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

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Climate change is progressively increasing severe drought events in the Northern Hemisphere, causing regional tree die-off events and contributing to the global reduction of the carbon sink efficiency of forests. There is a critical lack of integrated community-wide assessments of drought-induced responses in forests at the macroecological scale, including defoliation, mortality, and food web responses. Here we report a generalized increase in crown defoliation in southern European forests occurring during 1987–2007. Forest tree species have consistently and significantly altered their crown leaf structures, with increased percentages of defoliation in the drier parts of their distributions in response to increased water deficit. We assessed the demographic responses of trees associated with increased defoliation in southern European forests, specifically in the Iberian Peninsula region. We found that defoliation trends are paralleled by significant increases in tree mortality rates in drier areas that are related to tree density and temperature effects. Furthermore, we show that severe drought impacts are associated with sudden changes in insect and fungal defoliation dynamics, creating long-term disruptive effects of drought on food webs. Our results reveal a complex geographical mosaic of species-specific responses to climate change–driven drought pressures on the Iberian Peninsula, with an overwhelmingly predominant trend toward increased drought damage.

extreme events | earth system feedbacks | ecological networks | global change | Mediterranean biome

Global climate change is expected to cause progressively increased frequency and severity of drought events and heat waves in the Northern Hemisphere (1, 2). Globally, increased drought impacts have already been recorded over the last several decades, with anthropogenic forcing widely accepted as the most plausible cause (2–7). These drought impacts have presumably altered carbon cycling dynamics over extensive areas, possibly contributing to the progressive global reduction in the efficiency of terrestrial sinks (5, 7, 8). Major drought impacts on vegetation are to be expected in arid and semiarid biomes, which usually respond to increased water deficit with greater reductions in productivity, although drought-induced tree mortality occurs across a broad range of forest types and mean climate conditions (9). In semiarid and Mediterranean systems, several studies have recently reported increased plant mortality rates and die-off events, reduced seedling recruitment, long-term shifts in vegetation composition, reduced radial growth, and increased crown defoliation responses (9–13). Severe droughts also modify forest biogeochemical cycles by increasing nutrient loss through premature leaf fall without complete nutrient translocation (14). In addition, several studies have suggested the existence of important drought-induced cascading effects at higher trophic levels, affecting vertebrate, invertebrate, and fungal consumer populations; promoting insect outbreaks; and altering fundamental mutualistic processes, such as seed dispersal and pollination (10, 11, 15). Overall, the long-term effects of climate change–type droughts may alter forest physiological responses over extensive areas (10, 11, 15), potentially leading to extensive tree mortality and associated consequences for earth system processes (9, 16).

In the Mediterranean basin and meridional Europe, long-term climatic series and multiproxy studies have demonstrated an unprecedented and significant increase in heat waves and drought impacts over the last several decades (6, 12, 17–20). In line with these findings, the significant increase in the frequency of positive phases of the North Atlantic Oscillation during winter over the last several decades has promoted a northward shift of the Atlantic storm track and possibly triggered droughts and heat waves in southern Europe (21, 22). Comparisons of observational data over the last several decades and regional climate change simulations have identified the Mediterranean basin as a hot spot of hydrological cycle changes, and several regional and global models have consistently predicted increased drought impacts and heat waves in this area in the subsequent decades (23, 24). Droughts produce heterogeneous spatial and temporal impacts, however, and local studies have reported a wide variety of site-dependent and species-specific trends, including both positive and negative physiological responses in forest tree species (14). These differing findings preclude making generalizations based on available data at the local scale, and highlight the need for extensive community-wide assessments of the impacts of drought (11). We currently lack large-scale, integrative, community-wide assessments of drought-induced forest responses, such as tree crown defoliation, mortality, and food web responses.

European national crown condition inventories derived from the International Cooperative Program on Assessment and Monitoring of Air Pollution Effects on Forests (hereinafter the ICP Forest Inventory) provide yearly species-specific measures of the percentage of defoliation of tree crowns over a wide geographic area (25). During drought periods, a reduction in total leaf-transpiration area is a basic response of temperate and Mediterranean forests (26). Forests affected by drought reduce overall tree transpiration through adjustments in total leaf area, allowing improved tree water balance and restoring leaf-specific

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hydraulic conductivity (26). In the present study, we gathered crown defoliation data from the ICP Forest Inventories (25) to assess the macroecological impacts of drought on water-limited southern European forests over the 20-y period of 1987–2006.

Results

We first contrasted the defoliation patterns of southern water-limited forests relative to central and northern European forests. According to Fluxnet studies, the gross primary production and terrestrial ecosystemic respiration of European forests is limited by water deficit at latitudes below 52°N, whereas temperature effects predominate at latitudes above 52°N (27). Our analysis of temporal defoliation dynamics across latitudinal bands demonstrated a significant increase in crown defoliation rates over the last two decades only in southern European forests, in contrast to the stable and moderate to high defoliation levels seen in northern and central European forests (Fig. 1). From the mid-2000s to 2007, the highest defoliation levels were found in southern Europe.

To quantitatively assess the factors associated with this recent doubling of crown defoliation rates in southern European forests, we modeled crown defoliation and drought impacts in the Iberian Peninsula during 1987–2006. To study drought dynamics, we applied geographic information system–based interpolation techniques to obtain a monthly sequence of climatic maps for temperature, rainfall, and water deficit during 1951–2006. We then modeled defoliation responses using a battery of modeling approaches (*Materials and Methods*). We assessed the relative effect on defoliation of (*i*) climatic and topographic variables (i.e., temperature, rainfall, Emberger water deficit index, solar global radiation, and altitude); (*ii*) biological interactions (i.e., levels of vertebrate and insect herbivory, and fungal damage); (*iii*) soil structure (i.e., soil type and humus layer depth); (*iv*) forest management and fire damage; and (*v*) interactions between all of the independent variables explored (*SI Appendix*, Tables S1–S6). We also assessed the existence of drought-induced demographic responses by gathering tree mortality data from the Spanish National Forest Inventory (*Materials and Methods*).

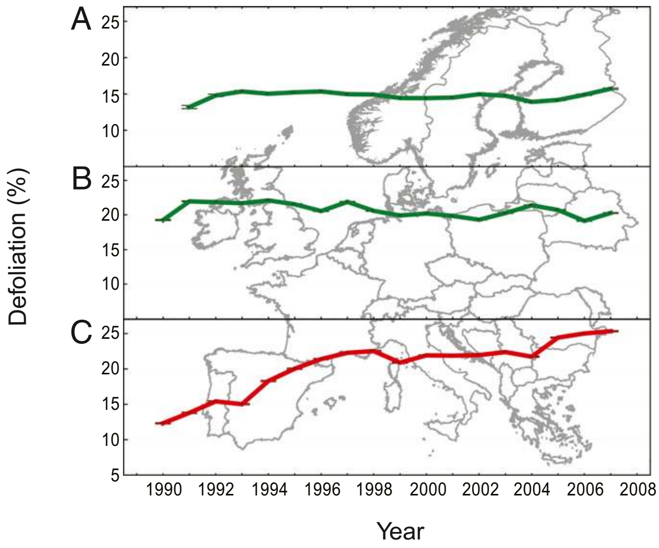

Fig. 1. A comparison of crown defoliation trends in northern, central, and southern European forests during 1990–2007. Annual trends in averaged defoliation per plot (for all species grouped) are plotted for three latitudinal bands: (*A*) northern European forests (>58°N of latitude); (*B*) central European forests (46°N < latitude < 58°N); and (*C*) southern European forests (<46°N of latitude).

We observed a significant tendency for increased mean annual temperatures and decreased annual rainfall ($P < 0.0001$) in 1951–2006, coinciding with recently published meteorological studies of the study area (28). We studied drought dynamics in the Iberian Peninsula during 1951–2006 and used time series analysis to identify trends (*SI Appendix*, Figs. S1 and S2). We found that severe droughts occurred in 2005–2006 and during a long period of drought from 1990 to 1995 that coincided with an anomalous general circulation situation (4, 22). Coinciding with this long drought in 1990–1995, we found a strong and generalized crown defoliation response in all of the tree species examined (Fig. 2). The increase in crown defoliation during 1987–2006 was statistically significant for all tree species examined (ordinary least squares fits, $P < 0.001$) (*SI Appendix*, Fig. S3).

The models indicated that drought damage was consistently the most important factor associated with the generalized increase in defoliation occurring during 1987–2006 (*SI Appendix*, Table S4). Associations with drought-related variables were significant and strongest in species distributed in more xeric areas (Fig. 3*A*). To more precisely assess how drought constrained the heterogeneity of tree physiological responses along climatic gradients, we divided the dataset for each species into quartiles of annual rainfall and independently modeled the defoliation and mortality responses to water deficit and temperature in each quartile (*SI Appendix, Materials and Methods*). We found close associations between water deficit and defoliation in the drier parts of the species' ranges (Fig. 3*A*), although each species demonstrated an idiosyncratic response pattern (*SI Appendix*, Fig. S4). The trends for increasing defoliation were consistent with mortality responses (Fig. 3 *C*–*F*). We found a significant and generalized increase of tree mortality rates between 1989–1996 and 1997–2007 by comparing the Second and Third Spanish National Forest Inventories (*SI Appendix*, Figs. S5 and S6). In turn, this increase in mortality was significantly associated with increased tree density and temperature effects in the 1997–2007 survey (*SI Appendix*, Fig. S7).

These results illustrate a complex geographical mosaic of species-specific responses to increased water deficit pressures. Our results show that most of the species studied experienced only partial recovery of crown condition after the 1990–1995 drought (Fig. 2), suggesting long-lasting chronic effects of drought on crown structure. This reduced capacity for recovery after drought is possibly due to a combination of limited investment in leaf production due to chronic stress and the presence of defoliated or dead modules in the crown that remain as nonfunctional units for several years (26).

The trophic cascade impacts of climate change–related droughts at the macroecological scale remain largely unexplored, although several previous studies have suggested the existence of important drought-induced cascading effects at higher trophic levels (10, 11, 15, 29–31). Forest drought usually results in reduced shoot growth, reduced nitrogen and water foliar concentrations, and increased allocation to secondary defensive metabolites, such as tannins. The combined effect of these factors can severely increase the mortality rates of insect herbivores during severe drought periods (29) and even truncate multiyear insect outbreak dynamics (32). Similarly, drought can significantly reduce the rate of fungal infection and sporulation capacity (33). We explored the existence of higher trophic-level effects by mapping insect- and fungal-related defoliation trends for each tree species, and compared the temporal dynamics of drought-induced defoliation, fungal damage, and insect herbivory damage. In the most widespread tree species, *Quercus ilex*, we found a sudden decrease in the impact of insect and fungal defoliation coincident with the abrupt increase of drought effects on trees in 1994–1995 (Fig. 4). We noted similar significant trends in insect defoliation in the less common, closely related species *Q. suber* (*SI Appendix*, Figs. S8 and S9). For all other tree

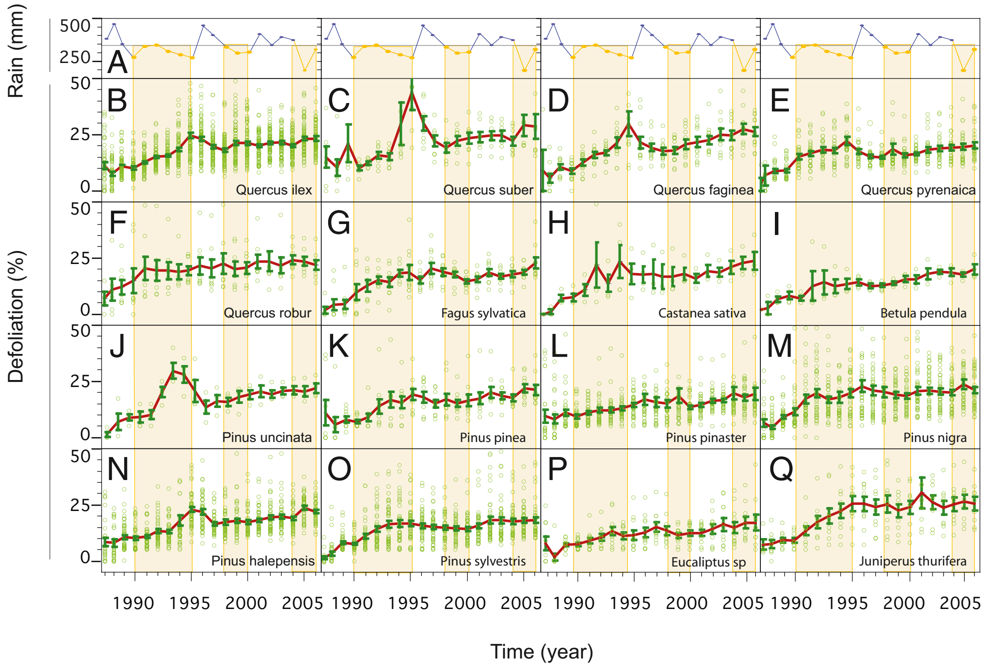

Fig. 2. Trends in crown defoliation for tree species in the Iberian Peninsula. (*Upper*) Spring–summer rainfall trends during 1987–2006. Orange bands indicate drought periods with spring–summer rainfall of <400 mm (1990–1995, 1999–2000, and 2005–2006). (*B–Q*) Crown defoliation trends for 16 main forest tree species (labelled in each panel).

species, fungal and insect defoliation patterns were unrelated or only weakly associated with drought dynamics. These results suggest the existence of species-specific drought-induced cascading effects at broad scales in the Iberian Peninsula.

Discussion

All of the forest tree species that we examined in the Iberian Peninsula have experienced a significant increase in crown defoliation over the last two decades, attributable mainly to the

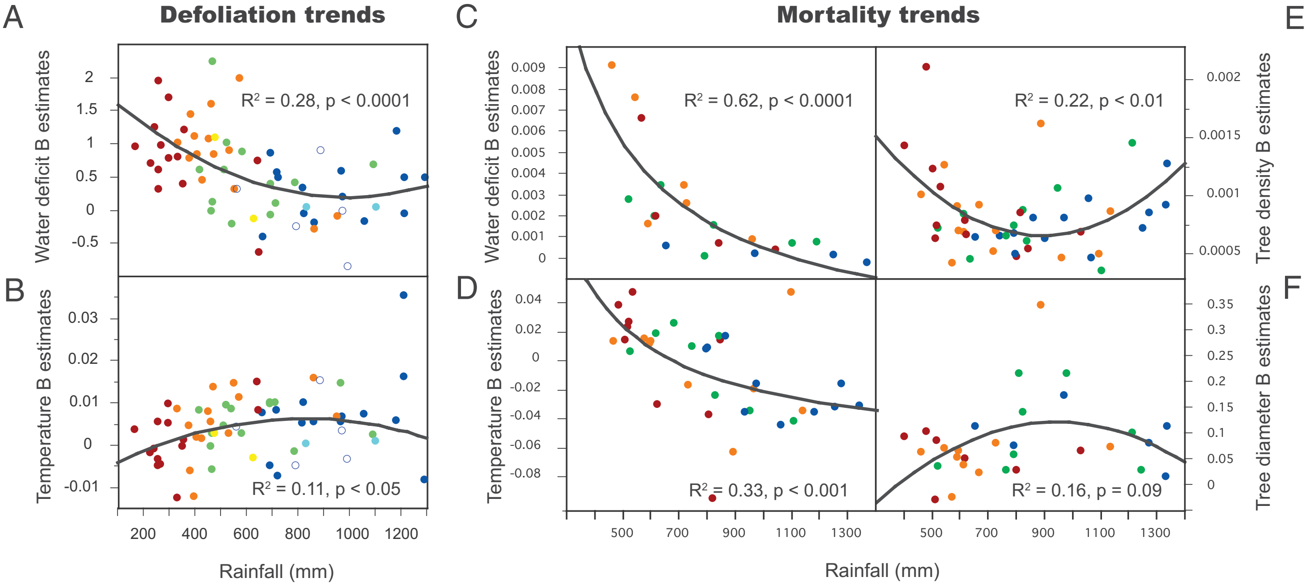

Fig. 3. Geographical variation in the effects of water deficit and temperature on crown defoliation and mortality. Defoliation is modeled as a function of Emberger water deficit and temperature in generalized linear mixed first-order autocorrelative models for each species and each rainfall quartile. Similarly, mortality is modeled as a function of temperature, water deficit, tree density, and tree diameter using generalized linear models for each species and quartile. Significant β estimates for all tree species are plotted. (*A*) Changes in Emberger water deficit β coefficient values with increased rainfall for defoliation models. (*B*) Changes in temperature β coefficient values with increased rainfall for defoliation models. (*C*) Changes in Emberger water deficit β coefficient values with increased rainfall for mortality models. Note that the water deficit variable was square-transformed to account for hump-shaped responses detected in exploratory graphical analyses. (*D*) Changes in temperature β coefficient values with increased rainfall for mortality models. (*E*) Changes in plot tree density β coefficient values with increased rainfall for mortality models. (*F*) Changes in tree diameter β coefficient values with increased rainfall for mortality models. The red dots represent 0–25 quantiles; orange dots, 25–50 quantiles; yellow dots, 0–50 quantiles; green dots, 50–75 quantiles; dark-blue dots, 75–100 quantiles; light-blue dots, 50–100 quantiles; white dots, species of restricted geographical distribution.

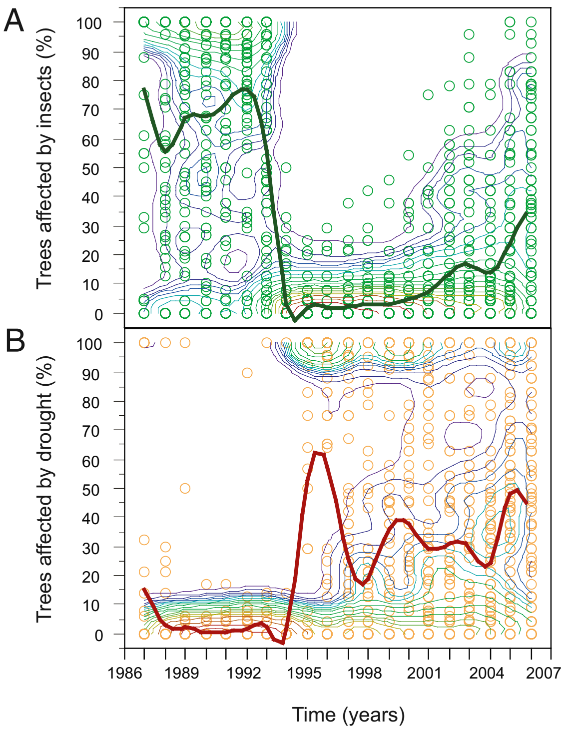

Fig. 4. Shift in insect herbivore dynamics associated with drought impacts in *Q. ilex*. (*A*) Temporal trends in the percentage of trees affected by insect defoliation in the Iberian Peninsula. (*B*) Temporal trends in the percentage of trees affected by drought. Dots represent sampled plots. A smooth 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.

impacts of drought. The observed defoliation trends are consistent with increased tree mortality rates in drier areas and with sudden dynamic changes at higher trophic levels. Our results show that Iberian forests are experiencing long-term chronic effects due to severe climate change–related droughts, and that these effects are progressively more pronounced in more xeric localities.

The reported trends toward increasing defoliation and mortality in southern European forests may have positive and negative effects on the climate system through diverse paths that remain to be quantified more precisely (34, 35). For instance, increased crown defoliation in more xeric forested areas might elevate the albedo of defoliated forests and increase sensible heat flux to the atmosphere (34, 36). Widespread crown decline also might reduce the effects of forest evaporative cooling (34), thereby possibly contributing to the reported declining trend of global land evapotranspiration (37). Notably, the increase in crown defoliation might reduce the evaporative cooling capacity of forests during hot periods and thus have a positive effect on extreme summer heat waves and long-lasting summer drought events (38). Moreover, widespread crown condition declines over large areas potentially could alter local or regional convective uplift dynamics and surface roughness effects (35, 36), as well as the production of volatile organic compounds and derived aerosols by forests, thereby possibly affecting the solar radiation balance and cloud formation processes (39).

In terms of chemical cycling dynamics, the trend of increasing defoliation (Fig. 2) suggests that the effects of drought are likely reducing the carbon sink efficiency of southern European forests, thereby contributing to the global reduction in carbon sink efficiency observed in the Northern Hemisphere and at the global scale (5, 8, 40). These results are in line with the recently reported global reduction in terrestrial net primary production over the last decade (7) and suggest that recurrent severe droughts may directly translate into generalized changes in carbon and nutrient cycling dynamics at the macroecological scale in more xeric Mediterranean areas. Indeed, previous empirical studies assert that severe defoliation events are also associated with increased nutrient cycling through leaf fall losses (14). Similarly, water availability has recently been described as a major determinant of terrestrial gross carbon dioxide uptake in Mediterranean and temperate regions (41). In line with this assertion, European carbon flux anomalies are correlated with water deficit anomalies (42), terrestrial ecosystems seem to respond to droughts with increased carbon flux to the atmosphere (27), and dendrochronological studies at the local scale suggest that important geographic areas in the Mediterranean basin are already experiencing chronic drought-induced effects on tree radial growth, growth variability, and crown condition (12, 19). In the same vein, several empirical studies have reported significant associations between crown condition decline and fine root mortality, reduced radial growth, and tree mortality (43–45).

Our present findings add to the increasing number of reports of drought-induced tree mortality responses, regional forest die-offs, and vegetation shifts around the globe (9). All of this empirical evidence highlights the need for improved long-term networks devoted to monitoring the impacts of climate change on forest health, functional trait variation, genetic variation, and forest demography (9). Critically, the diverse physiological mechanisms implicated in the reported defoliation and mortality responses also remain to be elucidated. These may include long-distance phloem transport effects, carbon reserve dynamics, metabolic unbalances, and/or hydraulic failure processes (46).

Finally, our results demonstrate that extreme droughts can substantially disrupt insect and fungi communities across extensive areas and induce long-term changes in community structure. These findings are consistent with previous studies that have reported 10-fold reductions in arthropod richness and abundance after long-lasting severe droughts and have identified foliage quantity and quality as important drivers of community structure (30, 31). Severe persistent droughts produce parallel disruptions in different groups, affecting ecto-mycorrizal fungi (15), defoliating fungi, herbivore and predator canopy insects, and parasitoids (30, 31). Bottom-up effects on vertebrate trophic chains have been poorly quantified but might occur, given the structural importance of insect resource channels in vertebrate networks in the Mediterranean basin (47, 48). Whether large-scale food web disruptions produced by drought can influence the extinction risk of vulnerable insect species and secondary consumers is an open question that warrants further research. This topic may emerge as a relevant concern related to the conservation of currently endangered biotic communities in the Mediterranean basin (49).

Materials and Methods

Data. Defoliation data 1987–2007 were gathered from the ICP Forests program (25), mortality data were provided by the Second and Third Spanish National Inventory (50), and climatic data were derived from records of the Spanish National Institute of Meteorology (*SI Appendix, Materials and Methods*).

Climatic and Crown Defoliation Maps. Interpolated climatic and crown defoliation maps were derived by applying mixed spatial interpolation methods that combine global and local interpolations (*SI Appendix, Materials and Methods*).

Statistical Analyses. For defoliation analyses, we contrasted a battery of modeling approaches including ordinary least squares, generalized linear models, spatial simultaneous autoregressive models, generalized estimating equations, and generalized linear mixed models. First-order autocorrelative terms were introduced to account for temporal autocorrelation in the models, using the CorAR1 function in the R package. Spatial autocorrelation was assessed by applying Moran's I correlograms and plotting spatial maps of the distributions of residuals. Mortality models were based on generalized linear models with a binomial error distribution (*SI Appendix, Materials and Methods*). Times series analyses were applied to assess the significance of temperature and rainfall trends during 1950–2006 (*SI Appendix, Materials and Methods*).

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

Supporting Information

Carnicer et al. / PNAS

Files in this Data Supplement:

- SI Materials and methods
- Tables S1 to S6.
- Figures S1 to S9.

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.

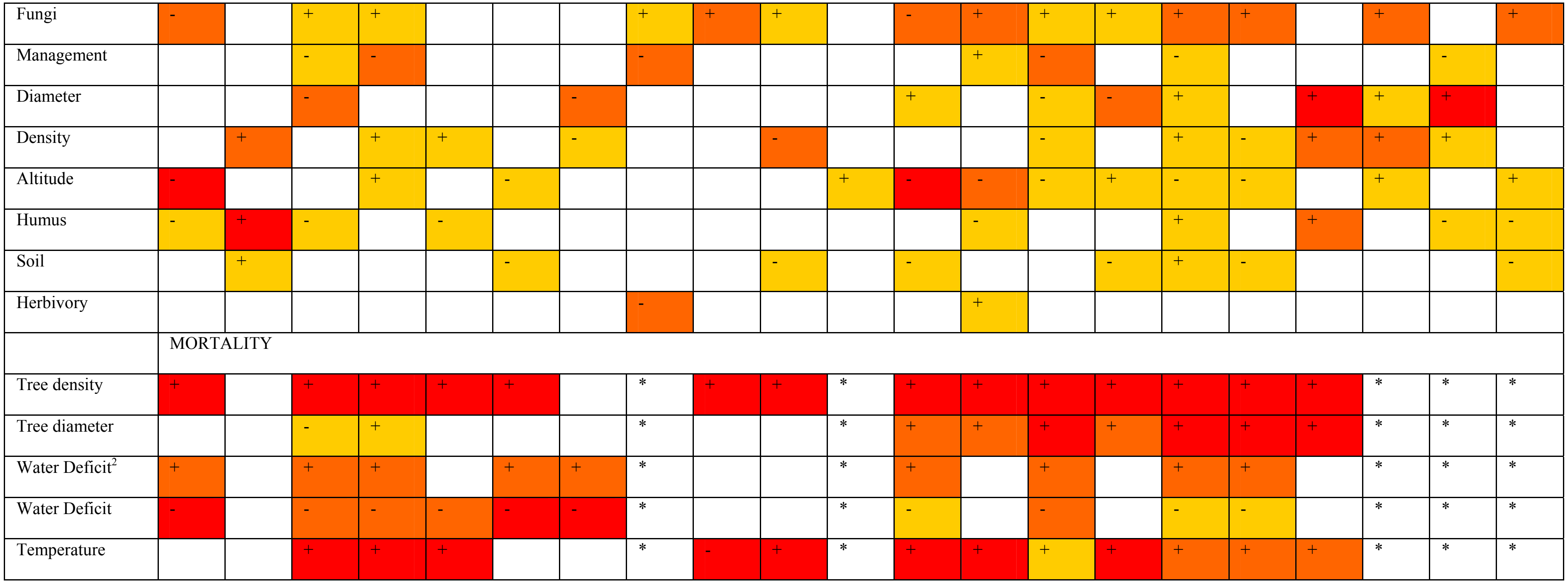
Species	*Crown Defoliation and Damage type Maps*	*GLMM-AR1 Model (All predictors)*	*GLMM-AR1 (REMB, Temp) Four Quartiles*	*GLMM-AR1 (REMB, Temp) Two Quantiles*	*GLMM-AR1 (REMB, Temp) Without Subgroups*	*Number of Plots*
Abies alba	√					2
Acer campestre	√					4
Betula pendula	√	√			√	7
Castanea sativa	√	√	√			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.

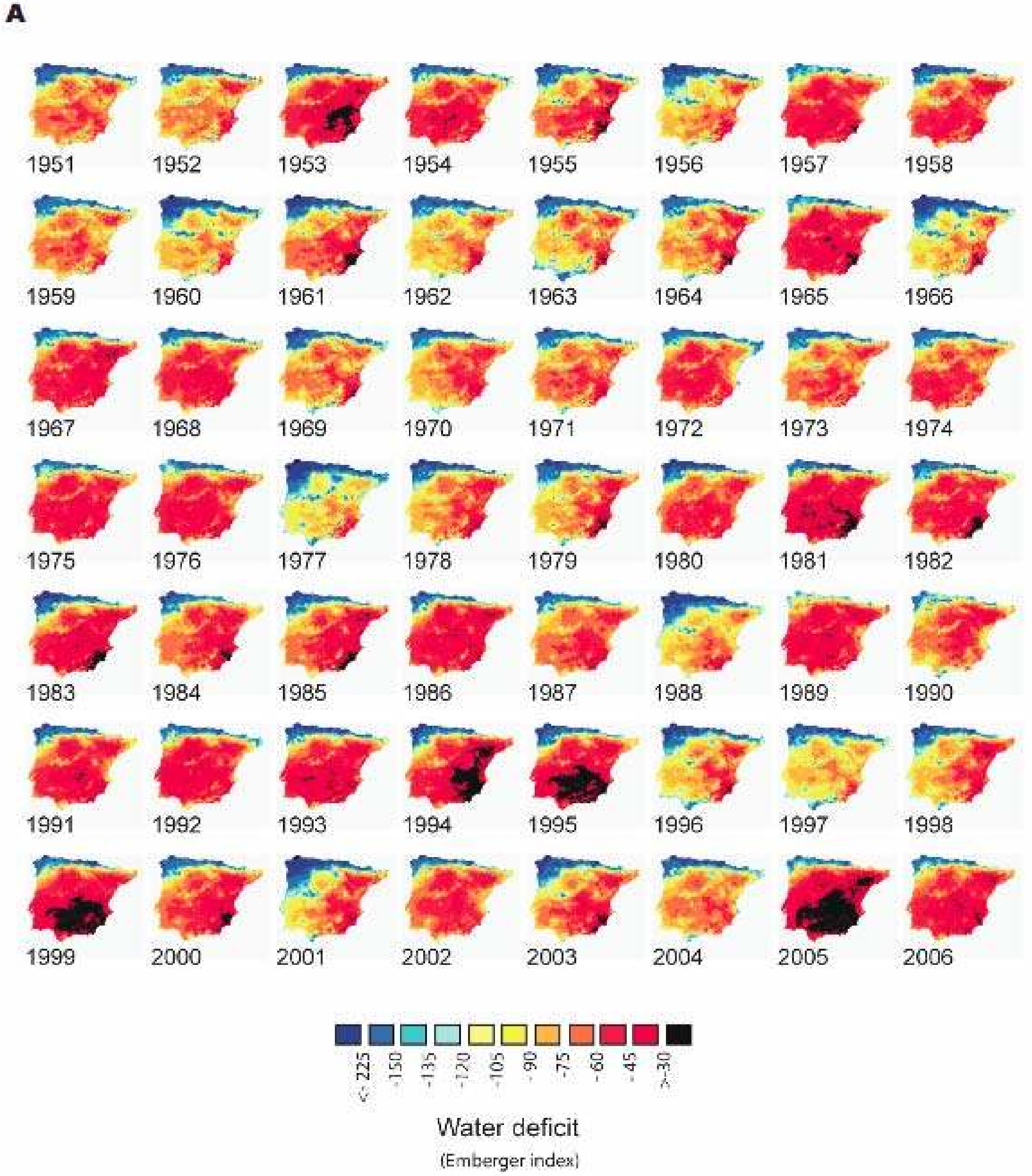
Species	Independent Variables	OLS	GLM	GLMM pql	GLMM Laplace	Spatial SAR	GEE AR1	GLMM AR1
Quercus ilex	Drought damage	+***	+***	+***	+***	+***	+***	+***
	Water deficit	+***	+*	+***	+*	+***	+***	+***
	Fire	+***	+***	+***	+***	+***	+***	+***
	Insect	-***	-***	-***	-***	-***	-***	-***
	Temperature	+***	+**	+***	+**	+*	+***	+***
	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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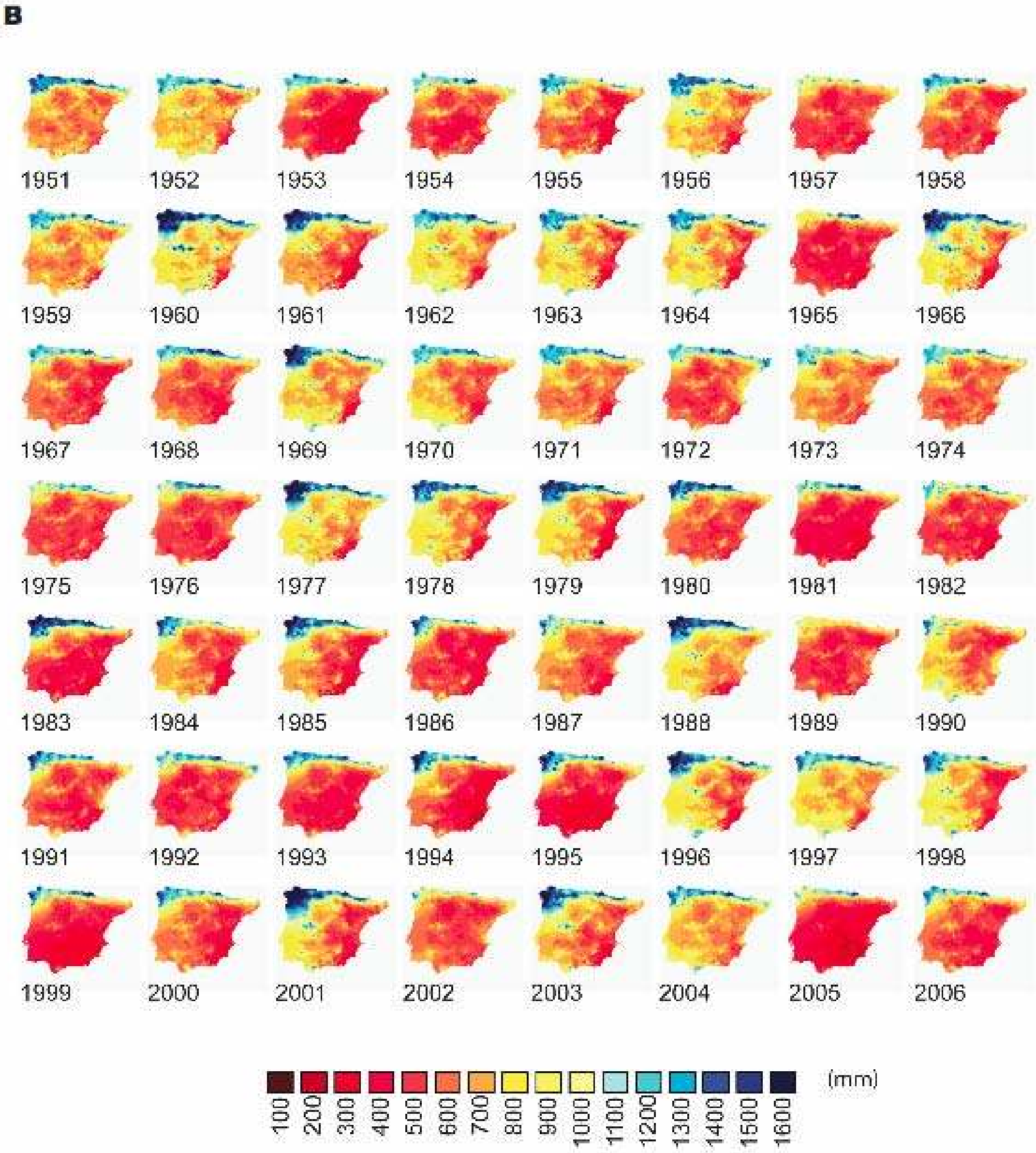
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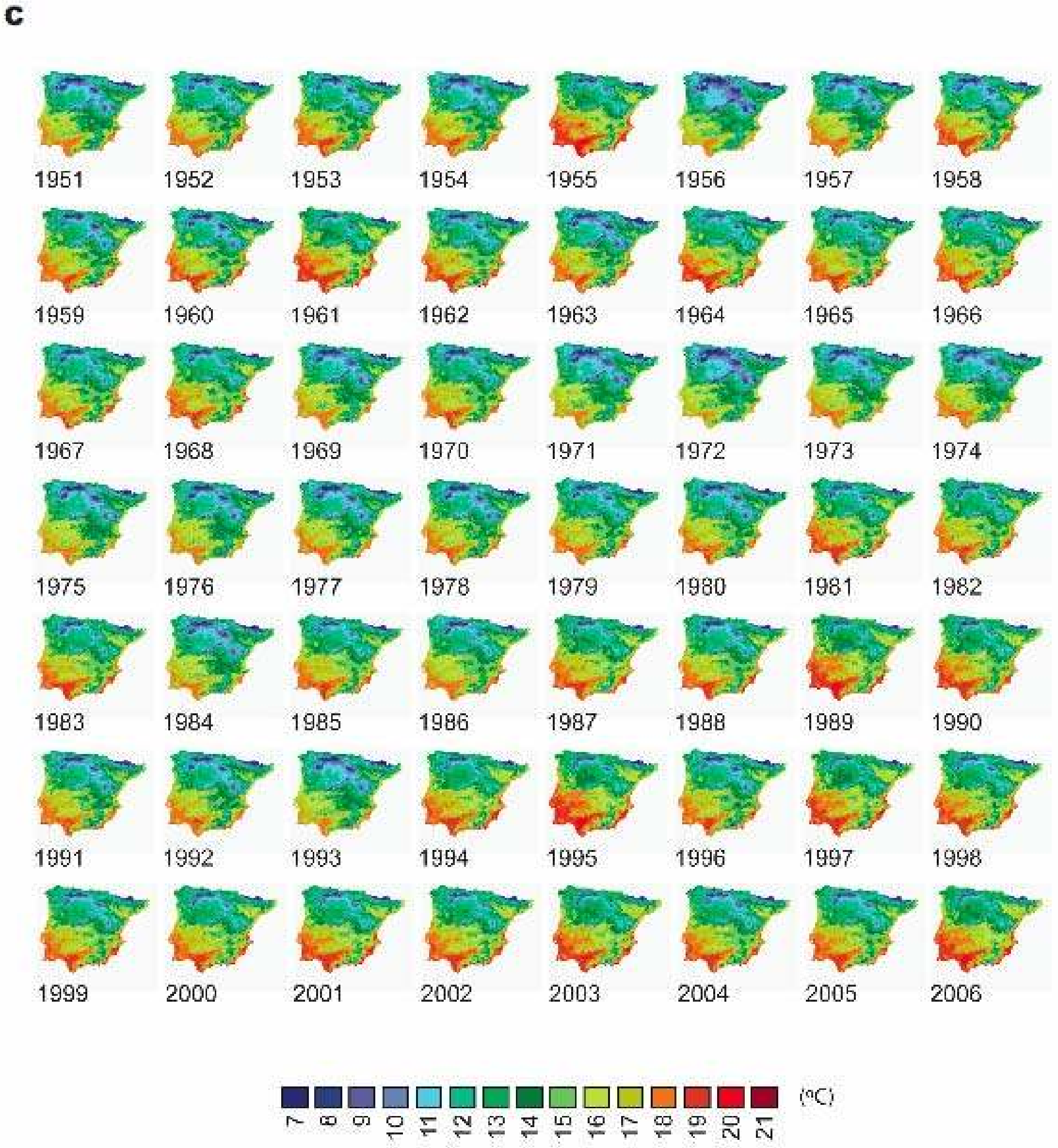
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Figure S2. Linear regression fits (black lines) and kernel smoothing functions (color lines) for one-year smoothed monthly temperature and monthly rainfall data in the sampled plots. The temporal increase of temperature and the decrease in rainfall 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; $t=15.13$; $p<0.0001$).

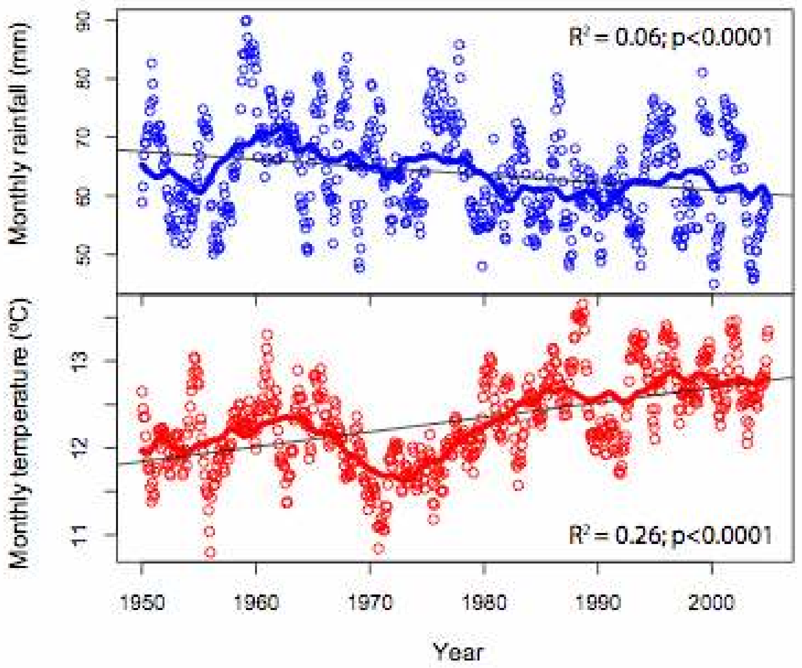
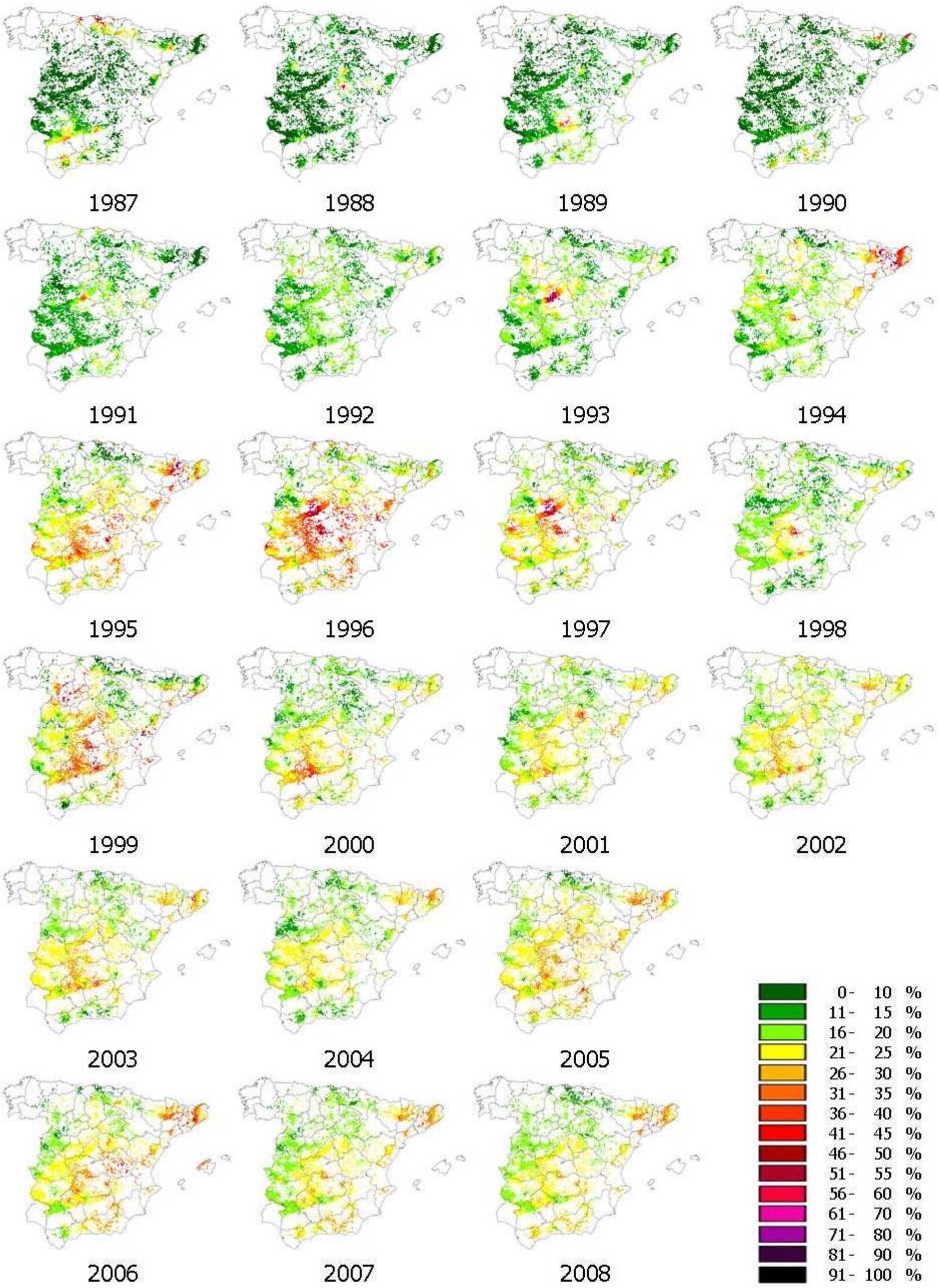
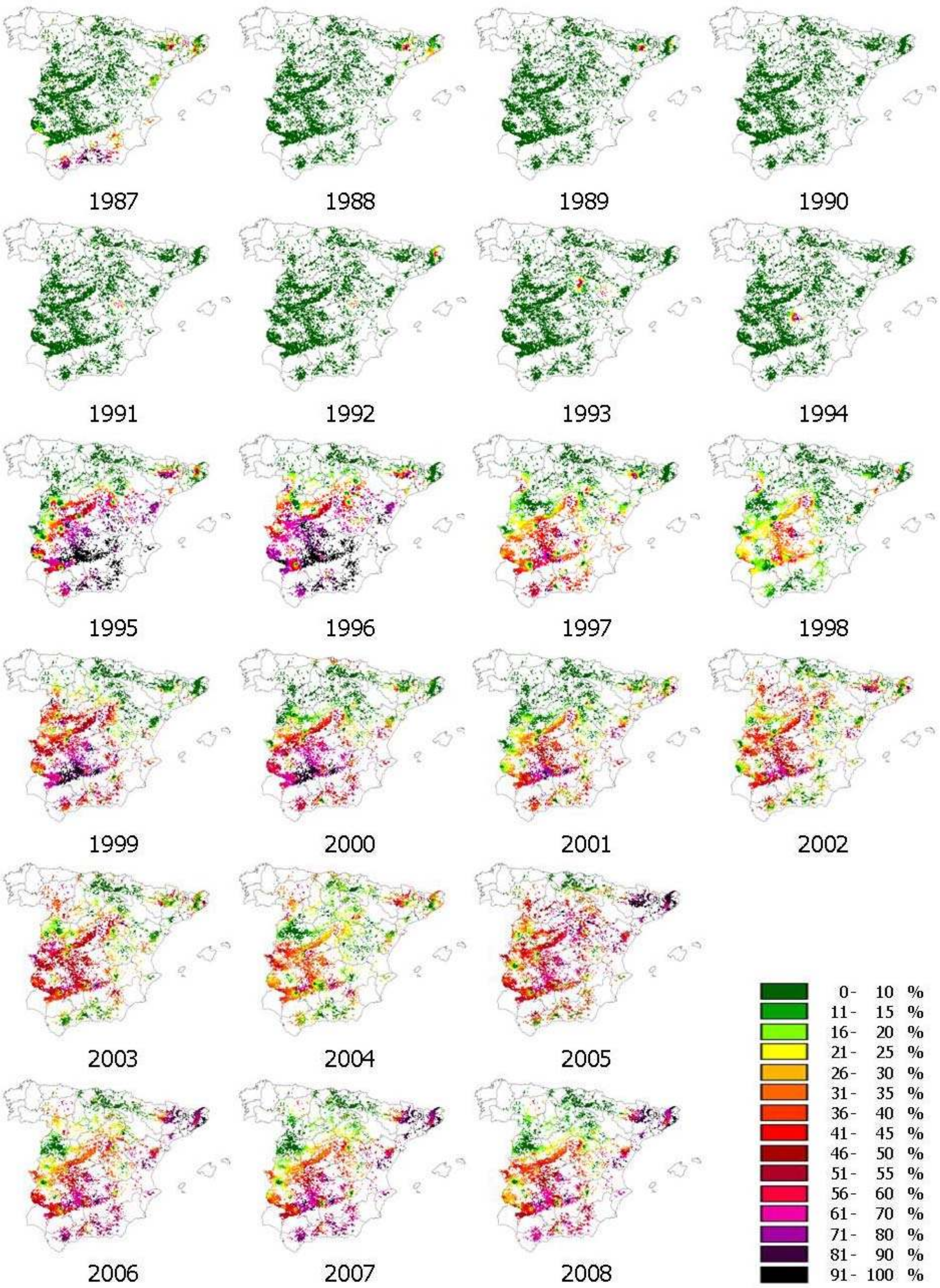


Figure S3. Maps of the percentage of crown defoliation and drought impacts (percentage of trees affected by drought per plot) for each tree species. *Quercus ilex* and *Pinus halepensis* maps are shown as illustrative examples.

Quercus ilex - Defoliation (%)



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



1987 1988 1989 1990

1991 1992 1993 1994

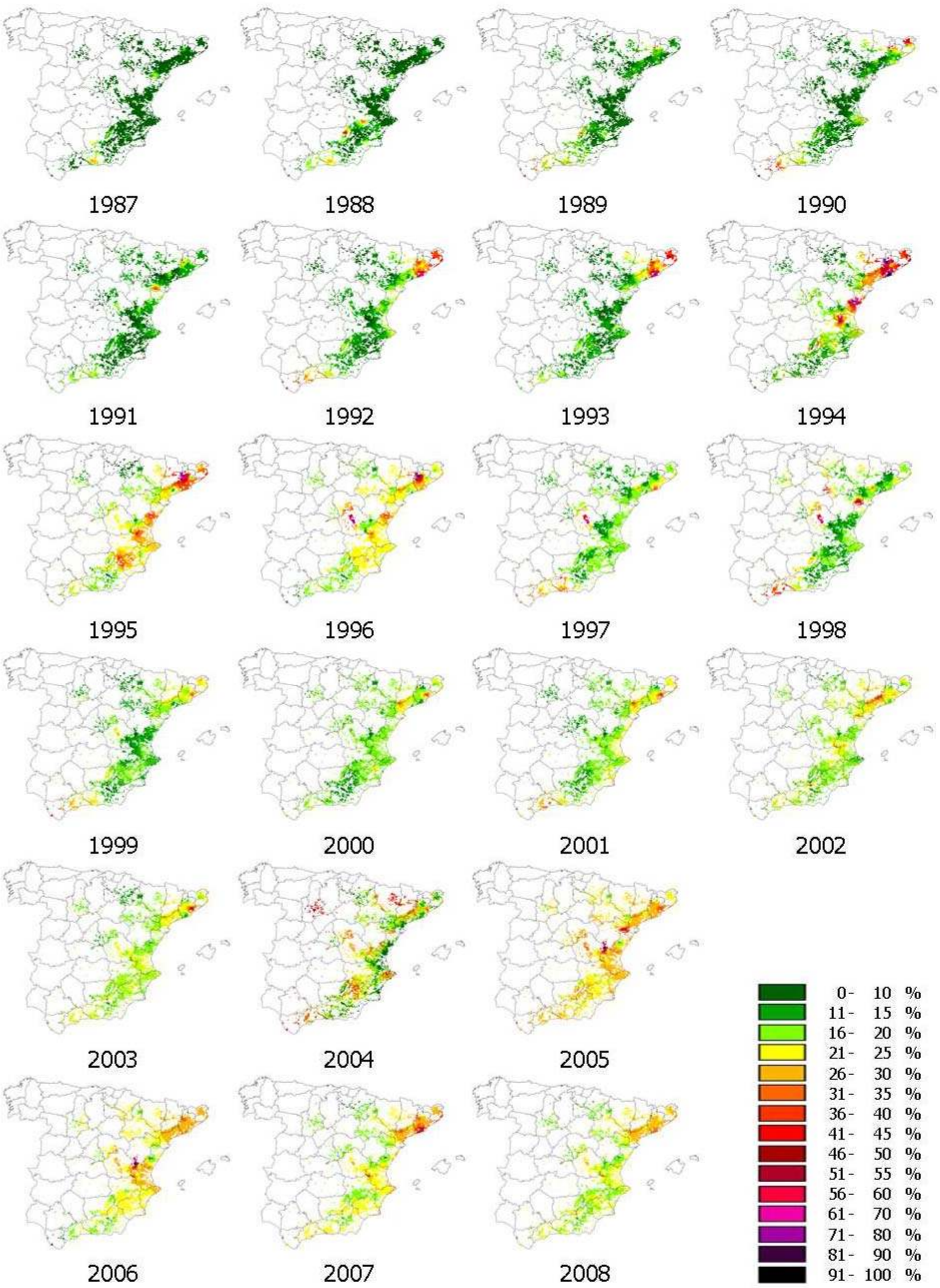
1995 1996 1997 1998

1999 2000 2001 2002

2003 2004 2005

2006 2007 2008

***Pinus halepensis* - Defoliation (%)**



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

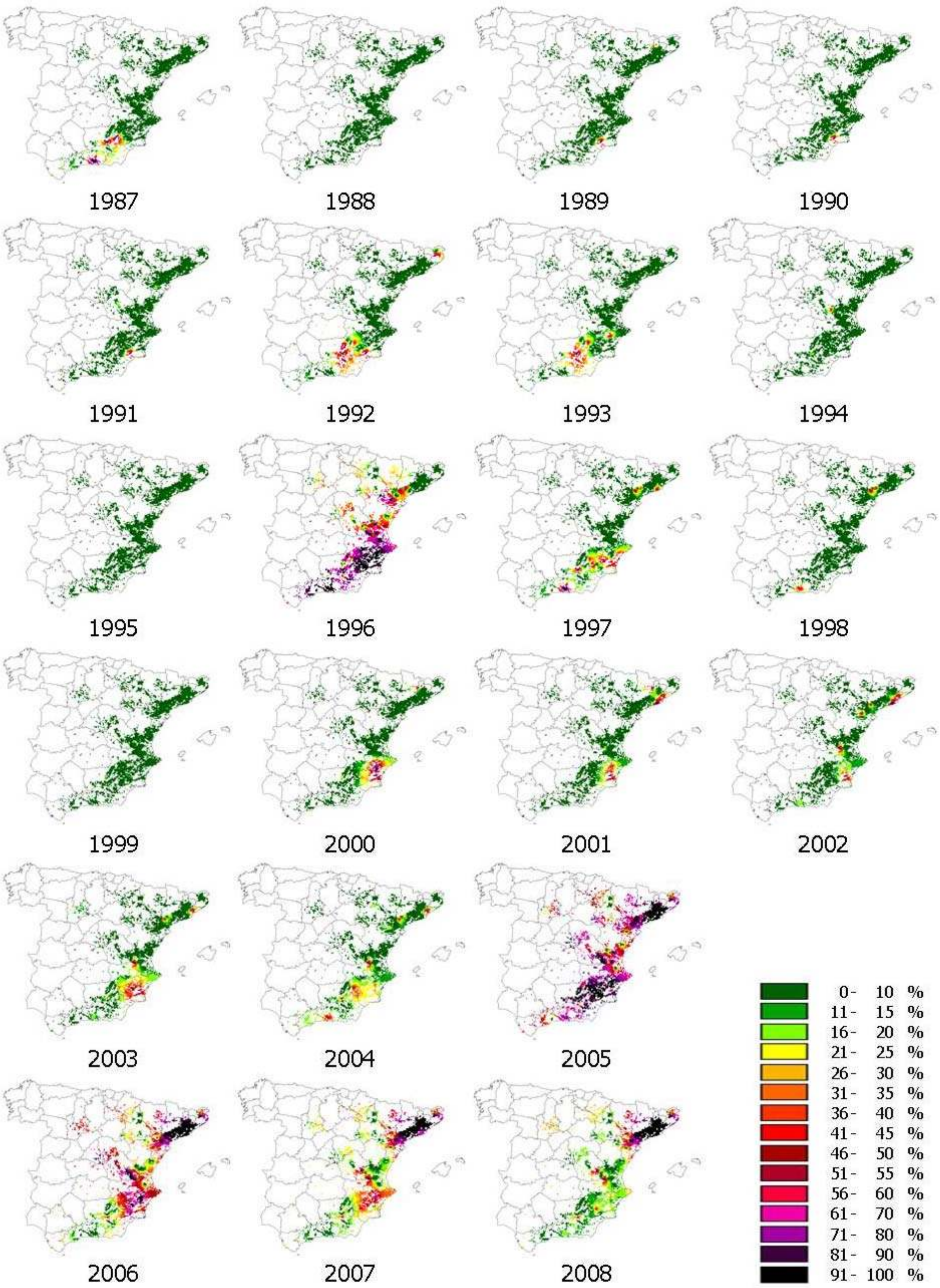


Figure S4. Observed variation in beta coefficients of GLMM-AR1 models in each rainfall quartile for tree species with large sample size (N plots ≥ 25) (Model: Crown Defoliation = b_1 REMB$_{i2}$ + b_2 Temperature). Red dots: Averaged two-year relative Emberger water deficit (REMB$_{i2}$) beta coefficients;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

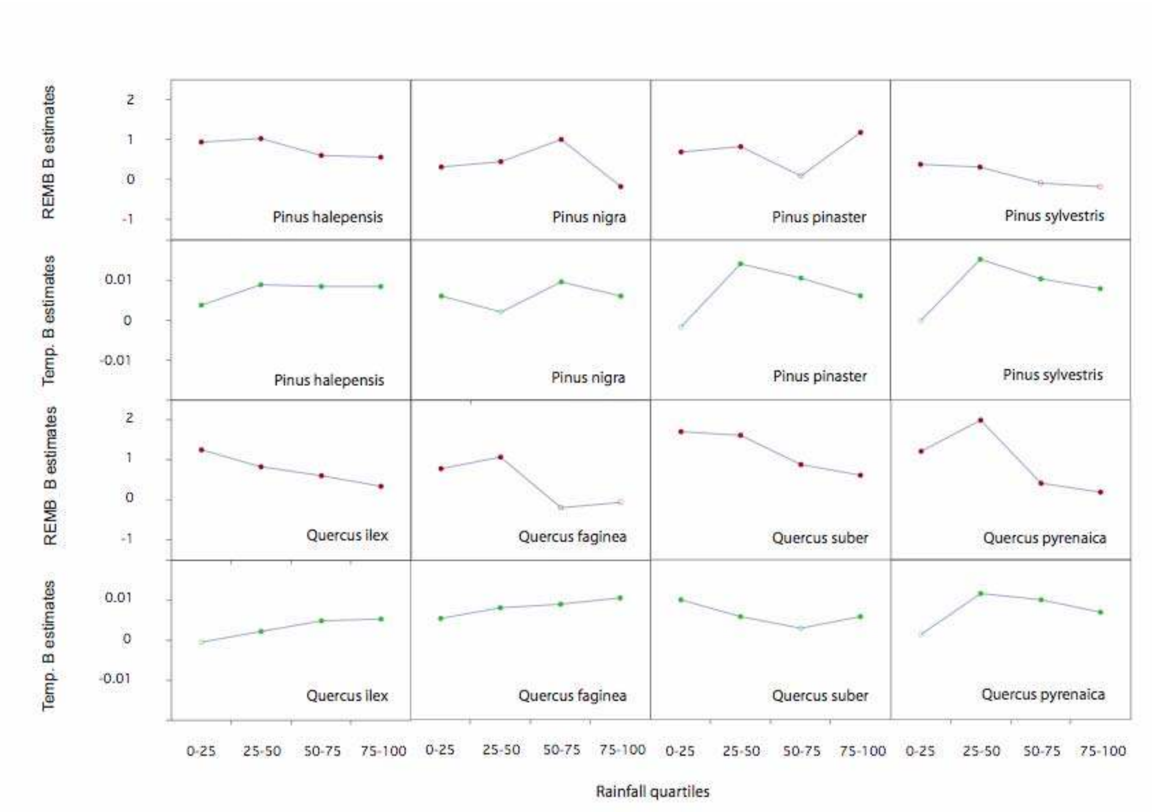


Figure S5. Observed mortality rates in the Second and Third Spanish National Forest Inventory Surveys. (*A*) IFN2 inventory (1989-1996); (*B*) IFN3 Inventory (1997-2007).

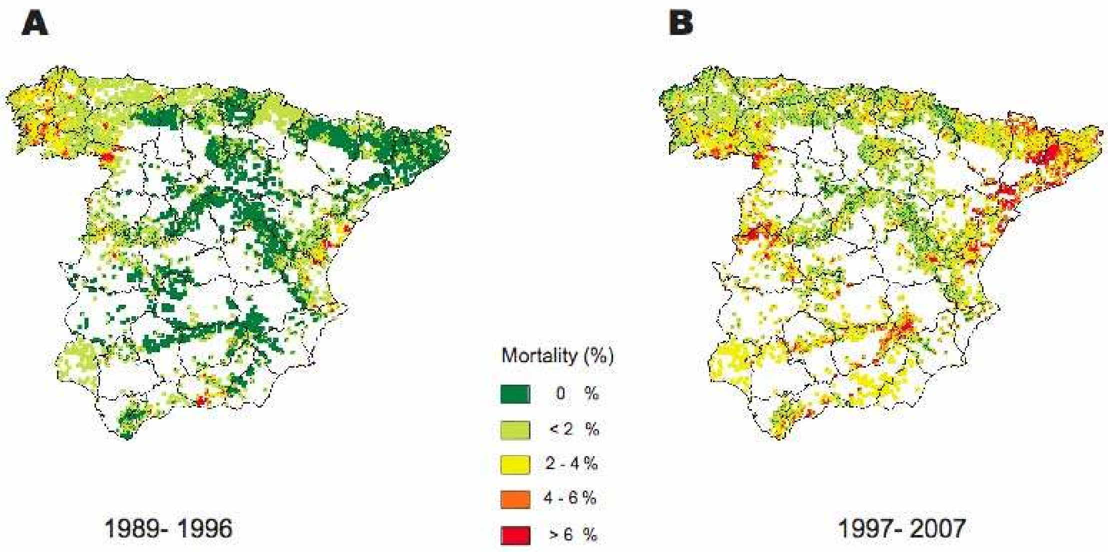


Figure S6. Observed changes in the mortality rates between the second and third Spanish National Forest Inventories (IFN2 and IFN3). Mortality rates significantly increased in all species with the exception of *Pinus radiata (F* test, ***p<0.001).

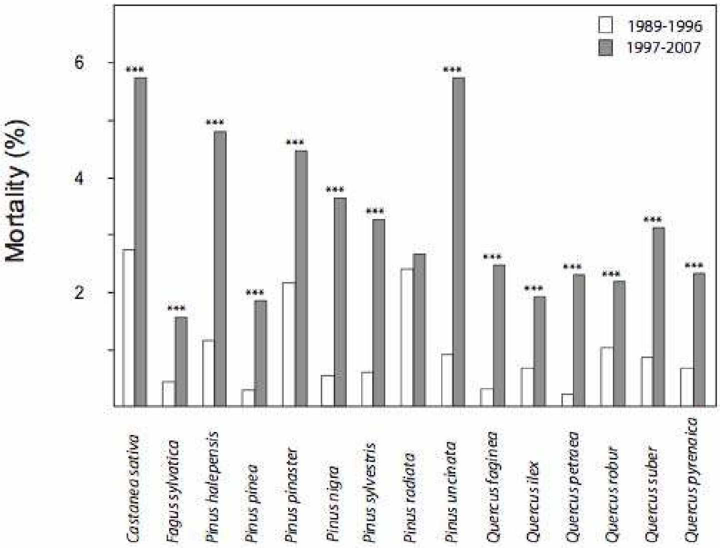


Figure S7. A comparison of tree density and temperature effects on mortality between the Second Spanish Forest National Inventory (1989-1996, IFN2) and the Third Spanish Forest National Inventory (1997-2007; IFN3). We compared 42.230 plots that were surveyed in both inventories, with a time lag of 10 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.

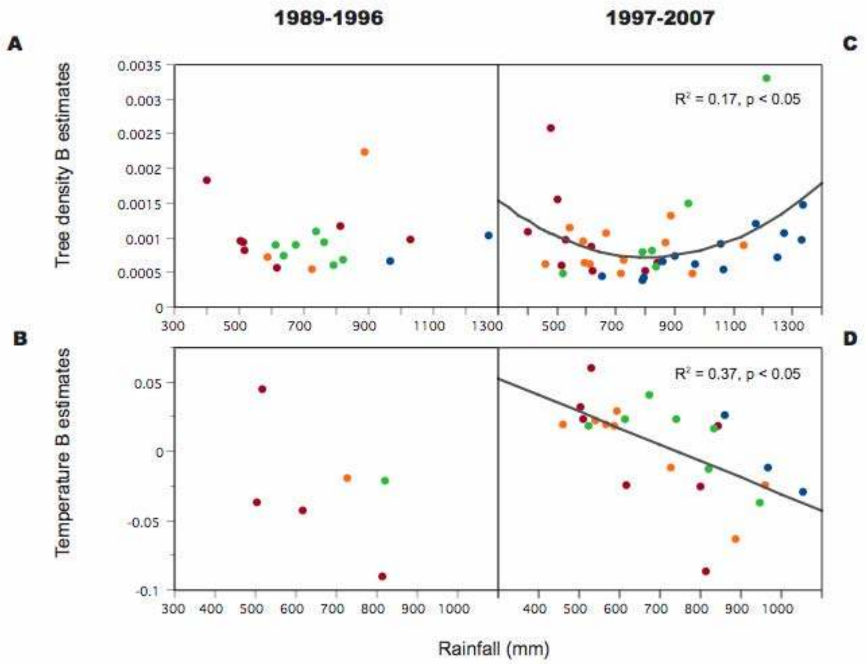
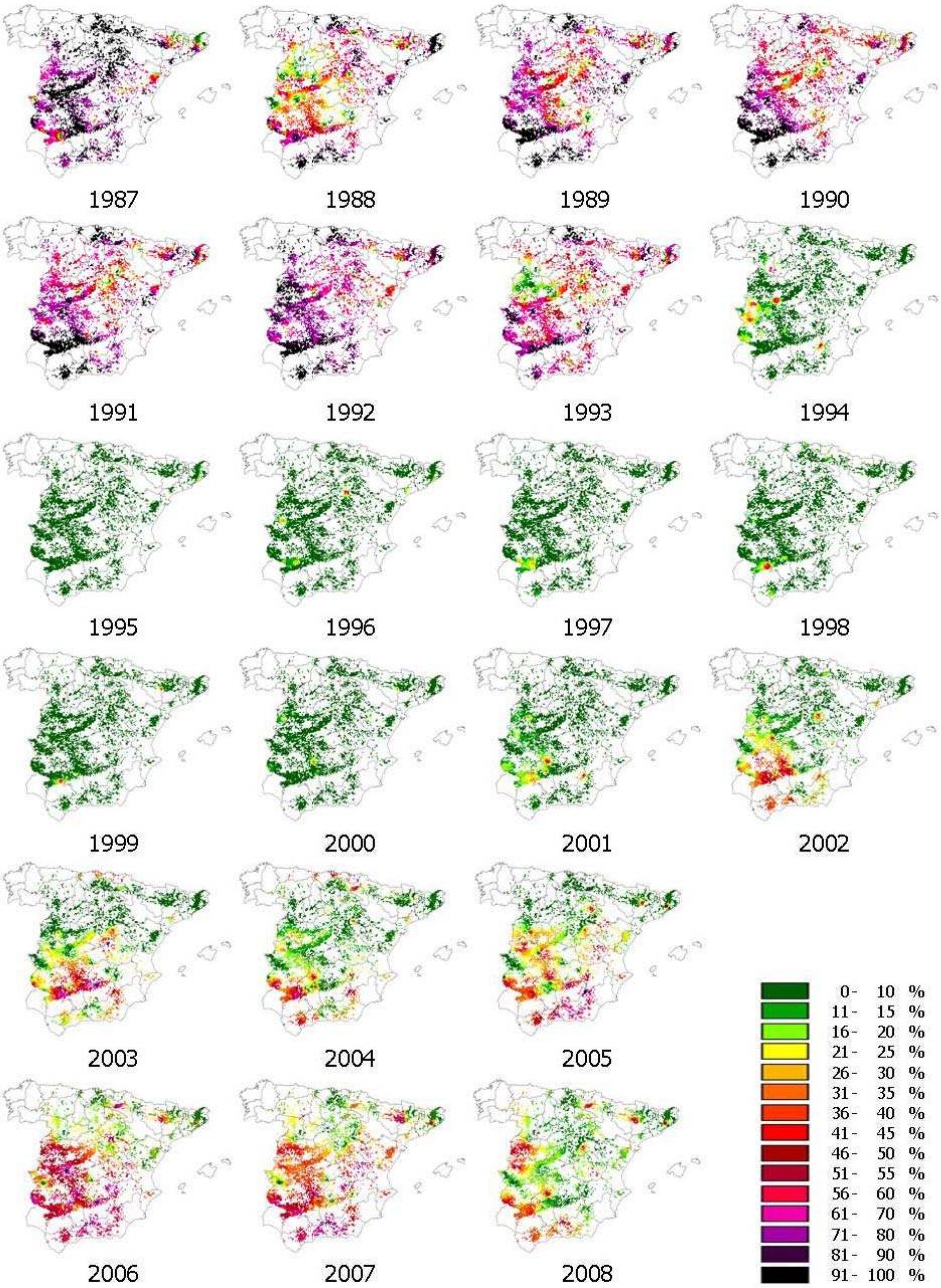
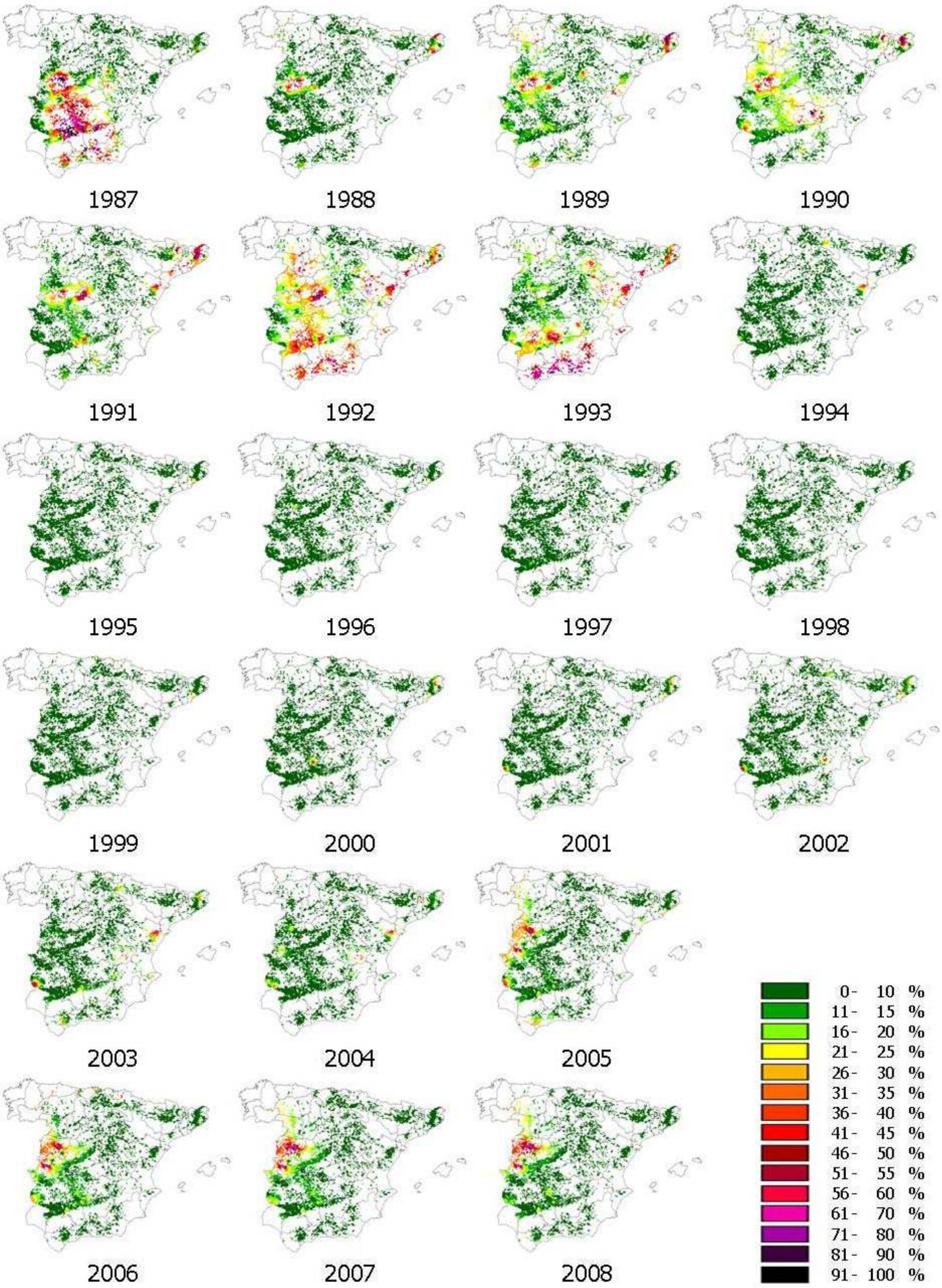

1989-1996
1997-2007
A
C
B
D
Tree density B estimates
0.0035
0.003
0.0025
0.002
0.0015
0.001
0.0005
0
300
500
700
900
1100
1300
500
700
900
1100
1300
$R^2 = 0.17, p < 0.05$
Temperature B estimates
0.05
0
-0.05
-0.1
300
400
500
600
700
800
900
1000
400
500
600
700
800
900
1000
$R^2 = 0.37, p < 0.05$
Rainfall (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)



1987 1988 1989 1990

1991 1992 1993 1994

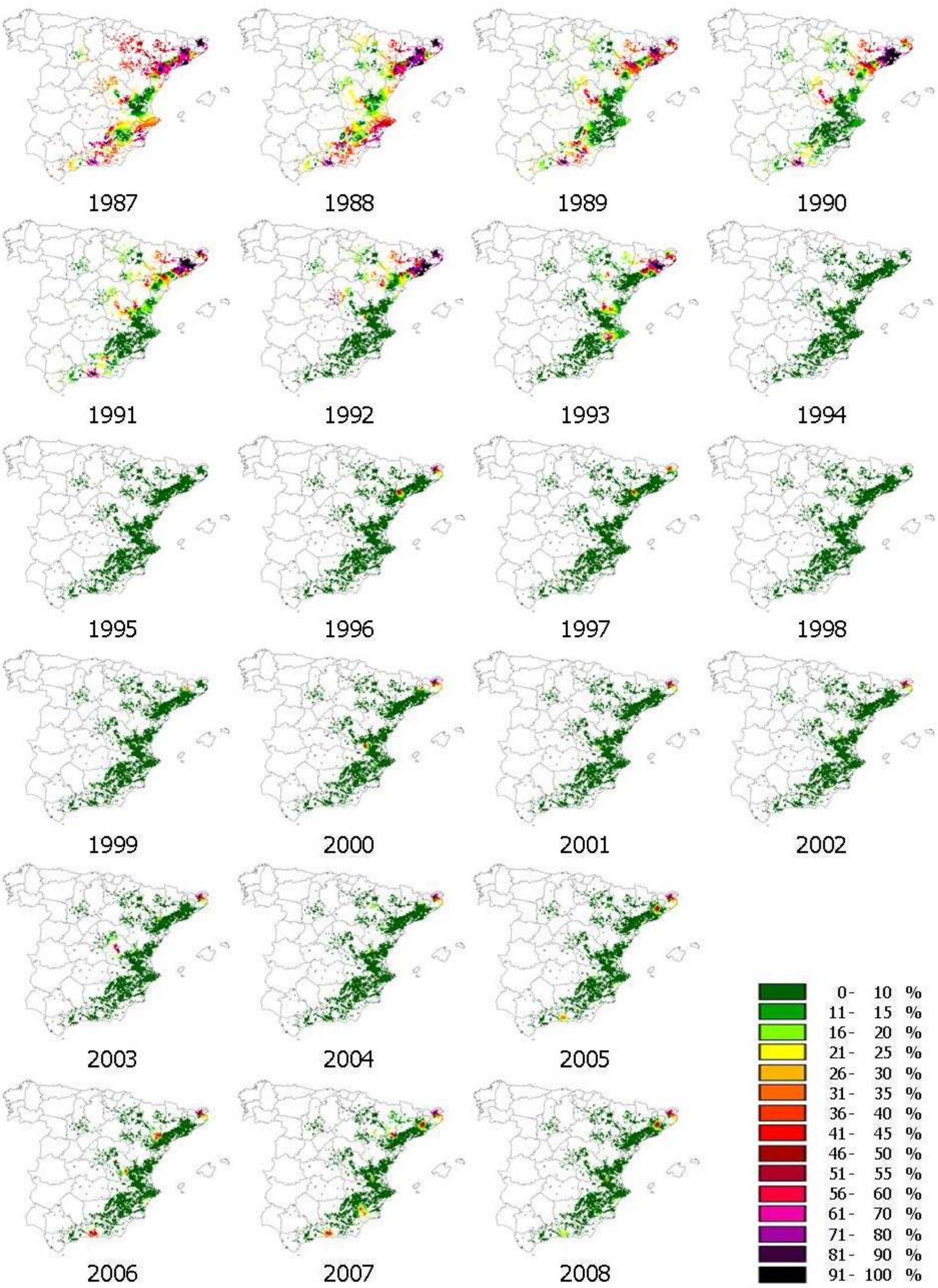
1995 1996 1997 1998

1999 2000 2001 2002

2003 2004 2005

2006 2007 2008

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



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

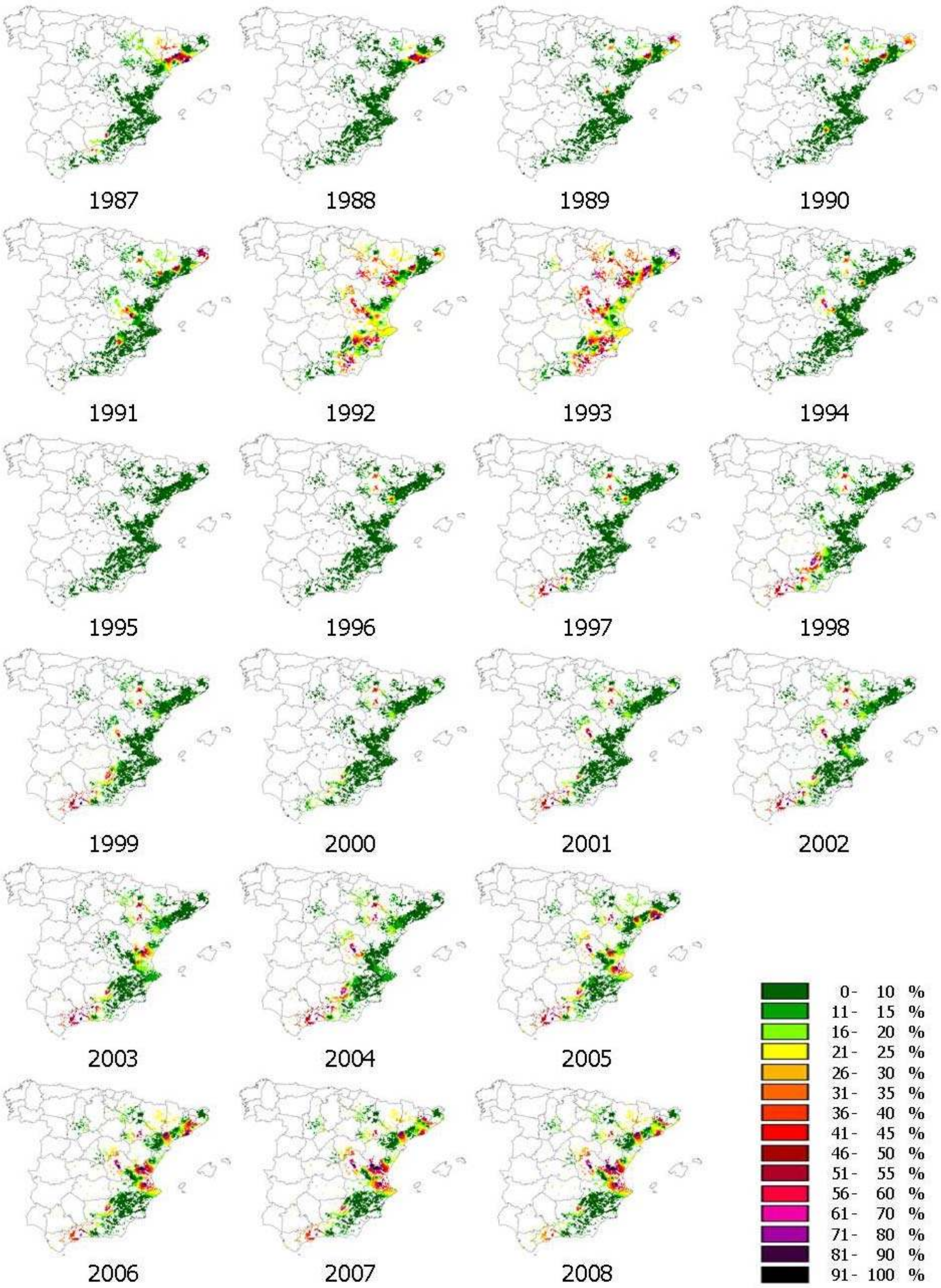
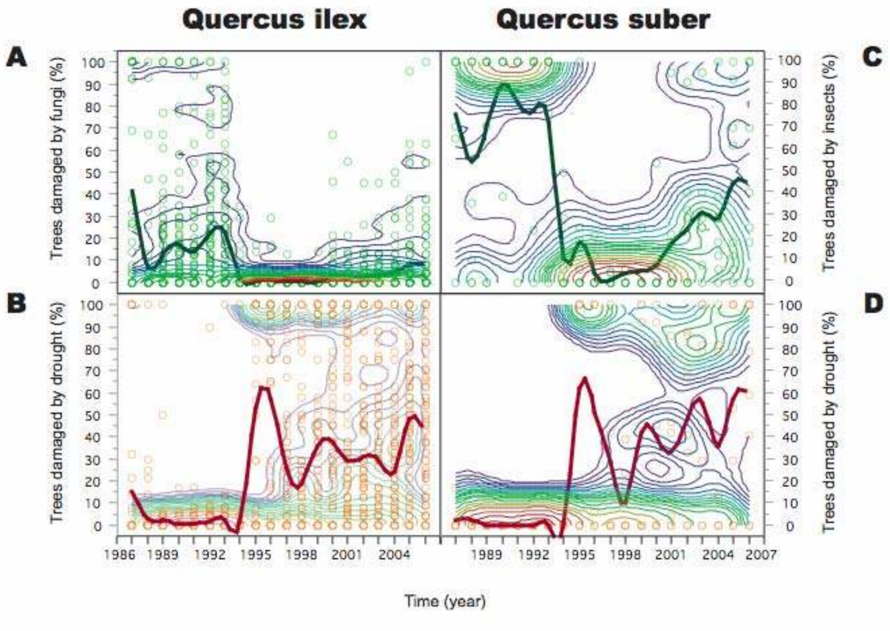


Figure S9. Shifts in fungal damage and insect damage dynamics associated to drought impacts in *Quercus ilex* and *Quercus suber*; (*A*) Temporal trends in the percentage of *Quercus ilex* trees affected by fungal defoliation in the Iberian Peninsula; (*B*) Temporal trends in the percentage of *Quercus 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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