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# Drought stress and pests increase defoliation and mortality rates in vulnerable *Abies pinsapo* forests

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# ABSTRACT

Forest ecosystems are increasingly exposed to the combined pressure of climate change and attacks by pests and pathogens. These stress factors can threaten already vulnerable species triggering dieback and rising defoliation and mortality rates. To characterize abiotic (drought, climate warmings) and biotic (pathogens) risks and their spatiotemporal patterns we quantified the recent loss of vitality for the endangered and relict Abies pinsapo forests from Andalusia, south-eastern Spain. Abies pinsapo is an iconic Mediterranean fir showing a high vulnerability to drought stress and also to several pests (Cryphalus numidicus) and root rot fungi (Armillaria mellea). We analyzed a monitoring network dataset of radial growth, defoliation and mortality from 2001 to 2017 including 1025 trees situated in three major mountain ranges (Sierra de Grazalema, Sierra de las Nieves, and Sierra Bermeja). We fitted several statistical models to determine the main drivers of changes in defoliation, a proxy of tree vigor, and mortality. Defoliation and mortality rates were much higher towards the East of the study area, mirroring the gradient from Atlantic to Mediterranean climatic conditions. In the most affected stands tree defoliation increased in response to a combination of long and severe droughts, with attacks by the beetle C. numidicus. Mortality rates increased in response to a higher defoliation rate, a lower relative radial-growth rate, long and severe droughts and a higher incidence of A. mellea. Our findings illustrate the value of monitoring networks recording changes in forest health to quantify and forecast future vulnerability of threatened tree species.

# 1. Introduction

Damaging biotic agents and climate change are two of the globalchange components tightly interrelated which negatively impact forest health and affect the sustainability of forest resources (Trumbore et al., 2015). For instance, an increasing frequency of extreme climatic events such as droughts has been shown to threaten forest health at a global scale (McDowell et al., 2020). There is also evidence for an increasing impact of forest pests and diseases contributing to changes in forest composition, structure, and ecosystem processes (Ayres and Lombardero, 2000; Cobb and Metz 2017). However, we still do not have full understanding on how forests respond to the interaction between these threats, particularly in small remnants of threatened and vulnerable tree populations. This is due to the complexity of understanding the mechanisms underlying the relationship between forest health and stress factors (Hartmann et al., 2018; Senf et al., 2018; Seidling, 2019). In this context, a loss in forest health and tree vigour may compromise the ability of forest to maintain productivity, long-term sustainability of related ecosystems services, and resilience.

Mediterranean fir forests are among the most threatened forest ecosystems in Europe (Linares 2011). For instance, several studies suggest that both abiotic and biotic stress factors significantly reduced radial growth in Mediterranean fir forests, causing extensive defoliation and triggering dieback and mortality events (Sánchez-Salguero et al. 2017; Gazol et al., 2020). This pattern is particularly relevant for those populations located at their southernmost or xeric limit of distribution, where they tend to form fragmented and relict populations. In these stands, additional stress imposed by climate change and droughts may

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make them more vulnerable to pest and pathogen attacks, ultimately threatening their existence. An emblematic species in this status is the Spanish fir (*Abies pinsapo* Boiss. subsp. *pinsapo*), currently occurring in small mountain areas in Southern Spain (Linares et al. 2010a). Abiotic stress factors such as drought seem to act simultaneously with biotic factors driving *A. pinsapo* forest dynamics (Linares et al., 2010a, 2011). In fact, the co-occurrence of drought and damage related to pests and pathogens such as the root rot fungus *Heterobasidion annosum* (Fr.) Bref. s.l. and the bark beetle *Cryphalus numidicus* (Eichhoff, 1878) have been related to periods of growth decline and high mortality rate of *A. pinsapo* (Navarro-Cerrillo and Calzado, 2004; Linares et al., 2010b). Lately, there is new evidence for the more widespread occurrence and effects of these mortality and defoliation events (Lechuga et al., 2017).

Understanding the relevance of the different stress factors driving the phytosanitary status of unique, relict *A. pinsapo* forests is of paramount importance to promote adaptive management strategies towards their conservation. Forest health status is the result of complex mechanisms acting in conjunction. Overall, we expect higher fitness (e.g., increased growth) in those areas where the environmental conditions match the optima for the species (Dobbertin 2005). In contrast, increasing levels of stress proxies such as defoliation and mortality should indicate problems in forest health and productivity (Teshome et al., 2020). Unfortunately, the relationships between these two groups of factors are not always clear, as there might be lagged responses and complex site-dependent effects between abiotic and biotic stress factors.

To address these uncertainties, systematic monitoring networks offer a unique source of information providing spatio-temporal information on forest health considering several proxies of tree vigour. Forest health assessment systems and networks are needed to understand current and future changes in biotic and abiotic stress factors and their relationship with tree health (Potter and Conkling, 2017). In Europe, the International Cooperative Programme on Assessment and Monitoring of Air Pollutant Effects on Forests (ICP Forests Network) has been monitoring forest condition using harmonized methods and criteria (Bussotti and Pollastrini, 2017). ICP assessments have allowed compiling detailed cases of forest dieback and growth decline throughout Europe, showing an increased impact of biotic and abiotic stress agents on forest health and ecosystem processes (Ferretti et al, 2014; Seidling, 2019), including drought-prone Mediterranean countries. For instance, in Spain several episodes of defoliation loss and increased mortality have been shown in several conifers (Carnicer et al. 2011; Cruz et al., 2014).

Since the late 1990 s, large areas of conifer forests in Andalusia (southern Spain) have shown dieback episodes characterized by high levels of defoliation and mortality (Sánchez-Salguero et al. 2012; Cruz et al., 2014). We used Spanish fir forests as study case to understand the critical factors affecting forest health on Mediterranean conifer forests. These forests have been monitored during the period 2001-2017 through an intensive Monitoring Forest Health Network using harmonized ICP methods (Navarro-Cerrillo and Calzado, 2004). This network is a unique setup towards understanding complex mechanisms behind species decline on its whole distribution geographical scale (Axelson et al., 2019). The objective of this research is to describe the current status of health condition of A. pinsapo forests and to analyse the temporal trends in defoliation and mortality to identify potential drivers (i. e., climatic, edaphic, dasometric and biotic variables) underlying these processes. Specifically, we aim to: (i) describe the spatial and temporal trends of annual defoliation and mortality rates, (ii) identify the main abiotic and biotic stress factors contributing to mortality and defoliation of A. pinsapo, and (iii) understand the relationships between two key forest health indicators (growth and defoliation) driving A. pinsapo forest dynamics. We discuss findings in relation to the future stability of A. pinsapo forests threatened under global change and suggesting adaptive management and mitigation strategies.

# 2. Material and methods

# 2.1. Study area

The study area consists of a long, northerly-running ridge located in southwestern Spain (Malaga and Cádiz provinces, Andalusia;  $36^{\circ}$  43' N,  $4^{\circ}$  58' W) (Fig. 1). The area ranges in elevation from 700 to 1800 m.a.s.l. with *A. pinsapo* occurring mainly in wet or mesic sites. The occurrence of these forests is concentrated in three distinct mountain regions: Sierra de las Nieves (hereafter SN), Sierra Grazalema (hereafter SG) and Sierra Bermeja (hereafter SB) (Fig. 1). These forests are subjected to water deficit in summer from June to September, a typical feature of Mediterranean climate. Average annual precipitation in the area is 1089 mm and mean annual temperature is 11.6 °C. Soils are predominantly calcareous. Most formerly pure *A. pinsapo* forests were converted by long-term human use to mixed forests with evergreen and deciduous oak species (*Quercus ilex* L. subsp. *ballota* (Desf.) Samp. and *Q. faginea* Lam., respectively), and natural and planted Mediterranean pine species (*Pinus halepensis* Mill., *Pinus pinaster* Aiton.).

# 2.2. Forest health diagnosis

In 2001, a Level I forest damage monitoring network (RED PINSAPO) was established according to a systematic sampling design  $(1 \times 1 \text{ km}; \text{N})$ = 43 plots) (Fig. 1). Plots were of variable radius, and 24 trees were selected according to ICP methodology (6 trees per quadrant, NE, SE, SW and NW) (Eichhorn et al., 2016; Consejería de Medio Ambiente y Ordenación del Territorio, 2018). Plots were dominated by A. pinsapo (cover over 50%). Tree diameter at breast height (dbh, measured at 1.3 m) was measured to calculate a relative growth rate from 2001 to 2017 (RGR). Annual monitoring of several variables used to describe tree health was performed on all tagged trees each year in August or September (i.e., crown defoliation and mortality, and biotic and abiotic damages). Defoliation was assessed visually on all the trees present in the plots into one of twenty percentage classes (intervals of 5 units between 0 and 100) in comparison to a local "reference tree" according to Level I ICP Forests standard (Eichhorn et al., 2010) by the same independent team. The use of defoliation as a tree health status condition is a practical convention, even though it cannot be considered a true tree physiological trait (Lorenz and Becher 2013). All dead trees were recorded and substituted by another tree of similar size and sociological status within the plot to estimate plot defoliation with the same number of individuals. For mortality analysis replacement trees were excluded from this study. The number of assessed trees in this period comprised 1025 A. pinsapo individuals.

The mortality rate was calculated as:

$$m = \left(1 - \frac{N_{t1}}{N_{t0}}\right)^{\frac{1}{2}} \times 100 \tag{1}$$

where  $N_{t1}$  is the number of trees that survived the census interval (2001–2017),  $N_{t0}$  the initial number of trees and *T* the time span (2001–2017). To provide a better understanding of the spatial drivers of mortality, mortality rates were also calculated for the three distribution areas (SB, SG and SN ranges) (Fig. 1).

Biotic and abiotic agents were described using standard symptoms, apparent severity (level of damage and abundance), and the inferred cause (when known) (see ICP Forests 2004). Pest severity was expressed as number of trees damaged in 2017 by several major pathogens or pests including fungi (*Armillaria mellea* (Vahl.: Fr.) Kumm.) and insects (*Cryphalus numidicus* Eich., and *Dioryctria auloi* Barbey). Finally, tree species richness per plot was also obtained (TDv).

## 2.3. Environmental variables

The dataset contains several categories of variables: mean climate (e.



Fig. 1. Location of the three major mountain ranges (sierras) where *Abies pinsapo* stands are located in south-eastern Spain (Sierra Bermeja, Sierra de Grazalema and Sierra de las Nieves).

g., temperature, precipitation), annual climate (temperature, precipitation and drought index), topographic (e.g., slope, aspect), and edaphic conditions (e.g., texture, soil pH) (Table S1, Supplementary Material). All data layers were downloaded from the Andalusian Environmental Information Network - REDIAM (http://www.juntadeandalucia. es/medioambiente/site/rediam/). Mean climate (period 1971-2000), topographic and edaphic data were extracted from the Forest Biomass project of Andalusia at a 100-m resolution (Table S1, Supplementary Material; see methods at Guzman-Álvarez et al., 2012). Annual climate variables were calculated from monthly precipitation and temperature interpolations of meteorological stations located in Andalusia at 500and 100-m resolution, respectively. To quantify drought severity, we obtained the Standardised Precipitation-Evapotranspiration Index (SPEI) calculated at 18- (SPEI $_{18}$ ) and 24-month resolutions (SPEI $_{24}$ ) from the SPEI global drought database at a 0.5° resolution (http://sac.csic. es/spei/index.html; accessed 12 December 2020). These two periods correspond to mid- and long-term duration droughts. This multi-scalar drought index allows characterizing deviations of normal waterbalance conditions by considering changes in precipitation and evapotranspiration rates (Vicente-Serrano et al. 2010).

Prior to analysis we checked potential collinearity problems among the explanatory variables using the Pearson correlation coefficient (Zuur et al., 2010). We selected variables with a pair-wise correlation lower than 0.6 (Fig. S1). From the sets of highly correlated variables, we selected those with the widest use in the literature and clearest biological meaning in relation to the study system (Table S1, Supplementary Material). The final selection included: drought index (24-month long SPEI in summer; SPEI24), average total precipitation (ptt), slope and insolation (ins) of each stand, soil depth (ps) as well as the relative growth rate (RGR) and stand Dbh in 2017 (D2017). Finally, we also considered the pest severity by *Armillaria mellea* (Am), *Cryphalus numidicus* (Cn) and *Dioryctria auloi* (Da) and tree diversity of the plot (TDv).

# 2.4. Spatio-temporal patterns of defoliation and mortality rates

Kernel Density Estimation (KDE) was used to assess the spatiotemporal correlation patterns of tree defoliation and mortality rates. This is a non-parametric method which estimates the probability density function of random variables and has been widely used in forest ecology (Wandresen et al., 2019). The distribution patterns of defoliation and mortality rates were explored based on finite data samples (O'Brien et al., 2012), and KDE was calculated for each year of the time series (2001–2017) weighting observations by the number of dead individuals recorded and the defoliation levels. We selected a Gaussian kernel density (KD) function, and the optimal bandwidth was estimated using leave-one-out least-squares cross-validation for bivariate KD bandwidths estimation in the *sparr* R package (Davies et al., 2018).

# 2.5. Relationships between abiotic and biotic strees factors and defoliation

The response function of defoliation with respect to environmental and management variables was studied in each of the monitoring network plots. We applied linear mixed-effects models (Pinheiro and Bates 2000) to study the relationship between stand defoliation and the climatic, topographic and forest related conditions of each stand in the period 2001-2017. Models were created for all sites and for each site, separately (excluding Sierra Bermeja due to the low number of points). We used plot identity as a random factor to account for the longitudinal structure of the data (i.e., defoliation was assessed in the same trees during the study period). Defoliation was log-transformed (log(x + 1)) prior to the analyses. As explanatory variables we included all noncollinear variables indicated in previous section. We also considered potential interactions between the drought index and other variables (see full model variables in table S3). To determine the impact in the results of outliers and extreme values, we evaluated the fit of the model graphically by examining the residuals and the fitted values (Zuur et al. 2010).

The resulting models that were generated with the different

combinations of the explanatory variables were ranked according to the second order Akaike Information Criterion (AICc). The  $\Delta$ AICc of each model was calculated as the difference between the AICc of each model and the minimum AICc found for the set of models. The  $\Delta$ AICc can be used to select those models that best explain the response variable because those  $\Delta$ AIC values lower than 2 indicate the suitability of the selected model while values above 7 indicate a poor fit as compared to the best model (Burnham and Anderson 2002). The relative importance of the explanatory variables included in the selected models was calculated based on the Akaike weights of each model. For each variable, the importance is calculated as the sum of model weights over all models including each variable. The larger the importance of the wariable is present the more relative importance the variable has.

Model comparison and averaging were used to select the best model and to assess the relative importance of each variable (Burnham and Anderson 2002). After selecting those models having a  $\Delta$ AICc lower than 10 (i.e., the best models), the coefficients for each one of the explanatory covariates included in the model were estimated by means of model averaging. To elucidate potential influences of outliers and extreme values, we evaluated the fit of the model by graphical examination of the residuals and the fitted values (Zuur et al. 2010).

Statistical analyses were carried out in the R environment v 3.6.3 (R Core Team, 2020). The "Ime" function of the *nlme* package was used to fit the linear mixed-effects models (Pinheiro et al., 2014). The *MuMIn* package was used to perform the multi-model selection (Barton 2012). The *visreg* package was used to visualize results of the linear mixed-effect models (Breheny and Burchett 2017).

## 2.6. Models of mortality rates

We studied the variability of mortality rates across regions and environmental factors with a combination of different analyses. First, we calculated the mortality time series for each individual tree. It comprised the number of years from the year of plot establishment (2001) to the date of tree death (up to 2017). Second, we used the Kaplan-Meier estimation method to create tree survival curves and to determine the unadjusted probabilities of survival (with associated 95% confidence intervals) for the studied period (2001-2017). Chi-squared test was performed to determine if significant differences were present among the survival probability of each mountain region, and pairwise multiple comparison adjustment with the Bonferroni's correction was used to test differences between groups (Logan et al., 2005). Third, we explored the relation between mortality (i.e. time to death) and the three sets of non-collinear variables (i.e. tree level characteristics, health status and site conditions) using Cox proportional hazard models (Cox 1972). As trees were nested in plots, we controlled by plot id using two separate methods, clustering and random effect (O'Quigley and Stare, 2002). As results were similar, we present for simplicity the clustering method. We implemented separate models for each group of variables and all combined. For each model we performed an automatic selection of variables based on AIC following a similar procedure that Esquivel-Muelbert et al. (2020). Finally, we carried out and compared separate cox proportional hazard models for the two mountain regions with mortality (SG and SN). These analyses were performed using the following R packages: stats, survival, survminer, ggplot2, ggfortify, and ranger (Kassambara and Kosinski, 2018; Therneau and Grambsch, 2000).

# 3. Results

# 3.1. Spatial and temporal trends in defoliation and mortality rates

Defoliation and mortality rates varied significantly across the distribution of *A. pinsapo* (Figs. 2–4, Supplementary Table S2). At the distribution area, defoliation (mean  $\pm$  SD) slightly increased from 2001



**Fig. 2.** Defoliation trends of *Abies pinsapo* in Sierra de Grazalema (green line), Sierra Bermeja (black line) and Sierra de las Nieves (red line). The solid lines and dots represent the average defoliation while the shaded area represents the standard error for the mean ( $\pm$ SE). The solid blue line shows the drought index (average SPEI) in the Sierra de las Nieves site. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 3.** Survival probability graph of *Abies pinsapo* using Kaplan-Meier mortality estimation for the three main distribution locations (SB, Sierra Bermeja, black line; SG, Sierra de Grazalema, green line; SN, Sierra de las Nieves, red line). X-axis, years since the beginning of the monitoring of the health status of the trees on the study plots (2001–2017); Y-axis, proportion of surviving trees (survival rate). The shaded area indicates the standard error of the estimate for each location. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

 $(D_{2001} = 16.67 \pm 1.66\%)$  to 2017  $(D_{2017} = 19.94 \pm 1.09\%)$ , decreasing in SB  $(D_{2017} = 13.12 \pm 2.24\%)$ , and increasing in SG  $(D_{2017} = 18.64 \pm 3.88\%)$ , and SN  $(D_{2017} = 20.98 \pm 0.98\%)$ . Defoliation of *A. pinsapo* showed a clear spatial pattern, increasing from western sites (SB) to the northeast (SN) (Fig. 4).

SG SG 4080000 08000 SN 000090t 0000090 SB 4040000 H040000 1040000 4020000 1020000 280000 300000 320000 340000 300000 320000 280000 340000 2017 SG SG 000080 SN 060000 SP SP

2001



Fig. 4. Kernel density analysis of A. pinsapo defoliation rate (left, percent defoliation over 24 trees per plot; adimensional density scale) and mortality (right, adimensional density scale) in 2001 (top) and 2017 (bottom) across the species distribution area based on a Kernel density model. X and Y axis showed longitude and latitude respectively (CRS: ETRS89 / UTM 30 N).

Mortality was also higher in SN (1.03  $\pm$  0.30 % year<sup>-1</sup>) than in SG (0.74  $\pm$  0.28 % year  $^{-1}$  ), with high differences until the year 2012, but without significant differences at the end of the period (P = 0.272) (Fig. 3). In SG we noticed a significant change in the mortality trend after this year, meanwhile the mortality trend was stable over the whole period in SN. There was not mortality in SB during the time span of this study. Similarly, the KDE approach highlighted some areas in SN with high mortality rates, with lower incidence in SG and no mortality in SB (Fig. 4).

# 3.2. Models of tree defoliation

Defoliation did not differ significantly (P < 0.01) between sites (Table S2 Supplementary Material). A. pinsapo defoliation was not directly associated with any of the tree, health or site factors considered (Table 1). We only found a significant interaction between the presence of C. numidicus and long-term droughts (SPEI24) (Table 1), indicating that higher defoliation levels appeared at the combination of higher pest and drought levels (Fig. 5).

# 3.3. Models of mortality rate

Tree mortality rates significantly differed among zones according to the Kaplan-Meier analysis (Fig. 3;  $\chi^2 = 11$ , P < 0.01). A. pinsapo mortality risk across the species distribution area depended on the characteristics of tree-level attributes, health status and site conditions (Table 2). Mortality models including all traits performed better than models with either group of risk factors alone (Table 2). Models with

#### Table 1

Defoliation model of *Abies pinsapo*. Multimodel inference results of the averaged best models explaining % defoliation (conditional average on models < 7 AICc). Defoliation factors include characteristics from the trees: size, represented by tree diameter at breast height in 2017 (D<sub>2017</sub>), tree species richness (TDv), relative stem diameter growth rates (RGR); health status: pest severity expressed as number of trees damaged by *Armillaria mellea* (Am), *Cryphalus numidicus* (Cn), and *Dioryctria aulloi* (Da); and site conditions: and site conditions: drought represented as the Standardised Precipitation-Evapotranspiration Index (SPEI24) for the 24-month in the period 2001–2017, insolation (ins), soil depth (ps), slope (pte) and total precipitation (ptt). Interactions between variables are indicated with ":". In bold, the coefficients that significantly differ from zero (p < 0.001).

	Value	Std.Error	Adjusted SE	z value	Pr(> z )
All locations					
(Intercept)	1.159	0.186	0.186	6.223	0.000
Cn	0.010	0.007	0.008	1.281	0.200
Da	-0.047	0.026	0.027	1.759	0.079
D <sub>2017</sub>	0.001	0.001	0.001	1.180	0.238
RGR	-0.138	0.093	0.096	1.436	0.151
SPEI24	-0.008	0.014	0.014	0.574	0.566
Cn: SPEI24	-0.005	0.001	0.001	3.682	0.000
D2017: SPEI24	0.000	0.000	0.000	1.860	0.063
ps	-0.001	0.001	0.001	0.813	0.416
ptt	0.000	0.000	0.000	0.824	0.410
TDv	0.030	0.045	0.046	0.664	0.507
Am	0.009	0.023	0.024	0.393	0.694
Di: SPEI24	-0.003	0.007	0.007	0.505	0.614
ins	-0.022	0.115	0.119	0.188	0.851
pte	0.000	0.004	0.004	0.072	0.943
ptt: SPEI24	0.000	0.000	0.000	0.122	0.903
Am: SPEI24	0.001	0.005	0.005	0.177	0.860



**Fig. 5.** Defoliation rate increased as a function of long droughts (quantified as the Standardised Precipitation-Evapotranspiration Index-SPEI24 for the 24-month period, x axis) and pest severity expressed as number of trees damaged by *Cryphalus numidicus* (Cn) (y axis).

only health plot status traits predict mortality better than models containing only tree-level attributes (Table 2).

Relative growth rates, defoliation changes and damage by *A. mellea* were the best predictors of tree mortality (Table 3). Specifically, we found higher mortality risk for slow growing trees, with defoliation above 50%, high occurrence of *A. mellea* and after drought events

# Table 2

Comparison between different Cox proportional hazard models predicting tree mortality across *Abies pinsapo* forests. Models are sorted according to AIC values.

Tree-level attributes	Health status	Site condition	AIC	Wald test	Model description
RGR***	$\Delta DF^{***} + Am^*$	SPEI24 ***+ins	1064	297.7***	Full model
	$\Delta DF^{***} + Am + Cn^*$		1119	579.7***	Health status only
$D_{2017}^{*} + RGR^{***}$			1300	133.1***	Tree-level only
		SPEI24 + ps + pte + ins	1596	0.54	Site conditions only

Models vary according to risk factors considered, including tree-level characteristics: tree size, represented by tree diameter at breast height in 2017 (D<sub>2017</sub>) and relative stem diameter growth rates (RGR), health status: defoliation rate between 2001 and 2017 ( $\Delta$ DF), pest severity expressed as number of trees damaged by *Armillaria mellea* (Am), and *Cryphalus numidicus* (Cn); and site conditions: drought represented as the average of Standardised Precipitation-Evapotranspiration Index (SPEI24) for the 24 month period, insolation (ins), soil depth (ps), slope (pte) and total precipitation (ptt). Significance levels: \*\*\*: p < 0.001, \*: p < 0.05.

### Table 3

Coefficients from the best (lowest AIC) Cox proportional hazard model of *Abies pinsapo* tree mortality for the full model and with mortality including interactions (":") between biotic agents (*Armillaria mellea* (Am) and *Cryphalus numidicus* (Cn)) and the rest of variables.

	coef	exp(coef)	se(coef)	robust se	z	Sig.		
All sites (n = 1023, d = 117)								
RGR	-1.85	0.16	0.79	0.51	-3.64	***		
Am	-1.21	0.30	0.63	0.38	-3.21	**		
Cn	-0.81	0.44	0.30	0.21	-3.92	***		
$\Delta DF$	0.06	1.06	0.00	0.00	11.89	***		
SPEI24	-1.62	0.20	0.52	0.62	-2.60	**		
ins	-2.28	0.10	1.29	1.12	-2.05	*		
RGR:Cn	-0.40	0.67	0.24	0.20	-2.00	*		
Cn:ins	1.22	3.39	0.40	0.30	4.04	***		
Am:ins	2.24	9.43	1.02	0.62	3.63	***		

For each risk factor selected in the best model we provide the coefficient (coef), its standard error (SE), exponent (exp(coef)), and statistical significance (\*\*\* < 0.0001, \*\* < 0.001, \*< 0.05). Risk factors include: stem diameter growth rates (RGR), defoliation rate between 2001 and 2017 ( $\Delta$ DF), number of trees damaged by *Armillaria mellea* (Am) and *Cryphalus numidicus* (Cn), drought represented as the average of Standardised Precipitation-Evapotranspiration Index (SPEI24) for the 24-month period and insolation (ins). The number of trees included in the analysis (n) and the number of dead trees (d) are shown.

(Fig. 6). Patterns were similar across sites, although the relevance of variables varied (Fig. 6, Table S7). In SN fast growing trees with higher defoliation were at higher risk, whilst in SG pests, mid-term droughts (SPEI<sub>18</sub>) and tree diversity impacted mortality (Table S7). Pest and pathogen incidence interacted significantly with tree and site factors (Table 3). Specifically, *A. mellea* and *C. numidicus* produced higher mortality risk at higher insolation levels (see Fig. 7).

# 4. Discussion

We provide here the first comprehensive, spatio-temporal assessment of *A. pinsapo* mortality and defoliation based on a systematic health monitoring network. Previous studies of health status in these forests have been highly localized or restricted to a small number of plots (Linares et al., 2009, 2010a; Lechuga et al. 2017). We show that a combination of stress factors is likely to be the most common cause of defoliation and mortality across the species distribution area in southern Spain. This is in line with previous studies showing how elevated tree mortality rates are one of the main symptoms of climate change impact



**Fig. 6.** Risk factors identified in the Cox proportional hazard models predicting tree mortality across *Abies pinsapo* forests for all the study area (black line) and the two areas with more mortality: Sierra de las Nieves (green line), and Sierra de Grazalema (red line). Shaded areas represent the standard error for each coefficient and dotted lines represent non-significant risk factors. Selected explanatory variables include relative stem diameter growth rates, defoliation rate between 2001 and 2017, pest severity expressed as number of trees damaged by *Armillaria mellea* and *Cryphalus numidicus*, and drought severity represented as the average of Standardised Precipitation-Evapotranspiration Index (SPEI24) for a 24-month period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

on drought-prone *A. pinsapo* forests (Linares et al., 2009, 2011, Navarro-Cerrillo et al., 2020a).

# 4.1. Spatial and temporal trends of defoliation and mortality rates

Species-oriented forest health networks can describe the spatial and temporal patterns of tree defoliation and mortality over large areas (Carnicer et al., 2011) but also the characteristic health patterns of forest ecosystems of regional concern (Duque Lazo et al., 2017; Sánchez-Cuesta et al., 2021). This information is of paramount importance for vulnerable populations situated at the geographic or climatic edges of their distribution or in xeric areas which are under high risk of being impacted by severe and long droughts. Specifically for *A. pinsapo*, we observed a consistent pattern in defoliation and mortality rates, which were higher in the North Eeastern part of the study area (i.e. Sierra de las

Nieves) and related to drought and key pest damages. In the other locations (Sierra Bermeja and Sierra de Grazalema) defoliation and mortality rates were lower, and health drivers could not be identified. These contrasting findings across regions coincide with the dissimilar bioclimate types developed for *A. pinsapo* (Fernández-Cancio et al., 2007). Sierra de Grazalema and Bermeja locations show a clear Atlantic influence in comparison with the Mediterranean character of the highly affected Sierra de las Nieves. The higher mortality and defoliation rates spreading to the east during the study period, partially agree with previous studies based on species distribution models (Fernández-Cancio et al., 2007; López-Tirado and Hidalgo, 2014; Navarro-Cerrillo et al., 2021), which reported a rapid reduction of the optimal areas for *A. pinsapo* in Sierra de las Nieves, probably connected with a decrease of Mediterranean convective conditions.



Fig. 7. Interaction between abundance two agents (*Armillaria mellea* and *Cryphalus numidicus*) and insolation to predict tree mortality across *Abies pinsapo* forests for all the study area. Shaded areas represent the standard error for each coefficient. Interaction is shown across three levels of abundance (1, 3 and 6 trees infected in the plot).

# 4.2. Drivers of defoliation rates

The annual defoliation rate of *A. pinsapo* showed moderate average values (17.6%), similar or slightly lower to those obtained for other European tree species (Klap et al., 2000; Cruz et al., 2014; Michel et al. 2014). The increasing defoliation trend showed here has been also identified in the European ICP Network for the most abundant tree species (Fischer et al., 2010). Particularly, defoliation of *A. pinsapo* was enhanced by an interaction of long droughts and damage related to attacks by the bark beetle *C. numidicus*. These results are consistent with spatial distribution models which identified drought-related climatic variables and microclimatic drivers (e.g., aspect) among the most relevant factors to explain current *A. pinsapo* distribution (Navarro-Cerrillo et al., 2021).

# 4.3. Drivers of mortality rates

Tree mortality is one of the most relevant variables assessed by European forest condition networks (Lorenz and Becher 2013; Neumann et al., 2017). Our empirical results from the A. pinsapo monitoring network show high values of accumulated tree mortality (11.53%), and mortality rates (0.90 % year<sup>-1</sup>), significantly higher than that obtained from other forest health networks (0.010–0.015 % year<sup>-1</sup>, Van Mantgem and Stephenson, 2007) and other Mediterranean species (e.g., Q. ilex, 0.153%) in southern Spain (Sánchez-Cuesta et al., 2021). High A. pinsapo mortality rates have been related to biotic (Navarro-Cerrillo et al. 2003; Sánchez et al., 2007) and abiotic stress factors (Linares et al. 2010a) such as pests, pathogens and drought. In our study, mortality was higher for slow growing trees, with defoliation above 50%, high occurrence of A. mellea and after major drought events. Tree diversity was not a significant factor, but recent studies have highlighted the relationship between drought impacts in forests and functional diversity modulating, among others ecosystem functions, their vulnerability to climate-related stresses (see Grossiord, 2020). It should be better investigated if more diverse neighbourhoods increase functional diversity and buffer or provide resilience to A. pinsapo as it has been indicated for A. alba during drought (Gazol and Camarero 2016).

Mortality risk increased with the occurrence of pathogenic fungi such as *A. mellea* and the insect *C. numidicus*. Both biotic agents are extremely relevant in the dynamic of *A. pinsapo* forests, particularly under stressing abiotic conditions (Arista et al. 1997). Specifically, we found higher mortality rates when these biotic agents occurred in sites of high insolation. We hypothesized that in these highly exposed areas (e.g. southern slope and higher altitudes) *A. pinsapo* is more vulnerable to the attack of pests, eventually producing mortality events. Other possible causes of the increase in mortality not studied here is the incidence of other pathogenic fungi such as *Heterobasidium annosum* (De Vita et al., 2010); or complex interactions (senescence with age, lack of suitable management, etc., Lechuga et al., 2017). Despite multiple causality of mortality, our results highlight some of the most relevant drivers of mortality on *A. pinsapo* forests, which can provide a better understanding of Spanish fir mortality.

Forest and natural resource managers must develop new adaptive strategies to respond to climatic changes (Nocentini et al., 2017). Those strategies should be supported by relevant information on observed and projected climate impacts. Regional and local forest health monitoring networks supply on-the-ground forest data for operational-scale adaptation measures to adapt forest ecosystems to climate change (Gustafson et al., 2020). Our results showed some key element for an adaptive silviculture for climate change on *A. pinsapo* forests: control of high-risk pests or maps of mortality pattern to orient the establishment of operational-scale adaptation plots to test specific ecosystem adaptation treatments to climate change through a gradient of adaptive approaches. Those actions contribute to integrate new conceptual tools and processes into silvicultural decisions and management in a context of climate change.

# 5. Conclusions

Regional and local forest-health monitoring networks are useful tools to provide robust data field changes in vigour and health of vulnerable tree species as we illustrated with the iconic Mediterranean fir A. pinsapo. The data recorded in the Spanish fir monitoring network allowed recording changes in forest health condition and assessing cause-effect relationships between tree status (defoliation and mortality), abiotic (drought, topography) and biotic (pests, pathogens) stress factors. Our results show that areas in the north-east part on the A. pinsapo distribution (Sierra de las Nieves) have shown increasing defoliation and mortality rates, which were overall related to drought severity, radial-growth loss and damage caused by pests and pathogens (Armillaria mellea and Cryphalus numidicus). Those processes seem to be related to two major stress factors: first, the increase of the aridity gradient from west to east areas influenced by different atmospheric patterns from the Atlantic Ocean and the Mediterranean Sea, respectively; and second, the spread and increase of severity of forest pest and diseases during the last decades (Navarro-Cerrillo et al., 2020b). Drought is supposed to be a predisposing factor which forces the sensitivity to other biotic and abiotic stress factors (Manion and Lachance, 1992). Those biotic stressors such as fungi of *Armillaria* species or beetles have been featured as major damage agents in other conifer forests (Müller et al., 2018). Finally, there are very few studies considering the impact of atmospheric pollutants over time, but some reports conclude that it could be also important to explain *A. pinsapo* defoliation (Blanes et al., 2013). Therefore, a continuous increase in *A. pinsapo* dieback incidence can be expected in the coming years in the most defoliated areas (Sierras de las Nieves) as has been illustrated under different growing conditions (Linares et al., 2009, 2011; Navarro-Cerrillo et al., 2020b). Future monitoring efforts must consider ecosystem function and stressor-indicator relationships within the framework of an appropriate statistical design.

# CRediT authorship contribution statement

Rafael M. Navarro-Cerrillo: Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. Pablo González-Moreno: Methodology, Formal analysis, Writing – original draft, Writing – review & editing. Francisco José Ruiz-Gómez: Methodology, Formal analysis, Writing – original draft, Writing – review & editing. Rafael Sánchez-Cuesta: Methodology, Writing – review & editing. Antonio Gazol: Formal analysis, Writing – review & editing. J. Julio Camarero: Methodology, Writing – review & editing.

# **Declaration of Competing Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary material

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# References

- Arista, M., Herrera, F.J., Talavera, S., 1997. Biología del Pinsapo. Junta de Andalucía, Consejería del Medio Ambiente, Seville, Spain.
- Axelson, J., Battles, J., Bulaon, B., Cluck, D., Cousins, S., Cox, L., Estes, B., Fettig, C., Hefty, A., Hishinuma, S., Hood, S., Kocher, S., McMahon, D., Mortenson, L., Koltunov, A., Kuskulis, E., Poloni, A., Ramirez, C., Restaino, C., Safford, H., Slaton, M., Smith, S., Tubbesing, C., Wayman, R., Young, D., 2019. The California tree mortality data collection network—Enhanced communication and collaboration among scientists and stakeholders. Calif. Agric. 73 (2), 55–62.
- Ayres, M.P., Lombardero, M.J., 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Sci. Total Environ. 262 (3), 263–286.
- Barton, K., 2012 MuMIn: multi-model inference. R package version 1.0.0. Available at: http://CRAN.R-project.org/package=MuMIn.

- Blanes, M.C., Viñegla, B., Salido, M.T., Carreira, J.A., 2013. Coupled soil-availability and tree-limitation nutritional shifts induced by N deposition: insights from N to P relationships in *Abies pinsapo* forests. Plant Soil 366 (1-2), 67–81.
- Breheny, P., Burchett, W., 2017. Visualization of regression models using visreg. R J. 9, 56–71.
- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach, 2nd edn. Springer-Verlag, New York.
- Bussotti, F., Pollastrini, M., 2017. Observing climate change impacts on European forests: what works and what does not in ongoing long-term monitoring networks. Front. Plant Sci. 8, 629.
- 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. P.N.A.S. 108 (4), 1474–1478.
- Cobb, R.C., Metz, M.R., 2017. Tree diseases as a cause and consequence of interacting forest disturbances. Forests 8 (5), 147.
  Consejería de Medio Ambiente y Ordenación del Territorio, 2018. Manual para el
- establecimiento y la evaluación de las parcelas de la Red Andaluza de Seguimiento de Daños sobre Ecosistemas Forestales: Red SEDA y Red de PINSAPO. Junta de Andalucía, Sevilla, Spain.
- Cox, D.R., 1972. Regression models and life-tables. J. R. Stat. Soc. Series B Stat. Methodol. 34 (2), 187–202.
- de la Cruz, Ana C., Gil, Paula M., Fernández-Cancio, Ángel, Minaya, Mayte, Navarro-Cerrillo, Rafael M., Sánchez-Salguero, Raúl, Grau, José Manuel, 2014. Defoliation triggered by climate induced effects in Spanish ICP Forests monitoring plots. Forest Ecol. Manag. 331, 245–255.
- Davies, Tilman M., Marshall, Jonathan C., Hazelton, Martin L., 2018. Tutorial on kernel estimation of continuous spatial and spatiotemporal relative risk. Stats. Med. 37 (7), 1191–1221.
- De Vita, P., Serrano, M.S., Luchi, N., Capretti, P., Trapero, A., Sánchez, M.E., 2010. Susceptibility of *Abies pinsapo* and its tree cohort species to *Heterobasidion abietinum*. For. Pathol. 40 (2), 129–132.
- Dobbertin, Matthias, 2005. Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review. Eur. J. Forest Res. 124 (4), 319–333.
- Duque-Lazo, J., Navarro-Cerrillo, R.M., 2017. What to save, the host or the pest? The spatial distribution of xylophage insects within the Mediterranean oak woodlands of Southwestern Spain. Forest Ecol. Manag. 392, 90–104.
- Eichhorn, J., Roskams, P., Ferretti, M., Mues, V., Szepesi, A., Durrant, D., 2010. Visual Assessment of Crown Condition and Damaging Agents. Manual Part IV, In: Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests. UNECE ICP Forests Programme Coordinating Centre, Hamburg. ISBN: 978-3-926301-1. <a href="https://www.icp-forests.org/Manual.htm">https://www.icp-forests.org/Manual.htm</a>.
- Eichhorn, J., Roskams, P., Ferretti, M., Mues, V., Szepesi, A., 2016. Visual assessment of crown condition and damaging agents. Manual Part IV, in: Manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on forests. UNECE ICP Forests Programme Co-ordinating Centre, Eberswalde, Germany, p. 49.
- Esquivel-Muelbert, A., Phillips, O.L., Brienen, R.J., Fauset, S., Sullivan, M.J., Baker, T.R., Chao, K.J., Feldpausch, T.R., Gloor, E., Higuchi, N., Houwing-Duistermaat, J., Lloyd, J., Liu, H., Malhi, Y., Marimon, B., Marimon Junior, B.H., Monteagudo-Mendoza, A., Poorter, L., Silveira, M., Galbraith, D., 2020. Tree mode of death and mortality risk factors across Amazon forests. Nat. Commun. 11 (1), 5515.
- Fernández-Cancio, A., NavarroCerrillo, R.M., Fernández, R.F., Hernández, P.G., Meneéndez, E.M., Martínez, C.C., 2007. Climate classification of *Abies pinsapo* Boiss. forests in Southern Spain. Forest Syst. 16 (3), 222–229.
- Ferretti, Marco, Nicolas, Manuel, Bacaro, Giovanni, Brunialti, Giorgio, Calderisi, Marco, Croisé, Luc, Frati, Luisa, Lanier, Marc, Maccherini, Simona, Santi, Elisa, Ulrich, Erwin, 2014. Plot-scale modelling to detect size, extent, and correlates of changes in tree defoliation in French high forests. Forest Ecol. Manag. 311, 56–69.
- Fischer, R., Lorenz, M., Granke, O., Mues, V., Iost, S., Van Dobben, H., De Vries, W., 2010. Forest condition in Europe. Institute for World Forestry, Hamburg, Germany.
- Gazol, Antonio, Camarero, J.Julio, Gomez-Aparicio, Lorena, 2016. Functional diversity enhances silver fir growth resilience to an extreme drought. J. Ecol. 104 (4), 1063–1075.
- Gazol, A., Sangüesa-Barreda, G., Camarero, J.J., 2020. Forecasting forest vulnerability to drought in Pyrenean Silver fir forests showing dieback. Front. For. Glob. Change 3, 36.
- Gustafson, Eric J., Kern, Christel C., Miranda, Brian R., Sturtevant, Brian R., Bronson, Dustin R., Kabrick, John M., 2020. Climate adaptive silviculture strategies: How do they impact growth, yield, diversity and value in forested landscapes? Forest Ecol. Manag. 470-471, 118208. https://doi.org/10.1016/j.foreco.2020.118208.
- Grossiord, Charlotte, 2020. Having the right neighbors: how tree species diversity modulates drought impacts on forests. New Phytol. 228 (1), 42–49.
- Guzman-Álvarez, J.R., Troncoso, J.V., Rengel, A., Sillero, M.L., Álvarez, J.A., Guerrero Álvarez, J.J., Sánchez, R., 2012. Biomasa Forestal en Andalucía. Consejería de Medio Ambiente, Junta de Andalucía.
- Hartmann, Henrik, Schuldt, Bernhard, Sanders, Tanja G.M., Macinnis-Ng, Cate, Boehmer, Hans Juergen, Allen, Craig D., Bolte, Andreas, Crowther, Thomas W., Hansen, Matthew C., Medlyn, Belinda E., Ruehr, Nadine K., Anderegg, William R.L., 2018. Monitoring global tree mortality patterns and trends. Report from the VW symposium 'Crossing scales and disciplines to identify global trends of tree mortality as indicators of forest health'. New Phytol. 217 (3), 984–987.
- ICP Forests, 2004. International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests operating under the UNECE Convention on Longrange Transboundary Air Pollution. http://icp-forests.net/.

Kassambara, A., Kosinski, M., 2018. Survminer: drawing survival curves using "ggplot2." Available online: https://cran.r-project.org/web/packages/survminer/survminer. pdf (accessed on 10 February 2021.

Klap, J.M., Voshaar, J.H., De Vries, W., Erisman, J.W., 2000. Effects of environmental stress on forest crown condition in Europe. Part IV: statistical analysis of relationships. Water Air Soil Pollut. 119 (1), 387–420.

- Lechuga, Victor, Carraro, Vinicio, Viñegla, Benjamín, Carreira, José Antonio, Linares, Juan Carlos, 2017. Managing drought-sensitive forests under global change. Low competition enhances long-term growth and water uptake in *Abies pinsapo*. Forest Ecol. Manag. 406, 72–82.
- Linares, J.C., 2011. Biogeography and evolution of Abies (Pinaceae) in the Mediterranean Basin. The roles of long-term climatic changes and glacial refugia. J. Biogeogr. 38, 619–630.
- Linares, J.C., Camarero, J.J., Carreira, J.A., 2009. Interacting effects of climate and forest-cover changes on mortality and growth of the southernmost European fir forests. Global Ecol. Biogeogr. 18, 485–497.
- Linares, J.C., Camarero, J.J., Carreira, J.A., 2010a. 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*. J. Ecol. 98 (3), 592–603.
- Linares, Juan Carlos, Camarero, Jesús Julio, Bowker, Matthew A., Ochoa, Victoria, Carreira, José Antonio, 2010b. Stand-structural effects on *Heterobasidion abietinum*related mortality following drought events in *Abies pinsapo*. Oecologia 164 (4), 1107–1119.
- Linares, Juan Carlos, Delgado-Huertas, Antonio, Carreira, José Antonio, 2011. Climatic trends and different drought adaptive capacity and vulnerability in a mixed Abies pinsapo–Pinus halepensis forest. Clim. Chang. 105 (1-2), 67–90.

Logan, Brent R., Wang, Hong, Zhang, Mei-Jie, 2005. Pairwise multiple comparison adjustment in survival analysis. Statist. Med. 24 (16), 2509–2523.

- López-Tirado, Javier, Hidalgo, Pablo J., 2014. A high resolution predictive model for relict trees in the Mediterranean-mountain forests (*Pinus sylvestris* L., *P. nigra* Arnold and *Abies pinsapo* Boiss.) from the south of Spain: A reliable management tool for reforestation. Forest Ecol. Manag. 330, 105–114.
- Lorenz, M., Becher, G., 2013: Forest Condition in Europe, 2013. Technical Report of ICP Forests. Work Report of the Thünen Institute for World Forestry 2013/1. ICP Forests, Hamburg.

Manion, P.D., Lachance, D., 1992. Forest Decline Concepts. APS Press.

- McDowell, Nate G., Allen, Craig D., Anderson-Teixeira, Kristina, Aukema, Brian H., Bond-Lamberty, Ben, Chini, Louise, Clark, James S., Dietze, Michael, Grossiord, Charlotte, Hanbury-Brown, Adam, Hurtt, George C., Jackson, Robert B., Johnson, Daniel J., Kueppers, Lara, Lichstein, Jeremy W., Ogle, Kiona, Poulter, Benjamin, Pugh, Thomas A.M., Seidl, Rupert, Turner, Monica G., Uriarte, Maria, Walker, Anthony P., Xu, Chonggang, 2020. Pervasive shifts in forest dynamics in a changing world. Science 368 (6494). https://doi.org/10.1126/ science:aa29463.
- Michel, A., Seidling, W., Lorenz, M., Becher, G., 2014. Forest Condition in Europe: 2013 Technical Report of ICP Forests; Report under the UNECE Convention on Long-Range Transboundary Air Pollution (CLRTAP). Johann Heinrich von Thünen-Institut, Eberswalde; Hamburg, 134 p, Thünen Working Paper 19.Müller, Michael M., Henttonen, Helena M., Penttilä, Reijo, Kulju, Matti, Helo, Teppo,

Müller, Michael M., Henttonen, Helena M., Penttilä, Reijo, Kulju, Matti, Helo, Teppo, Kaitera, Juha, 2018. Distribution of *Heterobasidion* butt rot in northern Finland. Forest Ecol. Manag. 425, 85–91.

Navarro Cerrillo, R.M., Calzado Martínez, C., 2004. Establecimiento de una red de equilibrios biológicos en ecosistemas con presencia de pinsapo (Abies pinsapo Boiss.) en Andalucía. Pirineos 158–159, 107–125.

Navarro-Cerrillo, R.M., Calzado, C, Quintanilla, J.L., Trapero Casas, A., 2003. Censo de focos de *Heterobasidion annosum* (Fr.) Bref. en ecosistemas de pinsapo. Bol. San. Veg. Plagas 29(4), 581-592.

Navarro-Cerrillo, R.M., Gazol, A., Rodríguez-Vallejo, C., Manzanedo, R.D., Palacios-Rodríguez, G., Camarero, J.J., 2020a. a. Linkages between Climate, Radial Growth and Defoliation in Abies pinsapo Forests from Southern Spain, Forests 11 (9), 1002.

Navarro Cerrillo, R.M., Duque-Lazo, J., Ríos-Gil, N., Guerrero-Álvarez, J.J., López-Quintanilla, J., Palacios-Rodríguez, G., 2021. Can habitat prediction models contribute to the restoration and conservation of the threatened tree *Abies pinsapo* Boiss. in Southern Spain? New Forests 52 (1), 89–112. Navarro-Cerrillo, Rafael M, Manzanedo, Rubén D., Rodriguez-Vallejo, Carlos, Gazol, Antonio, Palacios-Rodríguez, Guillermo, Camarero, J.Julio, 2020b. Competition modulates the response of growth to climate in pure and mixed Abies pinsapo subsp. maroccana forests in northern Morocco. Forest Ecol. Manag. 459, 117847. https://doi.org/10.1016/j.foreco.2019.117847.

Nocentini, S., Buttoud, G., Ciancio, O., Corona, P., 2017. Managing forests in a changing world: the need for a systemic approach. A review. For. Syst. 26 (1), eR01.

- Neumann, Mathias, Mues, Volker, Moreno, Adam, Hasenauer, Hubert, Seidl, Rupert, 2017. Climate variability drives recent tree mortality in Europe. Glob Chang Biol. 23 (11), 4788–4797.
- O'Brien, Susan H., Webb, Andrew, Brewer, Mark J., Reid, James B., 2012. Use of kernel density estimation and maximum curvature to set Marine Protected Area boundaries: Identifying a Special Protection Area for wintering red-throated divers in the UK. Biol. Conserv. 156, 15–21.

O'Quigley, John, Stare, Janez, 2002. Proportional hazards models with frailties and random effects. Stats. Med. 21 (21), 3219–3233.

Pinheiro, J.C., Bates, D.M., 2000. Mixed-Effects Models in S and S-PLUS. Springer, New York.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., 2014. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3, 1-117.

Potter, K.M., Conkling, B.L., 2017. Forest health monitoring: national status, trends, and analysis 2016. Gen. Tech. Rep. SRS-222. Asheville, NC: US Department of Agriculture, Forest Service, Southern Research Station.

R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Sánchez, M.E., Luchi, N., Jiménez, J.J., de Vita, P., Sánchez, J.E., Trapero, A., Capretti, P., 2007. An isolated population of *Heterobasidion abietinum* on *Abies pinsapo* in Spain. For. Pathol. 37 (5), 348–356.

- Sánchez-Cuesta, Rafael, Ruiz-Gómez, Francisco J., Duque-Lazo, Joaquín, González-Moreno, Pablo, Navarro-Cerrillo, Rafael M., 2021. The environmental drivers influencing spatio-temporal dynamics of oak defoliation and mortality in dehesas of Southern Spain. Forest Ecol. Manag. 485, 118946. https://doi.org/10.1016/j. foreco.2021.118946.
- Sánchez-Salguero, Raúl, Camarero, J.Julio, Carrer, Marco, Gutiérrez, Emilia, Alla, Arben Q., Andreu-Hayles, Laia, Hevia, Andrea, Koutavas, Athanasios, Martínez-Sancho, Elisabet, Nola, Paola, Papadopoulos, Andreas, Pasho, Edmond, Toromani, Ervin, Carreira, José A., Linares, Juan C., 2017. Climate extremes and predicted warming threaten Mediterranean Holocene firs forests refugia. P.N.A.S. 114 (47), E10142–E10150.
- Sánchez-Salguero, R., Navarro-Cerillo, R.M., Camarero, J.J., Fernández-Cancio, A., 2012. Selective drought-induced decline of pine species in southeastern Spain. Clim. Chang. 113, 767–785.

Seidling, Walter, 2019. Forest monitoring: Substantiating cause-effect relationships. Sci. Total Environ. 687, 610–617.

Senf, Cornelius, Pflugmacher, Dirk, Zhiqiang, Yang, Sebald, Julius, Knorn, Jan, Neumann, Mathias, Hostert, Patrick, Seidl, Rupert, 2018. Canopy mortality has doubled in Europe's temperate forests over the last three decades. Nat. Commun. 9 (1) https://doi.org/10.1038/s41467-018-07539-6.

Teshome, D.T., Zharare, G.E., Naidoo, S., 2020. The Threat of the Combined Effect of Biotic and Abiotic Stress Factors in Forestry Under a Changing Climate. Front. Plant Sci. 11, 601009.

Therneau, T.M., Grambsch, P.M., 2000. Modeling Survival Data: Extending the Cox Model. Springer-Verlag, New York, Statistics for Biology and Health.

Trumbore, S., Brando, P., Hartmann, H., 2015. Forest health and global change. Science 349 (6250), 814–818.

van Mantgem, Phillip J., Stephenson, Nathan L., 2007. Apparent climatically induced increase of tree mortality rates in a temperate forest. Ecol. Lett. 10 (10), 909–916.

Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscalar drought index sensitive to global warming: the Standardized Precipitation Evapotranspiration Index. J Clim. 23, 1696–1718.

Wandresen, Rafael Romualdo, Péllico Netto, Sylvio, Koehler, Henrique Soares, Sanquetta, Carlos Roberto, Behling, Alexandre, 2019. Nonparametric method: Kernel density estimation applied to forestry data. Floresta 49 (3), 561. https://doi. org/10.5380/rf.v49i310.5380/rf.v49i3.60285.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14.