



# Forest resilience to drought varies across biomes

Antonio Gazol<sup>1</sup>  | Jesus Julio Camarero<sup>1</sup>  | Sergio M. Vicente-Serrano<sup>1</sup> | Raúl Sánchez-Salguero<sup>1,2</sup> | Emilia Gutiérrez<sup>3</sup> | Martín de Luis<sup>4</sup> | Gabriel Sangüesa-Barreda<sup>1</sup> | Klemen Novak<sup>4,5</sup> | Vicente Rozas<sup>6</sup> | Pedro A. Tíscar<sup>7</sup> | Juan C. Linares<sup>2</sup> | Natalia Martín-Hernández<sup>1</sup> | Edurne Martínez del Castillo<sup>4</sup> | Montse Ribas<sup>3</sup> | Ignacio García-González<sup>8</sup> | Fernando Silla<sup>9</sup> | Alvaro Camisón<sup>10</sup> | Mar Génova<sup>11</sup> | José M. Olano<sup>6</sup> | Luis A. Longares<sup>4</sup> | Andrea Hevia<sup>12</sup> | Miquel Tomás-Burguera<sup>13</sup> | J. Diego Galván<sup>14</sup>

<sup>1</sup>Instituto Pirenaico de Ecología (IPE-CSIC), Zaragoza, Spain

<sup>2</sup>Depto. Sistemas Físicos, Químicos y Naturales, Univ. Pablo de Olavide, Sevilla, Spain

<sup>3</sup>Department of Evolutionary Biology, Ecology and Environmental Sciences, University of Barcelona, Barcelona, Spain

<sup>4</sup>Depto. Geografía y Ordenación del Territorio - IUCA, Univ. Zaragoza, Zaragoza, Spain

<sup>5</sup>Depto. de Ecología, Universidad de Alicante, Alicante, Spain

<sup>6</sup>Depto. Ciencias Agroforestales, EU Ing. Agrarias, iuFOR-Univ., Valladolid, Spain

<sup>7</sup>Centro de Capacitación y Experimentación Forestal, Cazorla, Spain

<sup>8</sup>Depto. Botánica, Escola Politécnica Superior, Campus Terra, Univ. Santiago de Compostela, Lugo, Spain

<sup>9</sup>Depto. Biología Animal, Parasitología, Ecología, Edafología y Química Agrícola, Univ. Salamanca, Salamanca, Spain

<sup>10</sup>Ingeniería Forestal y del Medio Natural, Univ. Extremadura, Plasencia, Spain

<sup>11</sup>Depto. Sistemas y Recursos Naturales, Univ. Politécnica de Madrid, Madrid, Spain

<sup>12</sup>Forest and Wood Technology Research Centre (CETEMAS), Grado, Spain

<sup>13</sup>Estación Experimental Aula Dei, Consejo Superior de Investigaciones Científicas (EEAD-CSIC), Zaragoza, Spain

<sup>14</sup>Ionplus AG. Lerzenstrasse, Dietikon, Switzerland

## Correspondence

Jesus Julio Camarero, Instituto Pirenaico de Ecología (IPE-CSIC), Zaragoza, Spain.  
Email: jjcamarero@ipe.csic.es

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## Abstract

Forecasted increase drought frequency and severity may drive worldwide declines in forest productivity. Species-level responses to a drier world are likely to be influenced by their functional traits. Here, we analyse forest resilience to drought using an extensive network of tree-ring width data and satellite imagery. We compiled proxies of forest growth and productivity (TRWi, absolutely dated ring-width indices; NDVI, Normalized Difference Vegetation Index) for 11 tree species and 502 forests in Spain corresponding to Mediterranean, temperate, and continental biomes. Four different components of forest resilience to drought were calculated based on TRWi and NDVI data before, during, and after four major droughts (1986, 1994–1995, 1999, and 2005), and pointed out that TRWi data were more sensitive metrics of forest resilience to drought than NDVI data. Resilience was related to both drought severity and forest composition. Evergreen gymnosperms dominating semi-arid Mediterranean forests showed the lowest resistance to drought, but higher recovery than deciduous angiosperms dominating humid temperate forests.

Moreover, semi-arid gymnosperm forests presented a negative temporal trend in the resistance to drought, but this pattern was absent in continental and temperate forests. Although gymnosperms in dry Mediterranean forests showed a faster recovery after drought, their recovery potential could be constrained if droughts become more frequent. Conversely, angiosperms and gymnosperms inhabiting temperate and continental sites might have problems to recover after more intense droughts since they resist drought but are less able to recover afterwards.

#### KEYWORDS

dendroecology, drought stress, forest growth, forest productivity, normalized difference vegetation index, resilience index, tree-rings

## 1 | INTRODUCTION

Climate warming is increasing drought frequency and severity in the Mediterranean region (Hoerling et al., 2012; Vicente-Serrano, Camarero, & Azorín-Molina, 2014). Forecasted climate conditions for the Mediterranean Basin point towards more frequent, lasting, and severe droughts during the 21st century (Giorgi & Lionello, 2008). Such trend will negatively impact forest productivity and growth, and lead to more recurrent and widespread events of forest dieback and tree mortality (Camarero, Gazol, Sangüesa-Barreda, Oliva, & Vicente-Serrano, 2015; Gazol, Camarero, Anderegg, & Vicente-Serrano, 2017; Gea-Izquierdo et al., 2017; Sánchez-Salguero, Navarro-Cerillo, Camarero, & Fernández-Cancio, 2012; Sarris, Christodoulakis, & Körner, 2007). Drought intensity is usually considered the main driver causing forest growth decline although functional traits of tree species may also confer dissimilar levels of resistance to drought (Greenwood et al., 2017; Peltier, Fell, & Ogle, 2016; Yin & Bauerle, 2017).

Some studies suggest that angiosperm tree species tend to be less sensitive to drought than gymnosperm species (Anderegg et al., 2015; Mitchell, O'Grady, Tissue, Worledge, & Pinkard, 2014) while others maintain that this is not always true (Carnicer et al., 2011; Yin & Bauerle, 2017). The dependence on stored carbohydrates for the formation of woody tissues differs between angiosperms and gymnosperms, which might consequently be involved in their different responses to drought (Hoch, 2015; Mitchell et al., 2014). Similarly, leaf investment cost and shedding strategies strongly differ between evergreen gymnosperms and deciduous angiosperms probably impacting their post-drought recovery (Sperlich, Chang, Peñuelas, Gracia, & Sabaté, 2015). Other research lines emphasize the role played by hydraulic traits suggesting little difference in drought-induced growth loss and tree mortality between angiosperms and gymnosperms when this component is factored out (Anderegg et al., 2016). Gymnosperms may diverge in their post-drought growth from angiosperms (Gazol, Camarero et al., 2017; Greenwood et al., 2017). Differential growth response to drought between taxonomic groups may be relevant in drought-prone and diverse regions such as the Mediterranean basin (Sperlich et al., 2015). Thus, this region could

be subjected to species' range shifts in the near future, as successional dynamics and climate warming may be favouring angiosperms to the detriment of gymnosperms (Coll, Peñuelas, Ninyerola, Pons, & Carnicer, 2013; Vayreda, Martínez-Vilalta, Gracia, Canadell, & Retana, 2016). Quantifying the resilience in response to drought of forests dominated by species with contrasting functional traits in different biomes is therefore a major knowledge gap and remains a research challenge (Gea-Izquierdo et al., 2017; Yin & Bauerle, 2017).

Current approaches to quantify forest resilience to drought include dendrochronology and remote sensing imagery. Specifically, changes in annual tree-ring widths provide a measure of growth response to drought at the individual tree scale (Camarero et al., 2015), while remote sensing imagery provides information on above-ground forest primary productivity, which is closely related to total canopy cover, leaf biomass and consequently to photosynthetic activity from stand to forest scales (e.g. Carlson & Ripley, 1997; Cihlar, St-Laurent, & Dyer, 1991; Vicente-Serrano, 2007). Long-term series of vegetation indices are available since the early 1980s, providing reliable information about temporal changes in vegetation activity and biomass (Beck et al., 2011; Myneni, Keeling, Tucker, Asrar, & Nemani, 1997; Nemani et al., 2003; Vicente-Serrano, Zouber, Lasanta, & Pueyo, 2012; Vicente-Serrano et al., 2015). Remote sensing information from the red and near-infrared electromagnetic spectrum is used to calculate the Normalized Difference Vegetation Index (NDVI; Tucker, 1979), which has been widely used to determine drought impacts on forest activity and biomass in several regions worldwide (e.g. Klisch & Atzberger, 2016; Kogan, 1998; Vicente-Serrano, 2007; Vicente-Serrano et al., 2013). Although linking tree-ring width and NDVI series may be limited by their different spatial and temporal scales, previous studies suggest a positive relationship between inter-annual NDVI variability and annual radial growth (Coulthard, Touchan, Anchukaitis, Meko, & Sivrikaya, 2017), despite discrepancies between different regions and forest types (Vicente-Serrano et al., 2016). Most research efforts on forest resilience have focused on the impacts of a single drought event on growth (cf. Gazol, Ribas, Gutiérrez, & Camarero, 2017; Lloret, Keeling, & Sala, 2011; Vitali, Büntgen, & Bauhus, 2017), and only few studies have evaluated forest response to drought across broad

environmental gradients, including several biomes, biogeographical regions, and tree species (but see Girardin et al., 2016; Gazol, Camarero et al., 2017; Sánchez-Salguero, Camarero, Carrer et al., 2017; Sánchez-Salguero, Camarero, Gutiérrez et al., 2017).

Here, we present a novel analytical approach, leveraging an extensive tree-ring network composed of absolutely dated ring-width indices (502 forests) and NDVI long-term (1981–2015) and high-spatial coverage data. This study aims to quantify forest growth responses to drought across a wide climatic and environmental gradient comprising 11 tree species (angiosperms and gymnosperms). We aim to know (i) if combined resilience components based on ring-width indices and NDVI improve our understanding of functional mechanics of adaptation to extreme droughts in angiosperms and gymnosperms, and (ii) to assess the intraspecific and interspecific variability in the responses of tree species to severe droughts. Our specific objectives are as follows: (i) to assess the impact of major droughts on different forest types and biogeographical regions by calculating resilience indices (Lloret et al., 2011) using NDVI and tree-ring width data, and (ii) to quantify how these indices vary at different temporal scales and environmental gradients, considering different species-specific responses and forest types.

## 2 | MATERIALS AND METHODS

### 2.1 | Study system

The study region includes peninsular Spain and the Balearic Islands (504,782 km<sup>2</sup>) in southwestern Europe (Figures 1 and S1). This area holds a great variability of climate conditions, including strong north–south and west–east humidity gradients with more arid conditions prevailing southeastwards (De Castro, Martín-Vide, & Alonso, 2005). The Iberian Peninsula is an area of transition from Eurosiberian climate in the north towards sub-tropical climate in the south. Along these lines, the Iberian Peninsula contains many climatic types from humid Atlantic types in the north and northwest to semi-arid Mediterranean types in the east and southeast (Martín Vide & Olcina, 2001). In addition, several mountain ranges increase the environmental heterogeneity and provide regional and local temperature and aridity gradients. Temperate climate prevails in northern Spain, and there are several Mediterranean-climate variants ranging from semi-arid conditions in the southeast to humid conditions in transitional areas between central and northern Spain (Martín Vide & Olcina, 2001). There is also a continentality gradient, with hot summers and cold winters inland and milder conditions near the coast. Average annual temperature ranges between <5°C on mountain peaks (up to ~3,500 m a.s.l.) to ca. 19°C in the south. Total annual rainfall ranges from over 2,000 mm at the most humid sites to less than 250 mm in the driest areas (Martín Vide & Olcina, 2001).

Spanish forests cover 18.2 million hectares, around 36% of its total land area (Forest Europe, 2011). We studied 11 species that belong to two gymnosperm families and one angiosperm family, respectively: Cupressaceae (*Juniperus thurifera* L.), Pinaceae (*Abies alba* Mill., *Pinus halepensis* Mill., *Pinus nigra* Arnold., *Pinus pinaster*

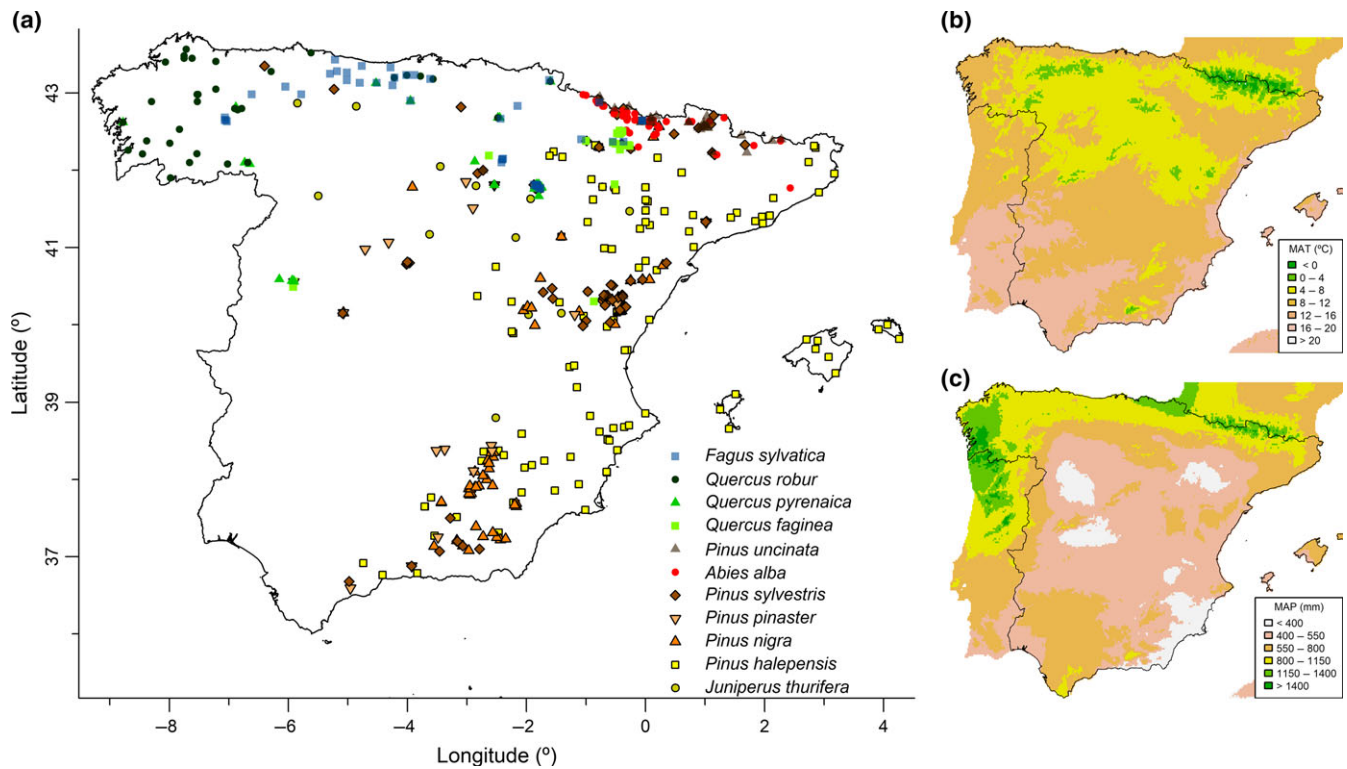
Ait., *Pinus sylvestris* L., *Pinus uncinata* Ram.), and Fagaceae (*Fagus sylvatica* L., *Quercus faginea* Lam., *Quercus pyrenaica* Willd., *Quercus robur* L.). All gymnosperm species studied are evergreen, and all angiosperms are winter deciduous (Table 1; Figure 1).

### 2.2 | Climate, NDVI data, and tree-ring datasets

To quantify drought events, we used climatic data from the Spanish Meteorological Agency (AEMET) for the period 1980–2015. This dataset is homogenized and quality-checked providing a reliable data source for the study area. The dataset contains records of daily mean temperature, sunshine duration, wind speed, relative humidity, and precipitation data (Vicente-Serrano et al., 2017). Data were gridded to one kilometre of spatial resolution and assembled at a weekly time-scale. Gridded Reference Evapotranspiration (ET<sub>o</sub>) was also calculated using the FAO-56 Penman–Monteith Equation (Allen, Pereira, Raes, & Smith, 1998). Finally, the Standardized Precipitation–Evapotranspiration Index (SPEI; Vicente-Serrano, Beguería, & López-Moreno, 2010; Beguería, Vicente-Serrano, Reig, & Latorre, 2014) was used to assess spatio-temporal differences in drought intensity (Figure S4). We selected SPEI as a measure of drought intensity instead of other metrics such as precipitation minus evapotranspiration (P–ET<sub>o</sub>) because absolute values of P–ET<sub>o</sub> were not useful to establish a spatial comparison of drought conditions given the strong differences among climates. For this reason, the so-called drought indices such as the SPEI are intentionally designed to allow spatial comparability of drought severity, independently of the climatology of each region. Negative/positive SPEI values indicate dry/moist conditions. We calculated 12-month long summer (June) SPEI values except for the 1994–1995 drought in which we considered a lag period of 24 months. A detailed explanation of the climate data processing and grid validation can be found in Vicente-Serrano et al. (2017).

To quantify temporal variability in aboveground forest primary productivity, we used bi-weekly time series of NDVI in continental Spain and Balearic Islands over the period 1981–2015 using a new high-resolution (1.1 km<sup>2</sup> grid) dataset from the entire available daily NOAA–AVHRR images covering the study period (see details in Martín-Hernández et al., 2017). This dataset has been processed including pattern recognition, geocoding, cloud removal (Azorin-Molina et al., 2013), topographic correction, temporal filtering, and calibration following NOAA recommendations (Robel & Graumann, 2014). The accuracy and quality of this database have been also checked with NOAA–AVHRR data from the Global Inventory Monitoring and Mapping Studies (GIMMS) database showing high temporal consistency but increased spatial resolution from the 64 km<sup>2</sup> of the original GIMMS to a finer resolution suitable for forest analyses.

We compiled raw tree-ring width information following dendrochronological methods, covering most of the Spanish forested areas (Figures 1 and S1). In each forest, at least 10–15 dominant or codominant trees located in undisturbed stands were selected and cored at 1.3 m using increment borers to obtain 2–3 cores per tree. Trees were cored on the cross-slope sides of the trunk. For each



**FIGURE 1** Studied forest stands in peninsular Spain and the Balearic Islands; (a) Location of the studied forest stands in peninsular Spain and the Balearic Islands. Latitude is N and longitude is E (positive values) or W (negative values); see also Table 1. Colours and symbols are used to identify different tree species; (b) mean annual temperature (MAT, in °C), and (c) total annual precipitation (MAP, in mm) in the study region for 1970–2000 according to WorldClim gridded climate data (Fick & Hijmans, 2017)

**TABLE 1** Tree species studied across the Iberian Peninsula, situation, elevation and number of forests considered for the following droughts: 1986, 1994–1995, 1999, and 2005. The mean latitude, longitude, and elevation of each species are shown. For detailed sampling locations, see Figures 1 and S1

Family <sup>a</sup>	Tree species (biogeographical region, main ecological zone) <sup>b</sup>	Latitude (N)	Longitude (–W, +E)	Elevation (m a.s.l.)	No. studied forests in each drought			
					1986	1994–1995	1999	2005
P	<i>A. alba</i> (E, T)	42.63	+0.02	1425	48	44	7	4
P	<i>P. uncinata</i> (E, C)	42.40	+0.32	2075	39	27	23	20
P	<i>P. sylvestris</i> (E, C)	40.88	–1.31	1526	76	71	59	39
P	<i>P. halepensis</i> (M, M)	39.88	–0.34	588	119	119	90	60
P	<i>P. pinaster</i> (M, M)	39.54	–2.98	993	20	20	20	18
P	<i>P. nigra</i> (M, M)	39.11	–1.87	1412	66	61	53	25
C	<i>J. thurifera</i> (M, M-C)	41.25	–2.46	1015	16	16	16	2
F	<i>F. sylvatica</i> (E, T)	42.55	–3.15	1145	51	51	44	36
F	<i>Q. robur</i> (E, T)	42.82	–6.62	539	34	32	19	10
F	<i>Q. faginea</i> (M, M-C)	42.04	–1.17	941	19	19	18	14
F	<i>Q. pyrenaica</i> (M, C)	41.78	–3.53	1000	34	34	30	27

<sup>a</sup>Family: C, Cupressaceae; F, Fagaceae; P, Pinaceae.

<sup>b</sup>Biogeographical regions: M, Mediterranean; E, Eurosiberian. Ecological zone: M, Mediterranean; T, temperate; C, continental.

study site, latitude, longitude, and mean elevation were recorded. Wood samples were sanded until rings were visible and then visually cross-dated. Tree-ring width was measured to the nearest 0.01 mm using binocular microscopes and measuring device systems (Lintab,

F. RinnTech., Germany; Velmex Inc., USA). The accuracy of visual cross-dating and measurements was checked using the COFECHA program, which calculates moving correlations between each individual tree-ring series and the mean site series (Holmes, 1983).



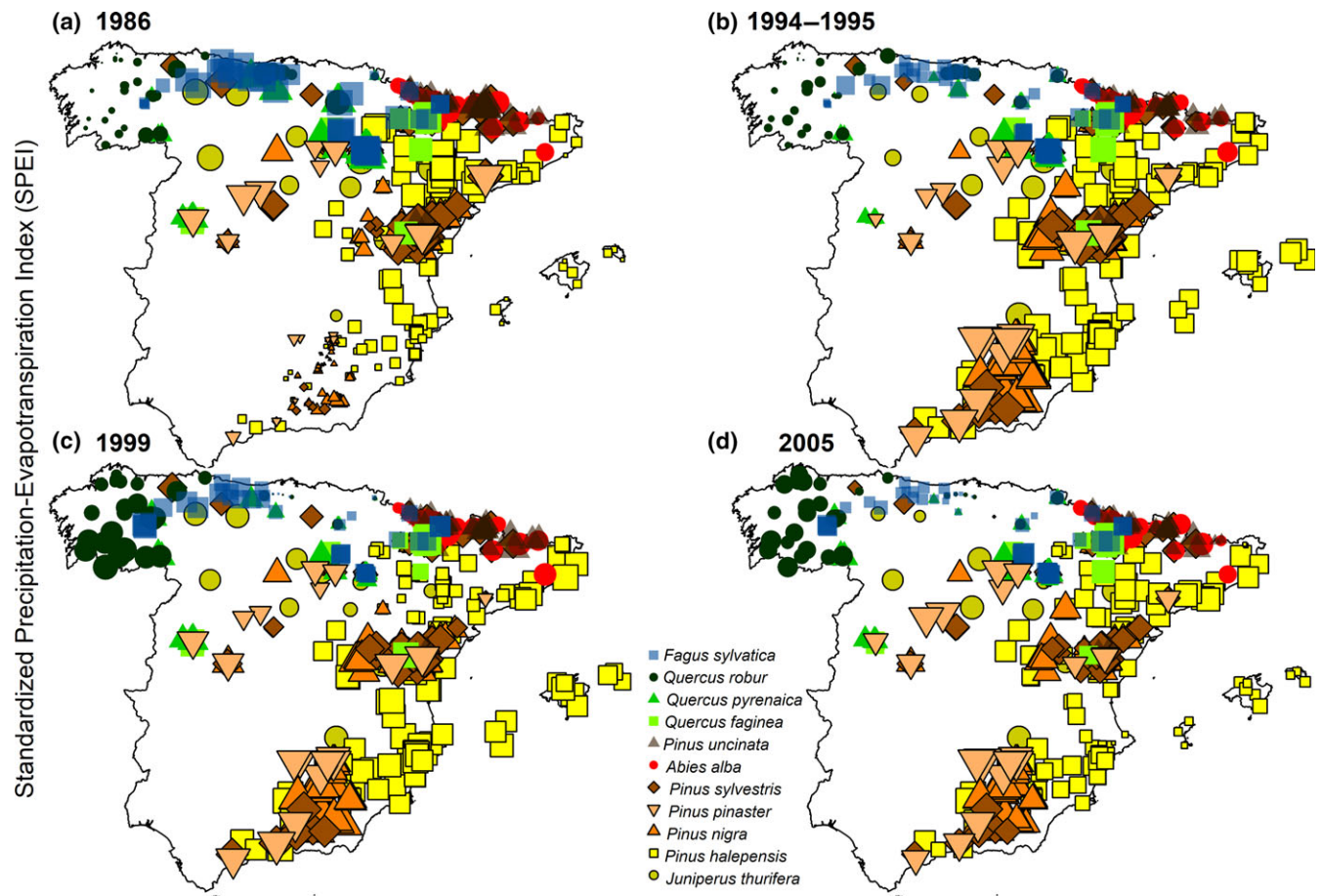
Tree-ring width measurements were filtered using standard dendrochronological protocols (Briffa & Melvin, 2011; Fritts, 2001). Specifically, we detrended individual series of tree-ring widths using a negative exponential curve and residuals were obtained by dividing the observed by the fitted values. Finally, we averaged the individual standardized series into site-level chronologies of ring-width indices (hereafter TRWi) following a hierarchical approach from tree to site and using bi-weight robust means. The mean site-level chronology represents the average growth series of a variable number of trees of the same species growing at the same site. This procedure was done using the “DPLR” package (Bunn et al., 2016). We removed the low-frequency variability while retaining both the high-frequency variability and the first-order autocorrelation since no autoregressive modelling was performed. Data on NDVI and climate variables were collected from the pixel coordinates in which each forest was located.

### 2.3 | Resilience to drought events

We assessed the impact of drought on NDVI and TRWi following a pointer-year approach (cf. Schweingruber, Eckstein, Serre-Bachet, &

Bräker, 1990). We calculated the annual percentage of TRWi or NDVI change of each site by calculating the ratio of TRWi or NDVI in year  $i$  and the average TRWi or NDVI of the three preceding years. The 1986, 1994–1995, 1999, and 2005 droughts were considered as the most severe droughts in the region during the second half of the 20th century affecting large areas of the country based on the pointer-year analyses (Figures 2 and S3; Vicente-Serrano, 2013). Another drought occurred in 2012, but we excluded it from the statistical analyses due to the low number of available tree samples for this extreme drought (Table 1 and Figure S3).

To quantify the response of TRWi and NDVI to drought, we calculated the four resilience components proposed by Lloret et al. (2011): resistance ( $R_t$ ), recovery ( $R_c$ ), resilience ( $R_s$ ), and relative-resilience ( $rR_s$ ) indices. These indices have been successful to quantify forest growth response to drought across varying spatial scales (Gazol, Camarero et al., 2017; Gazol, Ribos et al., 2017; Pretzsch, Schütze, & Uhl, 2013). We calculated them using annual TRWi and NDVI data (as sum of bi-weekly NDVI values throughout the year). We used the sum of NDVI values through the year rather than the mean value or the value for a shorter period because NDVI and tree-ring width are tightly coupled at annual scales (Vicente-Serrano



**FIGURE 2** Spatial distribution of drought intensity across sites and major drought years (1986, 1994–1995, 1999, and 2005). For each drought year, the intensity of drought is represented as the inverse of the Standardized Precipitation-Evapotranspiration Index (SPEI; symbols scaled to indicate higher drought intensity). The SPEI is a drought index and it was calculated considering a period of 12 months. Different colours and symbols correspond to different tree species for the selected droughts

et al., 2016). The resistance index ( $R_t$ ) quantifies the difference between TRWi or NDVI during the dry year and the preceding 3 years (i.e. the capacity of trees to buffer the drought stress and continue growing during drought), whereas the recovery index ( $R_c$ ) accounts for the growth reaction following the drought period (i.e. the difference in TRWi or NDVI between the dry year and the following 3 years). The resilience index ( $R_s$ ) quantifies the difference in TRWi or NDVI before and after the dry year (i.e. the capacity of trees to recover TRWi or NDVI values similar to those observed before the drought). Finally, the relative-resilience index ( $rRs$ ) is the difference between  $R_s$  and  $R_t$ , that is, the resilience weighted by the growth reduction experienced during drought (Lloret et al., 2011). To quantify the resilience indices, we defined a period of 3 years before and after the selected extreme drought based on previous analyses in similar forests (Gazol, Camarero et al., 2017).

## 2.4 | Data analyses

To test for the differences in forest resilience components across species, we used Generalized Least Squares models (GLS; Pinheiro & Bates, 2000). A separate model was built for each of the four resilience indices ( $R_t$ ,  $R_c$ ,  $R_s$ , and  $rRs$ ) based on TRWi (hereafter referred to as  $R_t$ -TRWi,  $R_c$ -TRWi,  $R_s$ -TRWi, and  $rRs$ -TRWi) and NDVI data (hereafter referred to as  $R_t$ -NDVI,  $R_c$ -NDVI,  $R_s$ -NDVI, and  $rRs$ -NDVI). The values of each resilience component were averaged over the four major droughts considered (1986, 1994–1995, 1999, and 2005). After that, we constructed a model including the averaged resilience component as response variable and tree species as explaining factor. When a significant effect of tree species was found, we used least-squares means based on Tukey HSD tests to analyse the differences among species (Bretz, Hothorn, & Westfall, 2010).

To study spatial and temporal differences in forest resilience components, we compiled a set of explanatory variables that would potentially influence the spatial and temporal responses of forest TRWi and NDVI responses to drought. Specifically, we considered the latitude, longitude, and elevation as spatial factors representing the biogeography of the study region. We also considered species as a factor to test for the potential different response of resilience components of each tree species. Finally, the SPEI was used to reflect drought intensity (Figure S4). We applied linear mixed-effects models (LMM) to test the effects of explanatory variables on resilience indices (Pinheiro & Bates, 2000), using the study site as a random factor since repeated measures (i.e. in different drought periods) were performed for each forest. To account for the potential different patterns in resilience components between species and functional groups, we included interactions between latitude, longitude, elevation, and drought year with tree species in the model. The presence of significant interactions between latitude, longitude, or elevation and tree species may indicate different biogeographical patterns in resilience components between functional groups (Gazol, Camarero et al., 2017). By contrast, the presence of significant interactions between drought events and tree species could indicate the

presence of different trends in resilience components, and thus reveal different adaptation strategies through time for the different functional groups.

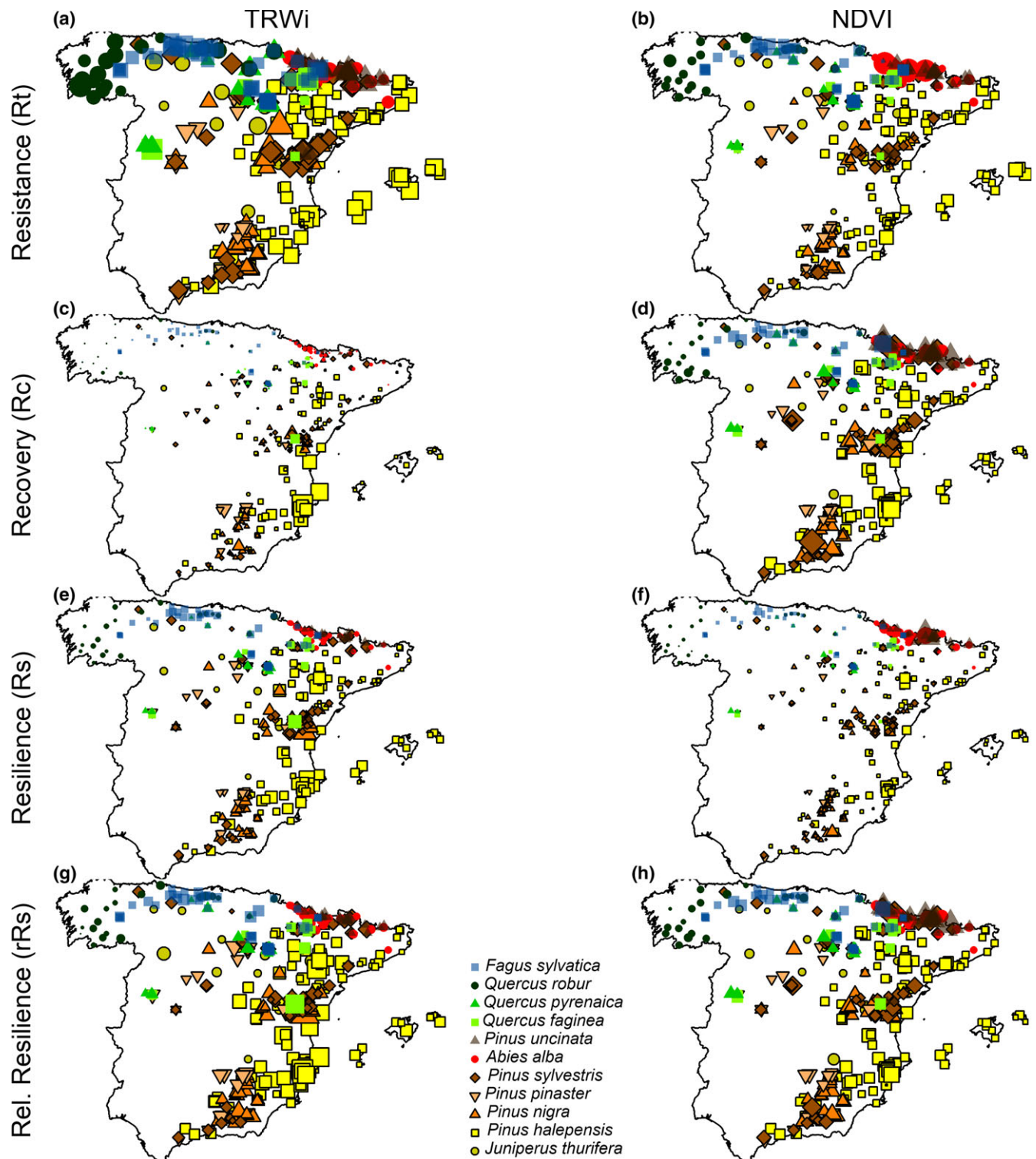
Separate models were constructed for each of the four components of tree resilience based on TRWi and NDVI data. To identify the set of predictors that better explained the observed patterns for each component of tree resilience, we used a multi-model inference approach based on information theory (Burnham & Anderson, 2002). This approach relies on the use of information theory to calculate the relative probability that a given model is more parsimonious than other competing models to explain the response variable. We ranked all potential models according to the second-order Akaike information criterion (AICc). The model showing the lowest AICc value and largest Akaike weight (relative probability quantifying if the selected model is the best one) was selected as the best model. We also calculated the  $\Delta AICc$  (AICc differences between each model and the best model) to rank competing models. For each explanatory variable, we calculated its relative importance across all the models. This value is obtained by summing the Akaike weights of all models that include the predictor of interest and considering the number of models. The larger the relative importance is, the greater the relevance of the predictor (Burnham & Anderson, 2002).

When significant interactions between latitude, longitude, elevation, or drought and tree species were found, we used least-squares means based on Tukey HSD tests to assess the differences between tree species (Bretz et al., 2010). To quantify the strength of the model, we calculated a pseudo- $R^2$  (Nakagawa & Schielzeth, 2013). Lastly, 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. All statistical analyses were performed in the R environment (R Development Core Team, 2017). The *lme* function of the “NLME” package was used to fit the linear mixed-effects models (Pinheiro, Bates, DebRoy, & Sarkar, 2014). The “MUMIN” package was used to perform the multi-model selection (Baron, 2012).

## 3 | RESULTS

The different components of forest resilience to drought ( $R_t$ ,  $R_c$ ,  $R_s$ , and  $rRs$ ), calculated for tree growth (TRWi) and forest primary productivity (NDVI), varied considerably among tree species, droughts, and the location of the studied forests (Figure 3, Tables 2 and 3; Figures S5–S12). Overall, TRWi showed a higher inter-annual variability than NDVI (Figures S3 and S13). Tree species, drought event, drought intensity, and the interaction between the first two factors were the most important variables (Figure S14; Tables 2 and S2).

Forest resistance ( $R_t$ ) calculated for TRWi and NDVI were correlated for the four extreme droughts considered (Table S1). These two proxies were also positively related (Table S1, Figure S15). Forest  $R_t$  was always negatively related to forest recovery ( $R_c$ ) after drought (Figure S16). The higher inter-annual variability of TRWi as compared with NDVI explained the higher standard deviation of



**FIGURE 3** Components of tree resilience in response to severe droughts based either on ring-width indices (TRWi, left column) or on Normalized Difference Vegetation Index (NDVI, right column) values for each species and study site. The symbol size is proportional to the represented index (the larger the symbol, the higher the index, i.e. the better the performance during/after drought). Different colours and symbols correspond to different tree species

TRWi resilience indices, particularly Rc (Figure S17). In general, the resistance to drought was higher in the wet north and northwestern Spain than in the dry southeastern regions (Figure 3). Larger values of Rt-TRWi were observed in tree species from temperate or

continental areas (*Q. robur*, *P. uncinata*, *F. sylvatica*, and *Q. faginea*) than in Mediterranean species as *P. halepensis* and *P. pinaster*, which dominate xeric areas and showed the lowest Rt-TRWi values (Tables 1 and 3). Less differences in Rt-NDVI values were found

**TABLE 2** Summary of the linear mixed-effect models (LMM) performed to study resilience components: resistance (Rt), recovery (Rc), resilience (Rs), and relative resilience (rRs) calculated using ring-width indices (TRWi) and forest primary productivity (NDVI)

	TRWi				NDVI			
	Rt	Rc	Rs	rRs	Rt	Rc	Rs	rRs
Elevation	<b>26.28</b>	<b>57.19</b>	–	<b>49.27</b>	–	–	–	–
Latitude	<b>87.26</b>	<b>145.30</b>	<b>15.48</b>	<b>125.08</b>	–	<b>31.55</b>	–	<b>32.40</b>
Longitude	–	–	–	<b>13.07</b>	2.80	3.19	–	2.51
SPEI	<b>195.56</b>	<b>217.31</b>	<b>13.99</b>	<b>192.63</b>	<b>33.21</b>	<b>59.68</b>	<b>19.07</b>	<b>57.67</b>
Tree species <sup>a</sup>	<b>3.72</b>	<b>3.62</b>	<b>4.10</b>	<b>3.74</b>	<b>4.69</b>	<b>3.35</b>	<b>3.34</b>	<b>3.03</b>
Elevation × Tree species	–	–	–	–	–	–	–	–
Latitude × Tree species	–	<b>4.21</b>	<b>3.72</b>	<b>4.23</b>	–	<b>3.25</b>	–	<b>2.80</b>
Longitude × Tree species	–	–	–	<b>3.86</b>	–	–	–	–
Drought year	<b>47.21</b>	2.85	<b>80.70</b>	<b>10.27</b>	0.62	<b>122.24</b>	<b>164.12</b>	<b>126.84</b>
Drought year × Tree species	<b>14.19</b>	<b>4.39</b>	<b>20.04</b>	<b>4.71</b>	<b>6.34</b>	<b>7.40</b>	<b>7.66</b>	<b>7.91</b>
ΔAICc	1.83	0.93	0.80	10.64	1.05	1.52	1.62	0.99
Akaike weight	0.60	0.50	0.29	0.99	0.41	0.43	0.36	0.41
Pseudo-R <sup>2</sup>	0.25	0.28	0.20	0.27	0.09	0.19	0.16	0.19

For each variable, we show the *t*-statistic of the variables included in the best model, the pseudo-R<sup>2</sup> (measuring the fraction of variation explained by the model), the difference between the second-order Akaike Information Criterion (AICc) of the selected model and the second minimum AICc found for the evaluated set of models (ΔAICc), and the Akaike weight of the selected model, that is, the probability that the selected model is the best model. Significant variables are included in bold. See Table S2 for details about model selection.

<sup>a</sup>Tree species: 1-*A. alba*, *F. sylvatica*, *J. thurifera*, *P. halepensis*, *P. nigra*, *P. pinaster*, *P. sylvestris*, *P. uncinata*, *Q. faginea*, *Q. pyrenaica*, *Q. robur*.

between some temperate species (*A. alba*, *F. sylvatica*), and the Mediterranean pine species (*P. pinaster*, *P. halepensis*, and *P. nigra*) presenting the highest and lowest values, respectively. Rt–TRWi and Rt–NDVI indices were positively related with drought intensity (Figure 4). Rt–TRWi increased along time for species such as *A. alba* and *Q. pyrenaica*, whereas it showed a marked decrease for species such as *P. halepensis* and *P. pinaster* (Table 3, Figure 5). Finally, Rt–NDVI in *Q. pyrenaica* showed a marked decrease.

Estimates of forest recovery after drought (Rc–TRWi and Rc–NDVI) were positively correlated (Table S1, Figure S15) and showed inverse patterns as compared to Rt (Figure 3). The species dominating the Mediterranean forests of the southeastern semi-arid Spain such as *P. pinaster* and *P. halepensis* presented higher values of Rc–TRWi than species from temperate and continental forests such as *Q. robur*, *P. uncinata*, *A. alba*, and *Q. pyrenaica* (Table 3). Rc–NDVI showed interspecific differences with *P. uncinata* displaying the highest values and *F. sylvatica* and *Q. robur* the lowest. Both Rc–TRWi and Rc–NDVI values were negatively related to drought intensity (Figure 4), but Rc–TRWi decreased with latitude whilst Rc–NDVI increased (Table S2). Rc–TRWi decreased considerably along time in *A. alba* and *Q. pyrenaica* but increased for species such as *P. pinaster*, *P. nigra*, and *Q. faginea*. Only *Q. pyrenaica* showed a positive trend for Rc–NDVI, whereas *J. thurifera*, *P. nigra*, and *A. alba* showed the most pronounced negative trends (Figure 5; Table 3).

Forest resilience to drought (Rs) for TRWi and NDVI was positively related for all droughts considered (Table S1, Figure S15). We found several differences between species' Rs–TRWi with the Mediterranean *P. halepensis* and *P. nigra* displaying the largest values,

and the temperate *Q. robur* and *A. alba* showing the lowest values. *P. uncinata* and *A. alba* showed the largest Rs–NDVI values, and *Q. robur* and *J. thurifera* presented the lowest values (Table 3). Rs–TRWi and Rs–NDVI decreased as drought intensity increased (i.e. SPEI decreased; Figure 4). Several tree species showed a negative trend in Rs–TRWi with *P. halepensis* displaying the strongest decreasing trend (Figure 5). Only *P. sylvestris*, *Q. robur*, and *Q. pyrenaica* showed non-negative trends. Similar patterns were observed for Rs–NDVI where all species showed negative trends, with *P. halepensis*, the species inhabiting the driest sites (Figure S2), displaying the most negative trend (Figure 5).

Forest relative resilience to drought (rRs) calculated for TRWi and NDVI showed a positive correlation for all the studied droughts (Table S1, Figure S15). The rRs–TRWi was higher for species inhabiting the southern and eastern dry Spain such as *P. halepensis* and *P. pinaster* than for species dominating the northwestern and northern wet areas as *Q. robur* and *A. alba*. Similar patterns were observed for rRs–NDVI with the exception of *P. uncinata* which displayed the highest values. Relative resilience decreased with drought intensity and presented species-specific latitudinal patterns: rRs–TRWi for *Q. faginea* decreased with latitude, whereas it showed slight increases for the remaining species. The rRs–NDVI values for *P. uncinata* and *F. sylvatica* increased with latitude, whereas they decreased for *P. halepensis*. The rRs–TRWi values showed a marked decrease with time in species such as *A. alba* and *P. halepensis*, whereas they increased in species such as *P. sylvestris*. rRs–NDVI values showed a negative trend in *J. thurifera*, *A. alba*, and *P. nigra*, whereas a positive trend was observed for *Q. pyrenaica* (Figure 5).



**TABLE 3** Differences in the resilience components between tree species and drought years considering TRWi and NDVI data

	TRWi				NDVI			
	Rt	Rc	Rs	rRs	Rt	Rc	Rs	rRs
Tree species								
<i>A. alba</i>	abc	a	a	ab	C	abc	c	ab
<i>F. sylvatica</i>	cd	ab	bcd	bcd	Bc	ab	ab	a
<i>J. thurifera</i>	abcd	abc	abcd	bcde	Ab	abc	ab	ab
<i>P. halepensis</i>	a	d	d	e	A	cd	b	bc
<i>P. nigra</i>	bc	bc	cd	d	Ab	bcd	ab	bc
<i>P. pinaster</i>	ab	cd	abcd	cde	Ab	abcd	ab	abc
<i>P. sylvestris</i>	cd	ab	ab	bc	Ab	bcd	ab	abc
<i>P. uncinata</i>	d	a	abc	ab	Ab	d	c	c
<i>Q. faginea</i>	cd	ab	abcd	abcd	Abc	abc	ab	ab
<i>Q. pyrenaica</i>	cd	a	abc	ab	Abc	ab	ab	ab
<i>Q. robur</i>	cd	a	ab	a	Abc	a	a	a
Tree species × drought year								
<i>A. alba</i>	d	a	b	ab	D	ab	c	a
<i>F. sylvatica</i>	bc	b	b	bc	Ab	c	c	c
<i>J. thurifera</i>	abc	abc	ab	abc	Abcd	a	abc	a
<i>P. halepensis</i>	a	ab	a	a	A	ab	a	ab
<i>P. nigra</i>	b	b	b	bc	Abc	a	ab	A
<i>P. pinaster</i>	ab	c	b	c	Abc	abc	abc	Abc
<i>P. sylvestris</i>	bc	b	b	c	Bc	ab	bc	Ab
<i>P. uncinata</i>	bc	ab	b	bc	Cd	ab	c	Ab
<i>Q. faginea</i>	bc	bc	b	bc	Abcd	abc	bc	Abc
<i>Q. pyrenaica</i>	cd	ab	b	abc	Ab	c	c	C
<i>Q. robur</i>	bcd	abc	b	abc	Abc	bc	bc	Bc

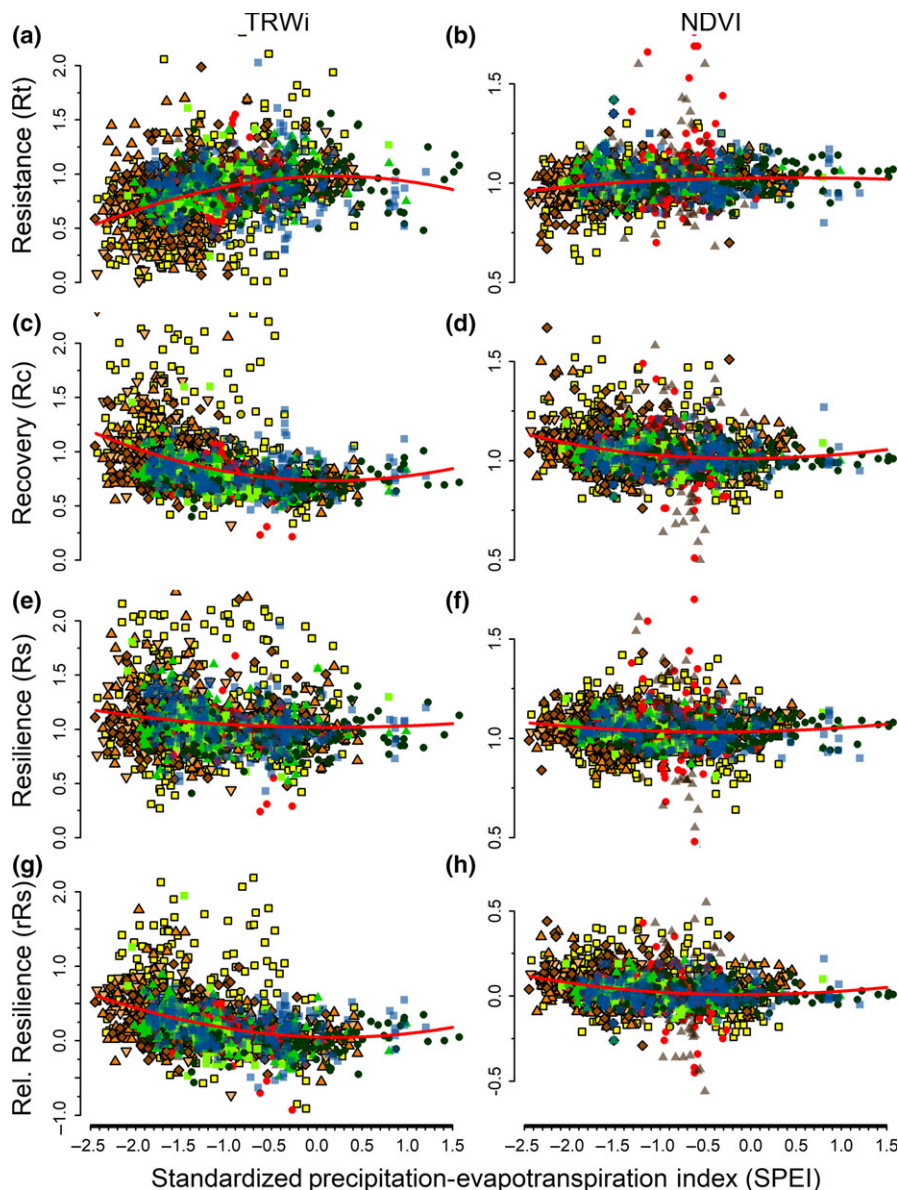
For the comparison of resilience components between tree species the least-squares means were computed using Generalized Least Squares (GLS) models containing each resilience component as a response variable and tree species as a covariate. For the comparison of the interaction between drought year and tree species, least-squares means were computed using linear mixed-effects models containing resilience components as response variables and the full subset of covariates considered in the study. For each resilience component, species are grouped according to their differences ( $p < .05$ ) indicated by letters. The  $p$  values were adjusted for multiple comparisons according to Tukey HSD tests. Two species that share one or more letters are not significantly ( $p < .05$ ) different.

## 4 | DISCUSSION

We analysed the resistance and resilience to drought of forests dominated by 11 species across wide climatic and environmental gradients in the Western Mediterranean basin using proxies of forest productivity (NDVI) and carbon accumulation (ring-width indices, TRWi) and considering four extreme drought events recorded between 1980 and 2005. Our results (Table 2) support that forest response capacity is strongly dependent on drought intensity (Greenwood et al., 2017), but also show contrasting functional responses to drought among tree species and forest biomes, and within the

species' distribution range (Anderegg & HilleRisLambers, 2016; Brodribb, McAdam, Jordan, & Martins, 2014; Choat et al., 2012). Furthermore, forest growth resilience seems to rely on the species considered, indicating species-specific responses to drought stress (Anderegg et al., 2015, 2016; Gazol, Camarero et al., 2017; Gea-Izquierdo et al., 2017; Peltier et al., 2016; Pretzsch et al., 2013; Sánchez-Salguero, Camarero, Gutiérrez et al., 2017; Yin & Bauerle, 2017). Evergreen gymnosperms dominating the semi-arid and drought-prone areas displayed lower resistance but faster recovery than evergreen gymnosperms and deciduous angiosperms dominating the temperate and wet regions, suggesting different adaptations and physiological mechanisms to cope with drought (Figure 3). Our results remark the existence of a positive correlation between resilience indices calculated for aboveground forest productivity (NDVI) and growth (TRWi; Vicente-Serrano et al., 2013; Zhang et al., 2017). Nevertheless, we detected a higher sensitivity of TRWi-based resilience components (see Figures S13 and S17). Our findings agree with previous research comparing climate sensitivity of dendrochronological networks and vegetation models (Babst et al., 2013; Coulthard et al., 2017; Zhang et al., 2017).

We found an overall positive correlation between TRWi- and NDVI-based forest resilience components (Figure S15) in line with previous research (Babst et al., 2013; Coulthard et al., 2017; Vicente-Serrano et al., 2015, 2016). Both, the TRWi- and NDVI-based resilience components captured the drop in forest growth and productivity related to drought occurrence (Figure 3). Nevertheless, the magnitude of the TRWi indices was much higher than the NDVI indices (Figures S13 and S17), suggesting that growth reduction is more mediated by sink (growing tissues as cambium) than by source (photosynthesis) limitations (Sarris et al., 2007; Zhang et al., 2017). This result is unexpected given that declining primary productivity is considered to be a major consequence of drought (Carnicer et al., 2011). Two reasons may explain these different responses. First, TRWi quantifies how wood cells form and expand, whereas NDVI quantifies the aboveground photosynthetic biomass. Growth and NDVI might be decoupled and respond to processes occurring at different temporal and spatial scales (Cuny et al., 2015; Vicente-Serrano et al., 2016). In this sense, primary growth has priority over secondary growth regarding the use of carbon reserves (Stoy, Richardson, & Baldocchi, 2009). In the case of drought-prone Mediterranean forests, leaf and wood formation are mainly constrained by water availability during spring and early summer, respectively (Camarero, Albuixech, López-Lozano, & Casterad, 2010; Montserrat-Martí et al., 2009). Second, tree-ring width data provide an accurate measure of growth responses to extreme climate events as droughts (Camarero et al., 2015; Fritts, 2001; Novak et al., 2016). However, classical dendrochronological studies are based on individual tree samples and data processing is aimed on emphasizing their common climatic signal (Cook & Kairiukstis, 1990). By comparison, satellite images reflect large-scale processes providing a synthetic overview of forest conditions, for instance at 1–50 km<sup>2</sup> large scales. However, the increase in the area covered by remote sensing data is accompanied by a loss in spatial resolution (pixel size), that is, tree-



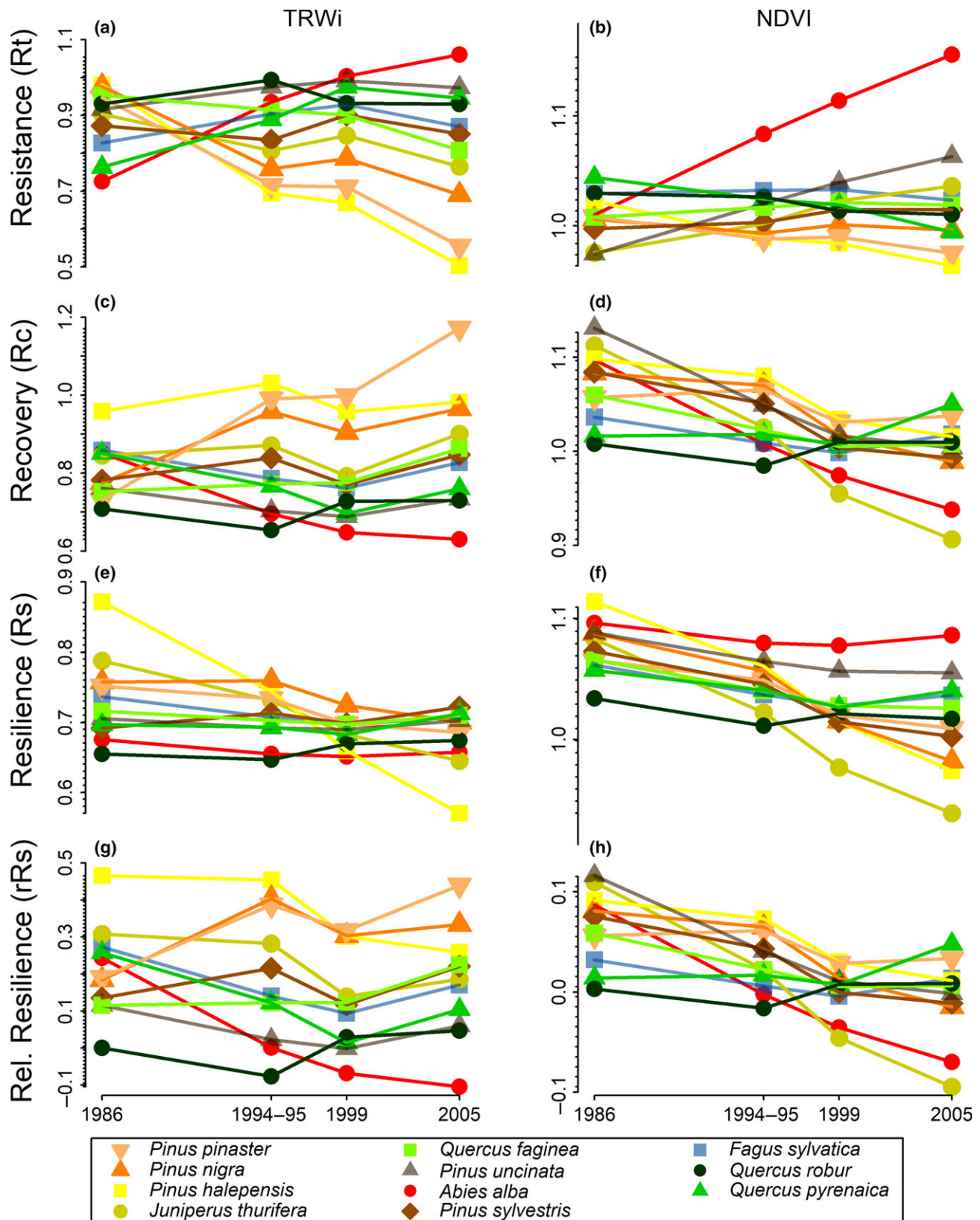
**FIGURE 4** Relationships between drought intensity and resilience indices based on ring-width indices (TRWi, left-column figures) and Normalized Difference Vegetation Index (NDVI, right-column figures) in response to selected droughts. The drought intensity is represented as the Standardized Precipitation-Evapotranspiration Index (SPEI) for June calculated for a period of 12 months. Different species are represented with different colours and symbols as in Figure 1

to-tree variability is blurred or lost since other vegetation formations can influence NDVI patterns (Vicente-Serrano et al., 2013).

Temperate forests situated in northern and northwestern Spain are dominated by more productive angiosperm and gymnosperm tree species in contraposition to the eastern and southeastern dry forests which harbour less productive Mediterranean gymnosperms (Dirección General de Conservación de la Naturaleza (DGMA), 2006). Drought intensity in the studied sites was higher in the eastern part (particularly in the southeastern semi-arid regions, Figure S2; see also Vicente-Serrano, 2006) coinciding with the forests that display the lowest resistance and greatest recovery after drought (Figure 3). Conversely, tree species dominating the more productive temperate forests in northern and northwestern Spain displayed higher resistance but a lower capacity to recover after drought (Figure 3).

Does drought intensity determine tree species plasticity in response to drought? Studies performed in North America have reported very low drought-legacy effects in junipers (Anderegg et al.,

2016). However, pine species tend to present larger legacy effects (Peltier et al., 2016). It is well established that some deciduous angiosperm species as oaks depend on sugar reserves to start secondary growth, whereas evergreen gymnosperms rely more on current photosynthetic activity (Michelot, Simard, Rathgeber, Dufrêne, & Damesin, 2012). However, different strategies to cope with drought, including stomatal regulation in dry periods, leaf desiccation, and shedding or shoot abscission may differ across gymnosperm taxa (Brodribb et al., 2014). The resistance of juniper to moderate drought stress (West, Hultine, Sperry, Bush, & Ehleringer, 2008) and few legacy effects after water shortage (Peltier et al., 2016) could be explained by their tendency to display anisohydric behaviour and a very negative hydraulic potential (Olano et al., 2017). Pine and fir species, by contrast, present longer recovery times, and are potentially more vulnerable to more intense and lasting droughts. It is plausible that a great capacity to recover after drought may be due to a greater plasticity in stomatal regulation (Klein, 2014). This will



**FIGURE 5** Temporal evolution of the components of tree resilience in response to extreme droughts based on ring-width indices (TRWi, left-column figures) and Normalized Difference Vegetation Index values (NDVI, right-column figures) for the different tree species and drought years (x-axes). Species are represented with different colours and symbols as in Figure 1



be the case of the Mediterranean gymnosperms that inhabit dry regions such as *P. halepensis* or *J. thurifera* which display great capacity to recover. However, there is a high variability in hydraulic potential among the gymnosperms. Species such as the drought-adapted *P. nigra* and the drought-sensitive *P. sylvestris* display marked differences in their post-drought recovery and drought resistance (Marqués, Camarero, Gazol, & Zavala, 2016). Conversely, other species from temperate or transitional sub-Mediterranean forests such as *Q. robur* or *Q. pyrenaica* may maintain growth during dry periods at the expense of a shorter vegetative period (Pérez-de-Lis et al., 2017). This trade-off between forest resistance to drought and recovery after drought has been reported previously (Gazol, Camarero et al., 2017; Gazol, Ribas et al., 2017), yet their mechanisms, causes, and consequences are still poorly understood. In addition, we found that similar patterns in the responses to drought are displayed by coexisting tree species, regardless of their functional strategy. For example, populations of *Q. faginea*, *P. halepensis*, and *J. thurifera* show similar patterns in their responses, which contrasts with the patterns presented by *Q. robur*, *Q. pyrenaica*, and *P. uncinata*, among others (Figure 3). Even if two contrasting strategies between species from the wet temperate forests and the dry Mediterranean sites are apparent, more research across the distribution range of each species is required to consider intraspecific variability in the species' responses to drought.

Phenotypic plasticity and genetic diversity may drive substantial differences in resilience to drought at species level (Savolainen, Pyhäjärvi, & Knürr, 2007). Our results show that some resilience components present species-specific latitudinal gradients. Benito-Garzón, Alía, Robson, and Zavala (2011) studied the distribution of *P. pinaster* and *P. sylvestris* across Spain and found contrasting responses to drought depending on their provenance. Gazol, Ribas et al. (2017) found that the resilience of *P. halepensis* to drought depended on forest latitude and longitude. In general, species-specific geographic patterns in the response to drought have been found in several regions of the world (Coulthard et al., 2017; Gazol et al., 2015; Martínez-Vilalta et al., 2009; Peltier et al., 2016; Sánchez-Salguero, Camarero, Carrer et al., 2017; Sánchez-Salguero, Camarero, Gutiérrez et al., 2017; Zhang et al., 2017). Thus, probably tree species with a wide biogeographical range may display contrasting responses to drought across the entire study region. In this sense, differences in drought intensity across regions may lead to intraspecific plasticity and genetic differentiation among tree populations (Benito-Garzón, Ruiz-Benito, & Zavala, 2013). Nevertheless, these ideas require further testing considering different provenances.

Each component of forest resilience to drought showed contrasting temporal trends, with different patterns depending on the species considered. In general, forest resistance to drought ( $R_t$ ) and forest recovery after drought ( $R_c$ ) showed contrasting patterns (i.e. they present a negative relationship; see Figure S16). The tree species dominating Mediterranean forests in the driest extreme of the studied gradient (*P. halepensis*, *P. pinaster*, and *J. thurifera*; Figure S2) showed a decrease in resistance and an increase in recovery, whereas the temperate species from the wettest end of the gradient presented no trends

(Figure 5). This pattern might be explained by the increase in drought frequency and severity in drought-prone regions from 1986 to 2005 (Spinoni, Naumann, Vogt, & Barbosa, 2015). In this sense, the 1999 and 2005 droughts are regarded as the most extreme dry spells in the Iberian Peninsula during the last half century (Trigo et al., 2013). However, the intensity of these "Mediterranean" droughts was higher in the central, eastern, and southern parts of Spain than in the north and north-western parts (García-Herrera et al., 2007). This increase in drought intensity resulted in a more pronounced response to drought in Mediterranean species from the south and southeastern drier Spain (Sánchez-Salguero et al., 2012, 2013). However, this can also be a consequence of the differences in the species dominating each region, drought-tolerant Mediterranean gymnosperms, and angiosperms in the dry region in contrast to more productive and frost-resistant temperate trees in the wet regions. Gymnosperms with a tight stomatal regulation such as pines (Klein, 2014) might display a lower resistance with increasing drought intensity. However, their increase in the relative resilience and recovery after drought suggests that these species are able to successfully recover growth and productivity after drought. This reinforces the hypothesis that different tree species display strategies to cope with drought that partially depend on the drought intensity of the region they inhabit.

There are some critical issues and potential shortcomings that might be considered when interpreting these findings. We considered a period of 3 years before and after drought events for the calculation of resilience components. In previous studies, we found similar behaviour of the resilience indices for periods lasting from 2 to 4 years (Gazol, Camarero et al., 2017; Gazol, Ribas et al., 2017). However, it has been suggested that lagged drought effects can last for longer periods (Peltier et al., 2016). In this sense, the temporal patterns observed in this study for some of the studied species might be influenced by these long-term legacy effects. For example, it is well established that the 1986 drought was a tipping-point for several Silver fir (*A. alba*) populations from the Pyrenees because it preceded dieback processes in some of these species (Camarero et al., 2015; Gazol et al., 2015). After that drought, these Silver fir populations showed a marked growth decline accompanied with a lower climatic response. Thus, the observed increase in resistance and resilience for this species after the 1986 drought can be a consequence of a less responsive growth and may not be related to a greater capacity to withstand drought (Gazol et al., 2015). A similar observation was made by Sánchez-Salguero et al. (2012) in pine plantations from southern Spain in response to the 1994–1995 and 2005 droughts. Resilience components can be affected by biological interactions before or after droughts, that is, growth reductions were observed in some pine species because of pine processionary moth (Sangüesa-Barreda, Camarero, García-Martín, Hernández, & de la Riva, 2014). This emphasizes that a thorough knowledge of the species under study is required before applying the resistance-resilience-recovery framework since it may not accommodate long-term drought legacy effects equally for all species.

Finally, drought-resilience analyses may be contingent on the definition of drought or other forest variables such as stand age



(Anderegg, Anderegg, & Berry, 2013). Here, we took the approach to define a set of four droughts with ample and strong impact across the entire study region. However, each forest may be differently impacted by the drought as a consequence of local or even regional climatic factors and also by the different duration of droughts (Vicente-Serrano et al., 2013). Similarly, differences in stand age between the studied forests can have an implication on growth resilience to drought since tree growth patterns strongly depend on tree age and size (Peters, Groenendijk, Vlam, & Zuidema, 2015). Nonetheless, we focused on mature and dominant individuals, a procedure that helps to minimize potential biases related to tree age and size.

We found robust patterns in the resilience to drought of forests based on growth (ring-width indices, TRWi) and forest productivity (NDVI) proxies. Nevertheless, TRWi data were more closely related to drought intensity at the tree and forest levels than the sum of yearly NDVI. Our results concurred with previous findings indicating the importance of drought intensity as a major driver of forest resilience to drought. Species inhabiting contrasting regions displayed multiple growth strategies to cope with drought. Despite their capacity to resist drought, Mediterranean forests dominated by gymnosperms in dry areas might be strongly impacted if droughts become more frequent because of limitations in their recovery potential. Conversely, temperate and continental forests dominated by angiosperms and gymnosperms in the wet regions might have problems to override more intense droughts since they are less able to recover after them.

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## CONFLICT OF INTEREST

Authors declare no conflict of interest.

## ORCID

Antonio Gazol  <http://orcid.org/0000-0001-5902-9543>

Jesus Julio Camarero  <http://orcid.org/0000-0003-2436-2922>

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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