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Impacts of droughts on the growth resilience of Northern Hemisphere forests

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ABSTRACT

Aim The intensity and frequency of drought have increased considerably during recent decades in some Northern Hemisphere forested areas, and future climate warming could further magnify drought stress. We quantify how forests resist drought events and recover after them, i.e. we determine their growth resilience.

Location North America and Europe.

Methods We use a large tree-ring database to study how drought influences forest growth resilience. We selected 775 tree-ring width chronologies and studied the occurrence of years with extremely dry conditions (low soil moisture and/or high evaporative stress; hereafter 'drought') in these forests. For each drought in each forest we calculated three indices that represent different components of growth resilience to drought: resistance (Rt), recovery (Rc) and resilience (Rs). We related the variation in these indices with geographical, topographic, climatic and ecological conditions from each region.

Results The three components of forest growth resilience were interrelated. Resistance and recovery were negatively related, and both were positively and nonlinearly related to resilience. Drought resistance increased with latitude, soil moisture and slope, whereas drought recovery decreased with latitude, soil moisture and summer normalized difference vegetation index. Drought resilience increased with elevation and decreased with the variation in soil moisture. Temperate broadleaf forests from wet regions showed a greater growth resistance (e.g. north-eastern USA, central Europe) while conifer forests from dry to semi-arid regions (e.g. south-western USA, southern Europe) presented a greater growth recovery.

Main conclusions The geographical patterns of growth resilience indices confirm the existence of different strategies among forests to cope with droughts, depending on the biome, the tree species and the prevailing climatic conditions. Geographical patterns in soil moisture availability tend to override species-specific responses to drought.

Keywords
Drought resistance, drought stress, forest growth, post-drought recovery, resilience indices, tree rings, water shortage.

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INTRODUCTION

Drought is a natural phenomenon characterized by the prevalence of low levels of water availability during long periods as a consequence of reduced precipitation levels, increased atmospheric evaporative demand or both (Wilhite, 1993). Some studies suggest that the frequency and severity of droughts has increased considerably in recent warm decades (Dai, 2013; Vicente-Serrano *et al.*, 2014). Thus, understanding how drought influences forest productivity and the ecosystem services provided by forests to humans has become a major focus in ecology (Allen *et al.*, 2010; Anderegg *et al.*, 2013a,b, 2015). Although droughts may increase in severity and duration due to climate warming, this may not necessarily translate into widespread forest dieback everywhere (Steinkamp & Hickler, 2015; but see Allen *et al.*, 2015). However, studies from regions where tree growth is not mainly constrained by drought, such as boreal forests, have reported reductions in productivity and widespread increases in tree mortality as a consequence of increasing drought stress (Peng *et al.*, 2011). Therefore, from a global perspective, it is challenging to predict how forests will resist drought stress and recover after it across different regions (Gonzalez *et al.*, 2010).

How forests and trees react to drought is complex and varies across stands, sites, regions and continents, depending on multiple factors such as species identity (e.g. Anderegg & HilleRisLambers, 2016), biome type (Vicente-Serrano *et al.*, 2013; Mitchell *et al.*, 2016) and prevailing climatic conditions (Pasho *et al.*, 2011; Brzostek *et al.*, 2014; Ivits *et al.*, 2014; Clark *et al.*, 2016) as well as tree species traits (Eamus, 1999; McDowell *et al.*, 2008; Martínez-Vilalta *et al.*, 2009; Hoffmann *et al.*, 2011; Brodribb *et al.*, 2012; Choat *et al.*, 2012; Lopez-Iglesias *et al.*, 2014; García-Forner *et al.*, 2016). Recent studies suggest that the effects of drought on forest growth can last for several years and lead to legacy effects (Camarero *et al.*, 2015). Such lagged growth sensitivity to drought was illustrated by Anderegg *et al.* (2015) at a global scale; they demonstrated that recovery of forest growth after a drought can take from 2 to 4 years. This has important implications in light of recent climate change if the frequency of drought events is higher than the time required for growth recovery (Clark *et al.*, 2016). However, the net effect of drought on forest health and productivity across regions is largely unknown (Allen *et al.*, 2010; Steinkamp & Hickler, 2015). In particular, understanding how forests and trees resist drought and recover after drought events in different regions is a crucial question for understanding how drought will impact forests and their ability to store carbon in long-term woody pools via growth (Anderegg *et al.*, 2015).

Variation in the functional response to drought between and within tree species and across distribution ranges may be a key factor for understanding how forests will respond to drought (Vilà-Cabrera *et al.*, 2015; López *et al.*, 2016). In general, gymnosperms are less diverse in terms of xylem cavitation resistance and anatomical characteristics than angiosperms (Brodribb *et al.*, 2012). However, the picture is more complex, as shown in a recent study by Anderegg & HilleRisLambers (2016), who found that two coexisting tree species, the conifer *Pinus ponderosa* and the hardwood *Populus tremuloides*, responded to drought by varying different suites of drought-response traits. In addition, different mechanisms exist within widely distributed tree species such as conifers to deal with water deficit (Brodribb *et al.*, 2014). For instance, some pine species show limited plasticity in their xylem functional responses to drought (Martínez-Vilalta *et al.*, 2009; Lamy *et al.*, 2014). Nevertheless, how tree species with different anatomical, hydraulic and functional traits respond to drought in terms of growth resilience remains unclear and little explored. Quantifying the growth responses of different tree species to drought across broad geographical gradients may help to understand what the main functional mechanisms are that drive forest resilience.

In this sense, tree rings can provide valuable information on how much a tree species is affected by drought and how tree growth reacts to drought (Camarero *et al.*, 2015). The dating and measurement of tree-ring widths across prolonged periods provide a retrospective picture of how forests grow before, during and after drought events, making it possible to compare the resilience of forests to drought (Lloret *et al.*, 2011). To quantify forest growth responses to drought and its consequences, Lloret *et al.* (2011) used the concept of tree resilience to drought and proposed three dimensionless indices that quantify different aspects of the reaction of radial growth to drought. These indices capture: (1) how tree radial growth 'resists' drought stress by continuing growth even during water shortage, (2) recovery of growth after the drought event, and (3) growth resilience by comparing pre- and post-drought growth values. These indices have been successfully applied to quantify differences in growth resilience to drought (Pretzsch *et al.*, 2013, Gazol & Camarero, 2016).

Here we evaluate the resilience of forest growth to drought in different regions across the Northern Hemisphere, particularly North America and Europe, by analysing an extensive database of tree-ring width and drought data. We make use of an extensive tree-ring database, the International Tree-Ring Data Bank (ITRDB; Grissino-Mayer & Fritts, 1997). First, we identify the droughts which occurred in each region, defined as those years displaying a reduced water budget, from climate data. Second, we assess the resilience of forest growth to the selected droughts by quantifying the resistance, resilience and recovery indices. Finally, we evaluate how these indices vary across the study regions as related to different site factors. We hypothesize that forests from drought-prone sites (e.g. semi-arid forests) have a great capacity to recover after droughts, whereas growth resistance is higher under mesic conditions where mild droughts occur frequently but productivity is relatively high (e.g. temperate forests).

MATERIAL AND METHODS

Climate data and definition of drought

To quantify drought events we used climate data from global gridded databases. In a recent study, Anderegg *et al.* (2015)

Figure 1 Geography of the study sites. The dots indicate the different locations included in the study. The colour palette represents the value of soil moisture from 0-100 cm depth minus potential evapotranspiration (SM-PET) in each location. Colour intensity scheme indicates the scale of SM-PET. Low values of SM-PET are mostly found in arid locations while high values of SM-PET are mostly found in humid locations.
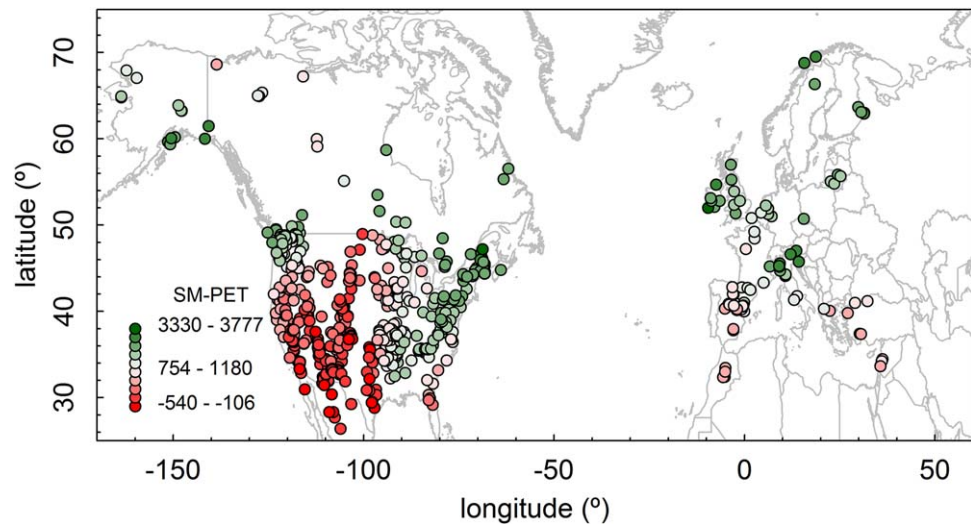
analysed monthly climate data from different sources in order to find a globally suitable climate index of water deficit for forests. In particular, they considered monthly precipitation and temperature data from three sources: (1) Climate Research Unit version 3.22 with gridded data at a 0.5° resolution (CRU; Harris et al., 2014), (ii) Global Precipitation Climatology Centre (GPCC; Schneider et al., 2014), and (iii) National Oceanographic and Atmospheric Administration Precipitation Reconstruction Over Land (NOAA PREC/L; Chen et al., 2002). Anderegg et al. (2015) used data on precipitation, potential evapotranspiration (PET) and soil moisture to search for a suitable metric of water deficit. Based on correlations calculated between tree growth and drought variables they selected an index calculated from the moisture at a soil depth of 0–100 cm minus PET calculated from the full Penman–Monteith equation (hereafter abbreviated as SM-PET). We use this metric here for our primary drought variable. The PET was calculated at 1.0° resolution using the Penman–Monteith equation and it was downloaded from http://hydrology.princeton.edu/~justin/ on 12 December 2014. The Penman–Monteith equation models PET as the combination of radiative and aerodynamic processes and it represents a more accurate and physically based model of PET than the overly simple Thornthwaite formulation, which is based solely on temperature (Vicente-Serrano et al., 2014). Modelled soil moisture at a soil depth of 0–100 cm was calculated by the Noah land surface model version 3.3, forced by the Princeton meteorological forcing data from the Global Land Data Assimilation System version 2 (GLDAS-2; Rodell & Beaudoing, 2015). The GLDAS-2 provides a series of land surface parameters which are modelled by combining satellite-based images as well as other land surface and climate data. The GLDAS-2 data had a geographical resolution of 0.25° and we aggregated them to a 1.0° resolution. These metrics of a plant's 'water budget' have proved to be more advantageous than just precipitation or temperature data to model vegetation patterns at regional scales (Dyer, 2004).

Here we define dry years as those showing the 10% lowest values of SM-PET. Using this definition, drought occurrence is calculated based on abnormal decrease in water availability in relation the average conditions of a region (e.g. Heim, 2002). In this way we ensure a large enough and comparable occurrence of drought events across regions despite the SM-PET values of dry years vary from one region to another (Fig. 1).

Tree-ring data

The International Tree-Ring Data Bank (ITRDB) (Grissino-Mayer & Fritts, 1997) is a virtual repository that contains tree-ring measurements from around 100 tree species in more than 2000 sites around the world. Dendrochronologists have generously made tree-ring data available to the scientific community and these are accessible online at http://www.ncdc.noaa.gov/paleo/treering.html. We downloaded 3117 files containing tree-ring width measurements as well as metadata when present (i.e. latitude, longitude and site elevation). Tree-ring width measurements were detrended and standardized using standard dendrochronological protocols (Briffa & Melvin, 2011). 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, a site-level chronology was obtained using a bi-weight robust mean. 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. With this procedure we removed the low- to medium-frequency variability but retained both the high-frequency variability and the first-order autocorrelation since no autoregressive modelling was performed. Finally, we considered a total of 775 site chronologies that fulfilled the following criteria: (1) geographical information of sampled sites was present; (2) tree-ring series contained at least 25 years in the period 1948–2008; and (3) chronology sites were distributed in regions of North America, particularly the conterminous USA, and Europe (Fig. 1; see also Fig. S1 in the Supporting Information).

Resilience growth indices

For every dry year and site, we calculated the resilience of tree growth using the three indices proposed by Lloret *et al.* (2011) in which the response of tree growth to dry conditions is decomposed in three components: resistance (Rt); recovery (Rc) and resilience (Rs). We considered every dry year as a single drought event and no drought periods lasting more than 1 year were considered. The resistance index Rt quantifies the difference between tree growth in the dry year and the years before it. Thus, it quantifies the capacity of trees to buffer the drought stress and continue growth during drought. The recovery index Rc quantifies the difference in growth between the dry year and a subsequent period. The resilience index Rs quantifies the difference in tree growth before and after the dry year. Thus, it measures the capacity of trees to recover the growth rates observed before the drought stress.

The three indices were calculated as follows:

$$Rt = G_d / G_{prev} \qquad (1)$$

$$Rc = G_{post} / G_d \qquad (2)$$

$$Rs = G_{post} / G_{prev} \qquad (3)$$

where G_d indicates growth (here quantified as mean tree-ring width) during the dry period and G_{prev} and G_{post} indicate mean growth during the 3 years before and after the dry period, respectively. We used a period of 3 years because we found similar results when comparing periods of two, three and four dry years (Fig. S2).

We studied how these three components of the response of growth to drought were interrelated and how they varied across forest types. We averaged the values obtained in each forest for the different dry years to obtain a unique measurement in each site.

Analyses

We compiled a set of explanatory variables that can influence the responses of forest growth to drought. Specifically, we considered factors operating at regional as well as local scales. Topographic factors such as elevation, slope and potential solar radiation, were used together with geographical coordinates (latitude and longitude), climate conditions (SM-PET; average value and interannual coefficient of variation) and changes in above-ground forest productivity as expressed by summer normalized difference vegetation index (NDVI). Latitude, longitude and elevation were obtained from the ITRDB database. Slope and potential incoming solar radiation were obtained from a digital elevation model at a spatial resolution of 1 km (GTOPO30) and the MiraMon Geographic Information System, and the summer NDVI at a resolution of 0.1° from the third generation Global Inventory Modeling and Mapping Studies (GIMMS) data set (Pinzon & Tucker, 2014).

We applied linear mixed-effects models (Pinheiro & Bates, 2000), using tree species and mean age of the chronology as random factors. The mean age of each chronology was quantified by calculating the mean length of ring-width series for the trees sampled in each site, in other words the mean length of the individual tree chronologies. Since not all ring-width series extend from the bark to the pith, this is a way to estimate a minimum mean age of trees sampled at each site. In order to avoid great differences between sites we classified the chronologies into five groups: less than 50 years; between 50 and 100 years, between 100 and 200 years, between 200 and 300 years and more than 300 years. A separate model was constructed for each one of the three components of tree resilience: Rt, Rc and Rs. For each model, we used a list of 10 potential explanatory variables. Specifically, we considered as potential predictors: latitude, longitude, elevation, solar radiation, slope, SM-PET mean and interannual coefficient of variation and summer NDVI.

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 probability that a given model is more appropriate than other competing models to explain the response variable. Therefore, the final output is a set of candidate models rather than a single model. We ranked all the potential models that could be generated with the different explanatory variables according to the second-order Akaike information criterion (AICc). For each explanatory variable we calculated its relative importance. 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 variable importance weight the greater the importance of the predictor variable (Burnham & Anderson, 2002). Finally, we estimated the coefficients for each of the explanatory covariates included in the model. Thus, the regression coefficient associated with each explanatory variable is a combination of coefficients from different competing models and not a single value. To quantify the strength of the model, we calculated a pseudo-R^2 as the squared value of the correlation between observed and fitted values. 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.
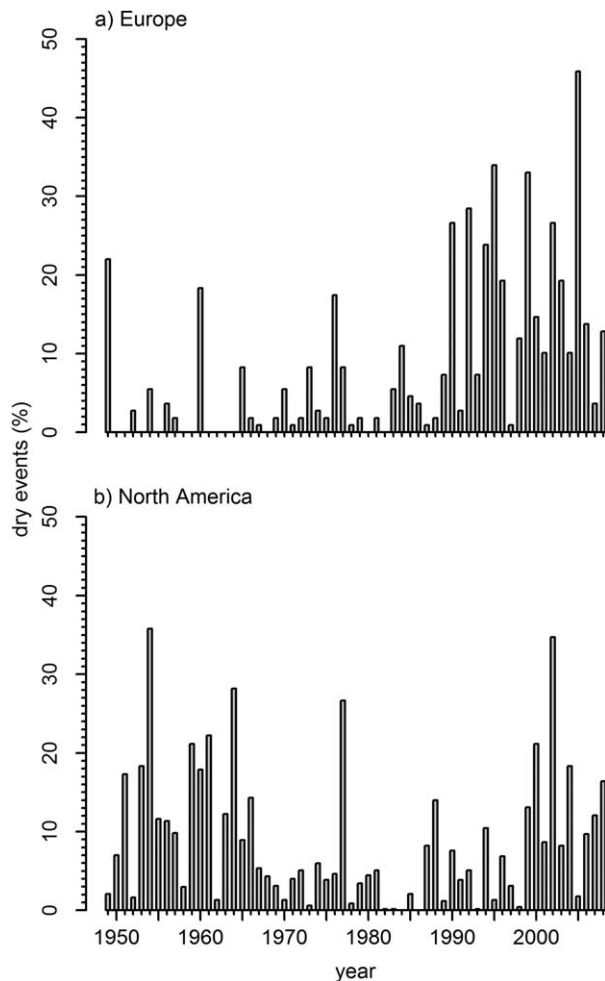
Finally, we performed simple correlation analyses at the species level to quantify the main factors driving the patterns of forest resilience for the most frequent species in North America and Europe. In particular we considered 10 tree species present in more than 13 sites: *Pinus ponderosa* (93 sites); *Pseudotsuga menziesii* (55 sites); *Quercus stellata* (43 sites); *Quercus alba* (41 sites); *Tsuga canadensis* (39 sites); *Picea glauca* (22 sites); *Taxodium distichum* (21 sites); *Pinus jeffreyi* (19 sites); *Pinus sylvestris* (15 sites); *Pinus nigra* (13 sites). For each species we correlated the Rt, Rc and Rs indices for each location in which the species was present with the same set of predictor variables as in the previous analyses: latitude, longitude, elevation, solar radiation, slope, SM-PET mean and interannual coefficient of variation and summer NDVI. Simple Pearson correlation analyses were used because the

number of occurrences of several species was not high enough to allow more sophisticated regression models.

All statistical analyses were performed in the R environment (R Development Core Team, 2014). The 'dplR' package was used to detrend tree-ring width indices and calculate mean chronologies (Bunn *et al.*, 2015). The *lme* 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).

RESULTS

The soil moisture minus PET (SM-PET) and the threshold value for the definition of dry years varied strongly around the world, closely related to the aridity conditions of each forest site (Fig. 1). The lower values are recorded in the arid sites of the central USA and north Mexico. Moreover, there exists a strong temporal variation in the occurrence of dry years with marked events (Figs 2 & S3). Forest growth responded positively to increased soil moisture, particularly
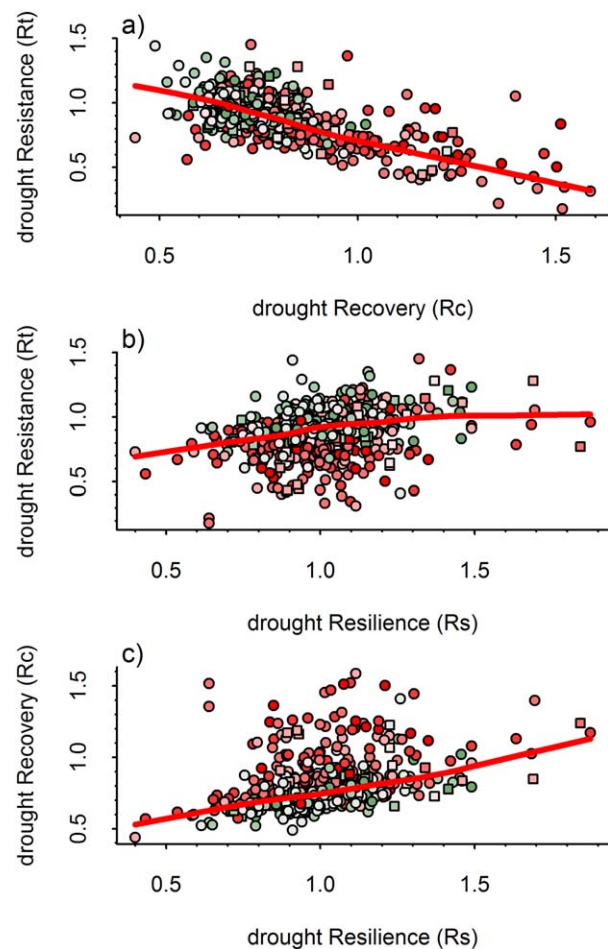
from April to July, in semi-arid regions such as the south-western USA or southern Europe but also in mesic sites from the north-eastern USA and central Europe (Figs S4 & S5).

We found strong relationships between the three indices used to capture drought resilience. The resistance of tree growth to drought (Rt) was negatively related with the recovery of tree growth after drought (Rc; Fig. 3). In addition, both indices were positively related to drought resilience (Rs).

In general, the drought metric models proposed explained around 30% of the variance in drought resilience components: 25% in Rt; 39% in Rc, and 38% in Rs. The fixed factors considered accounted for 16%, 20% and 5% of the variation in Rt, Rc and Rs, respectively. We found that the resistance of tree growth to drought increases as the latitude and SM-PET increase, whereas the recovery after drought (Rc) decreases as the latitude increases (Fig. 4, Table 1).

Figure 2 Number of drought events (defined when soil moisture at 100 cm depth minus potential evapotranspiration, SM-PET, was lower than the 10th percentile) observed in Europe (a) and North America (b) during the period 1949–2008.


Figure 3 Relationships observed between the components of drought resilience of tree growth. Relationship between: (a) drought resistance (Rt) and recovery (Rc); (b) drought resistance (Rt) and resilience (Rs); and (c) drought recovery (Rc) and resilience (Rs). The thick lines represent nonlinear relationships between the variables. The colour intensity of the points indicate the 10th percentile of the soil moisture at 100 cm depth minus potential evapotranspiration (SM-PET) index observed in each site (see Fig. 1).

a) Resistance (Rt)

b) Recovery (Rc)
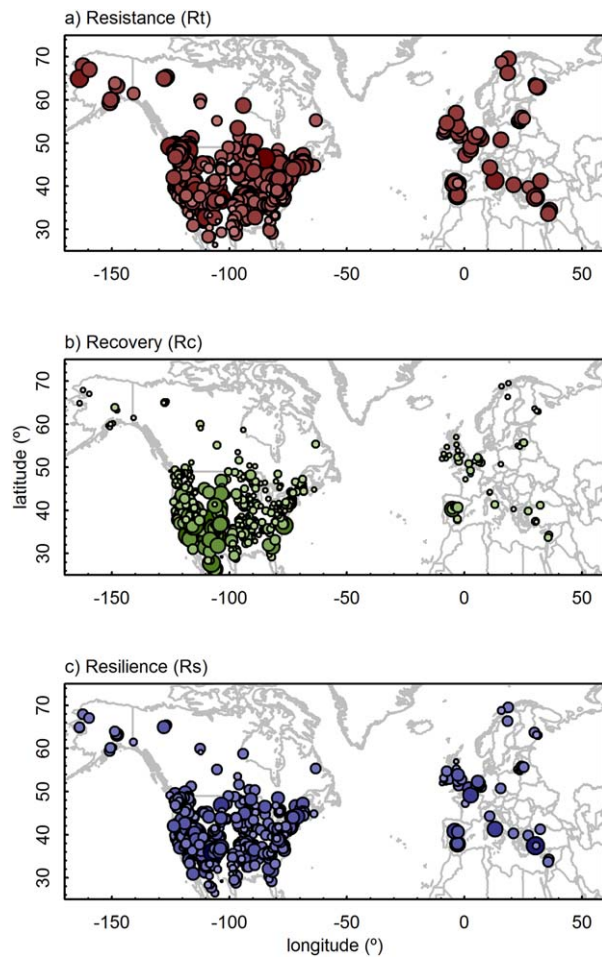
c) Resilience (Rs)

Figure 4 Components of resilience of forest growth in response to drought. The geographical pattern of the three components of drought resilience is presented: (a) resistance (*Rt*); (b) recovery (*Rc*); and (c) resilience (*Rs*). The size and the colour intensity are proportional to the represented index (the larger the index, i.e. the better the performance during/after drought, the darker the colour and the larger the symbol).

Forest growth resistance was strongly determined by the geographical location of the sites, with high resistance values in wet and cold sites such as temperate forests (north-western and north-eastern USA, central Europe, Balkans, some boreal forests), high recovery values in semi-arid or dry sites (south-western USA, Spain) and a less clear pattern for resilience values (Fig. 4). All of our tested explanatory factors showed important implications for at least one of the three components of forest resilience studied, although important explanatory factors varied by the component of resilience (Table 1, Fig. S6). Resistance of tree growth to drought increased with slope, latitude and SM-PET, whereas recovery of tree growth after drought decreased with latitude, slope and mean and interannual coefficient of variation of SM-PET. The resilience of tree growth to drought was positively linked to elevation (marginally significant; $P < 0.1$) and negatively to the interannual coefficient of variation in SM-PET.

Table 1 Model averaged coefficients for the different components of forest growth resilience.

|	Coefficient ($\pm$ SE)	Z-statistic
Resistance (*Rt*):		
Latitude	0.255 ± 0.049	5.227**
Slope	0.152 ± 0.044	3.903**
SM-PET CV	0.034 ± 0.042	1.079
SM-PET mean	0.214 ± 0.055	3.903**
Elevation	-0.006 ± 0.035	0.0922
Longitude	0.054 ± 0.05	0.280
Solar radiation	-0.006 ± 0.035	0.867
NDVI_JJA	0.028 ± 0.064	0.922
Recovery (*Rc*):		
Latitude	-0.247 ± 0.051	4.80**
Slope	-0.141 ± 0.051	2.791**
SM-PET CV	-0.234 ± 0.040	5.803**
SM-PET mean	-0.233 ± 0.057	4.099**
Elevation	0.102 ± 0.060	1.694
Longitude	-0.014 ± 0.057	0.249
Solar radiation	-0.026 ± 0.032	0.821
NDVI_JJA	-0.053 ± 0.046	1.166
Resilience (*Rs*):		
Latitude	-0.064 ± 0.058	1.112
Slope	-0.101 ± 0.067	1.778
SM-PET CV	-0.183 ± 0.047	3.863**
SM-PET mean	0.042 ± 0.072	0.583
Elevation	0.133 ± 0.071	1.877
Longitude	0.109 ± 0.067	1.634
Solar radiation	-0.008 ± 0.049	0.233
NDVI_JJA	-0.025 ± 0.049	0.496

The coefficient associated with each explanatory variable (mean $\pm$ adjusted SE) is shown together with the Z-statistic. Significance levels are indicated with asterisks (*$P < 0.05$; **$P < 0.01$).
SM-PET, soil moisture at 100 cm depth minus potentia evapotranspiraton (PET) used as a proxy of drought severity (mean and coefficient of variation, CV); NDVI_JJA, summer normalized difference vegetation index.

The analyses revealed that the growth resilience index *Rs* of each species varied across the studied sites and responded to different factors (Figs 5 & S7, Table S1). The recovery, and to a lesser extent, the resistance of conifers such as *Pinus ponderosa*, *Pseudotsuga menziesii*, *Pinus sylvestris* and *Pinus jeffreyii* was more variable than that of oak species (Fig. 5). The resistance of the four most common species varied strongly along the latitudinal and longitudinal gradients. The recovery of some conifers (e.g. *Pinus ponderosa*, *Pseudotsuga menziesii*) and oak species from mesic sites (*Q. stellata*, *Q. alba*) depended on site longitude and soil moisture. However, the recovery of some conifers varied as a function of elevation (*Pinus ponderosa*, *Pseudotsuga menziesii*, *T. distichum* and *Pinus sylvestris*). Finally, we found few significant influences of the variables studied on the resilience index.

DISCUSSION

Our results support the idea that forests display different strategies to withstand the impacts of drought. In this sense, the
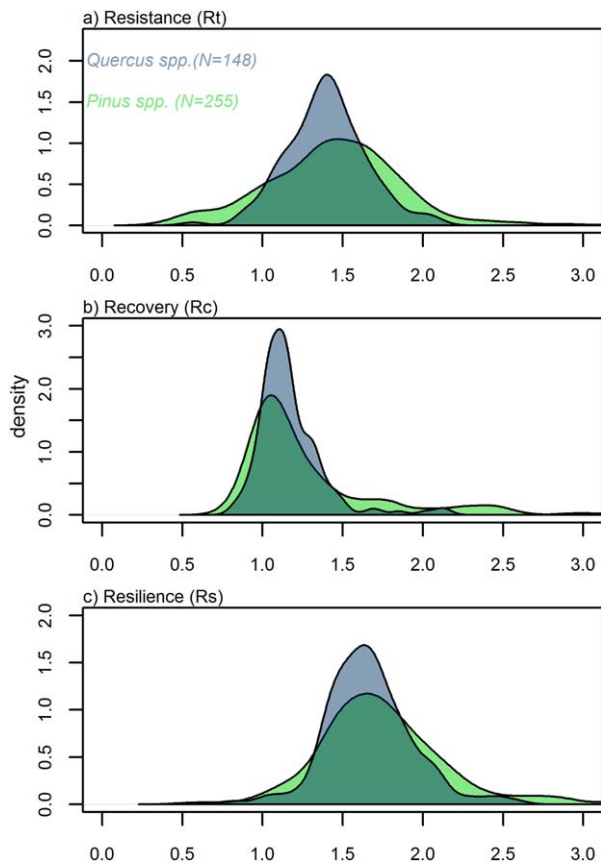
Figure 5 Components of forest growth resilience for oak (n = 148 sites) and pine (n = 225 sites) species and their variation across the geographical range of the species: (a) resistance (Rt); (b) recovery (Rc); and (c) resilience (Rs). The figure shows a kernel density distribution graph of the values of the Rt, Rc and Rs indices for oak and pine species. The x-axis represents the range of Rt, Rc and Rs values and the y-axis shows the potential density for each value. The figure shows a greater tendency across the mean for pine species and the lower bandwidth of oak species.

three components of growth resilience displayed different geographical patterns across North America and Europe and were influenced by the different explanatory variables. The negative relationships observed between resistance of forest growth to drought and forest recovery from drought (Fig. 3) suggests the existence of two strategies. While drought resistance increases along gradients of latitude and soil moisture, drought recovery decreases. In addition, recovery after drought is strongly sensitive to variability in soil moisture during the year (Table 1). This suggests the existence of a trade-off between the resistance of growth to drought and the recovery of growth after drought. Finally, it is possible that considering stand (functional and structural diversities) and tree (size) factors in future models would increase the amount of explained variation in the resilience of growth to drought.

The approach used to determine the occurrence of drought, based on an abnormal decrease in water availability in relation to the average conditions of a region (e.g. Heim, 2002), makes it possible to study how forest resilience reacts to the same relative (from a statistical standpoint) drought in regions with contrasting climate. We cover many drought-prone regions in which drought-induced mortality events have been widely reported such as the south-western USA (e.g. Breshears *et al.*, 2005; Clark *et al.*, 2016). Other regions, such as temperate broadleaf forests from eastern North America, are expected to be less impacted by drought due to the abundant and well-distributed precipitation they receive. However, during recent years it has been reported that these forests can suffer from reduced levels of soil water availability and are vulnerable to global change (Gonzalez *et al.*, 2010; Martin-Benito & Pederson, 2015). This extensive coverage of climatic conditions in North America (spanning semi-arid to cool temperate regions) contrasts with data from Europe in which semi-arid regions are underrepresented (Fig. 1). There are therefore very few chronologies available from the Mediterranean Basin where forests are facing drought-induced die-back (Camarero *et al.*, 2015; Dorman *et al.*, 2015; Gazol *et al.*, 2015). Moreover, several studies have demonstrated that extreme droughts, such as the heat wave of 2003, have negatively affected the productivity of European forests during the last decades (Ciais *et al.*, 2005; Ivits *et al.*, 2014). This lack of representation in some regions is influenced by sample availability in the ITRDB (Vicente-Serrano *et al.*, 2013; Anderegg *et al.*, 2015). Although our approach loses power in the spatial representation of areas with very fragmented forests such as southern Europe, where there is a deficit of ITRDB tree-ring chronologies, the long time-scale covering the past half century still provides useful inferences.

The resistance of forest growth to drought tends to increase as latitude and soil moisture increase (Table 1, Fig. 4). In terms of drought recovery, higher values of forest growth recovery were found in the south-western USA and southern Europe (Fig. 4), which are among the driest regions of the studied area (Fig. 1). These contrasting patterns in resistance of forest growth to and recovery from drought suggest the existence of different strategies to cope with drought. The great recovery capacity of trees from these drought-prone regions after drought suggests a great ability of tree species from these regions to adapt and respond to periods of water deficit. In particular, some tree species have shown substantial xylem plasticity related to hydraulic conductivity following drought, which might allow them to acclimate to drought and increase their resilience (Lopez-Iglesias *et al.*, 2014; Anderegg, 2015; Anderegg & HilleRisLambers, 2016; López *et al.*, 2016). Other species such as holm oak can increase leaf-specific conductivity by a reduction in the transpiring leaf area (Limousin *et al.*, 2010). The potential for tree species to acclimate to drier conditions through phenotypic plasticity could significantly buffer forests under climate change scenarios, but is rarely considered in ecosystem models (Anderegg, 2015; but see Wang *et al.*, 2010; Benito Garzón *et al.*, 2011; Leites *et al.*, 2012). Quantification of phenotypic plasticity in drought response traits,

especially across many species, is logistically challenging but greatly needed (Valladares *et al.*, 2014). Crucially, our study reveals that tree species vary in the resilience of growth to drought and this points to the importance of phenotypic plasticity for understanding a species' response to drought across its distribution range (Fig. 5).

We found that gymnosperms (mainly pines) were more plastic in their resistance to drought across geographical gradients than angiosperms (mostly oaks; Table 1, Fig. 5). In this sense the two conifers more frequently sampled in the ITRDB (*Pinus ponderosa*, *Pseudotsuga menziesii*) displayed a greater plasticity in resistance to drought that the two more frequently sampled oaks (*Q. alba* and *Q. stellata*; Fig. S8). These results largely agree with those of other studies that found little hydraulic variation between some pine species but large variation in growth-related traits, such as the Huber value (e.g. Martínez-Vilalta *et al.*, 2009; Lamy *et al.*, 2014; Anderegg & HilleRisLambers, 2016). However, it is important to note that both conifers and oak species presented strong intraspecific variation in growth resistance to and recovery after drought, as represented by correlations with longitude, which represents an important gradient of increasing aridity westward within North America (Fig. 1). Oak and pine species are located at opposite extremes of the leaf–wood functional spectrum since oaks present resource-acquisitive leaf traits and a high wood density whilst pines present resource-conservative traits and a low wood density (Vilà-Cabrera *et al.*, 2015). Thus it is plausible to think that these groups of species may have different strategies for coping with drought that involve a wide suite of traits and not simply xylem growth rates (Brodribb *et al.*, 2014; Anderegg & HilleRisLambers, 2016).

It is possible that, on average, gymnosperms have a great capacity to resist a drought event, which is consistent with their generally more drought-tolerant xylem (Maherali *et al.*, 2004), but they need more time to recover growth after a water shortage than angiosperms (Anderegg *et al.*, 2015). This is also consistent with anatomical differences such as the lower proportions of living tissue in gymnosperm wood and greater longevity (Brodribb *et al.*, 2012; Johnson *et al.*, 2012). Further research considering additional traits (stomatal conductance, water storage in sapwood, rooting depth) and their intraspecific variation across species distribution ranges and how they relate to drought is required.

Differences between regions in the response to drought can thus be partially explained by the different species that dominate each region which are the product of human landscape transformation. Western North American forests are dominated by coniferous species well adapted to drought such as *Pinus ponderosa* and *Pseudotsuga menziesii* (Clark *et al.*, 2016). Conversely, in eastern North America drought-tolerant forest tree species have been replaced by more productive mesophytic tree species during the 20th century as a consequence of fire suppression (Nowacki & Abrams, 2008). In this sense, Brzostek *et al.* (2014) suggested differences in vessel size and distribution, and the preference of arbuscular versus ectomycorrhizal symbiosis as the main factors driving the growth responses of trees to drought across eastern North American hardwood forests. These results emphasize the idea that climate, through the influence of extreme events such as severe droughts, but also through mild droughts and changes in management, may interact to determine forest productivity and composition over broad geographical scales (Vanderwel *et al.*, 2013).

The occurrence of growth-sensitive droughts is not restricted to dry or temperate regions. Thus, it could be hypothesized that an increase in drought events may reduce forest productivity and increase the mortality rate in non-water limited regions, or at least in the driest sites of these regions (Dietze & Moorcroft, 2011). At a continental scale, it seems that Europe has experienced an increase in dry years since 1950, whereas North America as a whole has not (Fig. 2). This could negatively affect European forests, whose resistance to drought increases northwards (Fig. 4) and is negatively correlated with drought recovery. If growth resistance is the preferred strategy for overcoming droughts by boreal forests, which are not used to extreme droughts, a certain threshold of 'resistance' may exist. If such a threshold is reached under future drier and warmer conditions, some high-latitude tree populations may be more endangered than those inhabiting low latitudes. This in turn may also favour the northward expansion of species from low latitudes. However, whether this will translate into changes in forest composition requires a more holistic approach taking into consideration mortality and recruitment (Clark *et al.*, 2016), as well a more detailed exploration of how tree species from drought-prone and mesic regions vary in their functional traits across their distribution ranges (Vilà-Cabrera *et al.*, 2015; Anderegg & HilleRisLambers, 2016). At local scale it is plausible to think that forests located on steep slopes or shallow and rocky soils are adapted to drier conditions and present lower growth rates and thus a greater resistance and lower recovery after drought. However, why these factors have an impact on the resilience of trees to drought requires a better understanding of the links between radial growth and functional traits related to physiological mechanisms (photosynthesis, water and carbon use).

There is a lack of studies evaluating the long-term impacts of drought on forest growth at continental to global scales, despite a few exceptions (e.g. Vicente-Serrano *et al.*, 2013; Anderegg *et al.*, 2015). The consequences of the forecast increase in the severity and intensity of droughts are largely unknown. Retrospectives studies aiming to understand how forest growth has reacted to drought may help to advance our knowledge. This study represents one of the first attempts to illuminate the resilience of forests to drought. We conclude that there exist different resilience strategies in response to drought, with some forests showing a greater growth resistance while others present a greater growth recovery. Species with different ecophysiological characteristics show varied responses to drought in terms of growth resilience, but our findings indicate that geographical changes

and soil moisture gradients override species-specific responses. This highlights key future avenues for research into how forest composition might enhance or mitigate the vulnerability of forests to drought under a warmer climate.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Correlations (Pearson coefficients) calculated between site features and the three indices representing components of forest growth resilience in response to drought for the major tree species.

Figure S1 Map of the tree-ring width chronologies considered in this study.

Figure S2 Relationships observed between the three indices representing the forest growth resilience to drought considering periods of several lengths after a drought.

Figure S3 Forest sites showing selected drought years.

Figure S4 Associations calculated between growth and the drought index.

Figure S5 Associations (Pearson coefficients) calculated between growth and the drought index at a monthly scale.

Figure S6 Determinants of forest growth resilience in response to drought.

Figure S7 Geographic patterns of the tree-ring width chronologies of the most frequently studied tree species.

Figure S8 Components of forest growth resilience for the most frequent species and its variation across the geographical range of the species.

BIOSKETCHES

Antonio Gazol is a researcher mainly interested in how plant populations and communities respond to environmental drivers at varying spatial and temporal scales.

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