suber* trees affected by drought. Dots represent sampled plots. A smooth surface showing the density of sampled plots is provided. Red contour lines indicate maximum point density. Spline fits describing the temporal variation in the percentage of trees affected by insect damage and drought are shown.



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