SHORT-TERM FOREST RESILIENCE AFTER DROUGHT-INDUCED DIE-OFF IN SOUTHWESTERN EUROPEAN FORESTS

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Abstract

Drought-induced die-off in forests is becoming a widespread phenomenon across biomes, but the factors determining potential shifts in taxonomic and structural characteristics following mortality are largely unknown. We report on short-term patterns of resilience after drought-induced episodes of tree mortality across 48 monospecific forests from Morocco to Slovenia. Field surveys recorded plants growing beneath a canopy of dead, defoliated and healthy trees. Site-level structural characteristics and management legacy were also recorded. Resilience was assessed with reference to forest composition (self-replacement), structure, and changes in the climatic suitability of the replacing community relative to the climatic suitability of the dominant pre-drought species. Species climatic suitability was estimated from species distribution models calculated for the baseline 1970-2000 period.

Short-term resilience decreased under higher levels of drought-induced damage to the dominant species and with evidences of management legacy. Greater resilience of structural features (fewer gaps, greater canopy height) was observed overall in forests with a larger basal area. Less gaps were also associated with greater woody species richness after drought. Overall, Fagaceae-dominated forests exhibited greater structural resilience than conifer-dominated ones. On those sites that were more climatically suited to the dominant pre-drought species, replacing communities tended to exhibit lower climatic suitability than pre-drought dominant species. There was a greater loss of climatic suitability under a legacy of management and drought intensity, but less so in the replacing communities with higher woody species richness.

Our study reveals that short-term forest resilience is determined by pre-drought stand characteristics, often reflecting previous management legacies, and by the impact of drought on both the dominant pre-drought species and post-drought replacing species in terms of their climatic suitability.

Keywords

climate change, drought-induced die-off, drought events, forest mortality, forest resilience, species climatic suitability.

1. Introduction

There have been an increasing number of reports on mortality in many forest types across forested biomes (van Mantgem et al. 2009; Allen et al. 2015, Neumann et al. 2017). Climate changes, and particularly extreme drought episodes, have often been associated with this phenomenon (Allen et al. 2010; Carnicer et al. 2011; Peng et al. 2011; Williams et al. 2013; Evans and Lyons 2013; Senf et al. 2020), with drought intensity being an important determinant of such mortality episodes (Greenwood et al. 2017). Other drivers, such as pests, management legacy and species biogeographical context, usually interact with climate to increase mortality rates above the historical baseline (Clark et al. 2016; Sommerfeld et al. 2018). This leads to a high degree of local idiosyncrasy in terms of the extent, duration and identity of the affected tree species (Lloret and Batllori 2021). Despite the relevance of these forest mortality events to the future of forests and the services that they provide (Anderegg et al. 2013), their consequences in terms of forests' compositional and structural characteristics have been insufficiently investigated. For instance, vegetation-type conversion following drought has been reported at multi-regional scale (Batllori et al. 2020), but our understanding about the mechanisms of resilience in forests affected by drought-induced mortality still remains largely uncertain (Martinez-Vilalta and Lloret, 2016).

From the perspective of the resilience theory, engineering resilience (*sensu* Pimm 1984; see Gunderson 2000) refers to the capacity of the ecosystem to recover its pre-disturbance properties, which are considered to define its ecological state of reference. In forests experiencing drought-induced die-off, their state of reference can be estimated as the pre-drought levels of dominance of overstory species. Alternatively, ecological resilience (*sensu* Holling 1973; see Gunderson 2000) refers to the capacity of a system to remain in a state of dynamical equilibrium until it reaches a tipping point that leads to a new equilibrium state. In drought-affected forests, this would correspond to shifts towards a non-forested community. Long-term monitoring of drought-affected areas is needed to gain conclusive data about tipping points, but the assessment of the short-term replacement patterns after mortality events (Batllori et al. 2020) can provide important insights into future trajectories (Johnstone et al. 2016). For instance, the absence of woody species replacing dead trees following drought can be considered a preliminary indicator of potential tipping points, which will be confirmed if tree species are not able to establish themselves in the long term. In other words, measures of engineering resilience, such as short-term replacement patterns, are also informative of long-term ecological resilience.

Canopy replacement largely determines the initial stages of forest dynamics in different ways after a mortality event. Drought mortality can ‘push back’ successional trajectories towards early stages if pioneer species are favored, or it may ‘push forward’ successional processes if replacement by late-successional species is promoted (Batllori et al. 2020). Alternatively, new successional trajectories may also appear following drought if species turnover leads to novel community assemblages (Hobbs et al. 2006). Gap-dynamics approaches based on tree-level observations and modelling, eventually scaled-up to stand level, are suitable for capturing such processes (Ibáñez et al 2019).

Stand characteristics - including basal area, tree density, and species richness - determine forest dynamics after gap opening to some extent (e.g., Rebertus and Veblen 1993; Gray and Spies 1996) and, therefore, they are likely to explain the replacement patterns of the dominant species in the canopy following drought, including the self-replacement of a tree species. Furthermore, stand characteristics closely reflect management legacy - including planting, clearing and cutting - and forest stage, which is linked to successional trajectories.

While the contribution of stand-level characteristics to forest vulnerability to drought-induced die-off has been widely explored (Galiano et al. 2010; Bell et al. 2014; Crouchet et al. 2019), its relevance to post-drought forest dynamics remains largely unexplored. For instance, large stand basal area reflects suitable growth conditions for dominant trees, often associated with late successional stages, which would endow such species with a greater higher capacity to recover for such species. In turn, stand tree density likely reflects the availability of trees in the understory ready to replace dead trees. Finally, greater richness of woody species, would likely be associated with the presence of species with different light requirements, thus limiting the continuation of the open spaces which resulted from tree death.

The effects of drought episodes on tree populations are also expected to be strongly determined by the suitability of affected sites' climatic conditions for different species. Species Distribution Models (SDMs) provide a quantitative characterization of species' requirements by correlating their occurrences in a territory with their respective environmental conditions (often climatic), as obtained from georeferenced sources (Franklin, 2010). These models can then be projected under given sets of climatic conditions to obtain climatic suitability indexes, which synthetizes the degree to which such climatic conditions are adequate for the species, according to the climatic conditions that the species encounter through their entire distribution range (Soberón and Peterson 2005). A key feature of species distribution models is that their standardization (through suitability indices) the way that different populations and species experience the climatic environment. This approach has been used to explain the impact of extreme drought episodes on co-occurring species (Sapes et al. 2017, Perez-Navarro et al. 2019) and on populations of dominant tree species across regions (Lloret and Kitzberger 2018, Margalef et al. 2020).

In this context, we could expect resilience patterns after disturbance to be determined by the climatic suitability of the dominant species on a given site. For instance, on those sites that have been historically suitable for a particular species, a higher availability of its recruits would be expected (Sexton et al. 2009), thus enhancing self-replacement. However, recruiting populations living in historically suitable and stable conditions can be less successful under the harsh conditions of a drought episode (Walck et al. 2011). The balance between such processes could determine the eventual relationship between historical climatic suitability and resilience patterns (Lloret and Kitzberger 2018, Margalef et al. 2020).

Climatic suitability indexes also make it possible to scale up from coexisting populations of different species to community-level estimates. Community-weighted means can be calculated from the abundance of the species present on a site in order to estimate the overall suitability of the community's climatic conditions. Higher values of community climatic suitability would indicate that most species growing on that site find optimal climatic conditions there. In this case, the climatic disequilibrium, defined as the difference between the climate existing on that site and the climate inferred from the community composition (Davis 1986; Svenning and Sandel 2013; Blonder et al. 2015), would be minimal. After disturbance, differences between the climatic suitability of the previously dominant tree species and the climatic suitability of the replacing species would indicate trends in the emerging community's suitability with respect to the recent climate. Accordingly, negative trends (i.e., lower climatic suitability of the replacing community) would entail an increase in climatic disequilibrium, in relation to the historical conditions. In contrast, positive suitability trends after disturbance (i.e., higher climatic suitability of the replacing community) would indicate that the formerly dominant species exhibited greater climatic disequilibrium than the potential replacers. Both positive and negative changes in community-level suitability and, therefore, climatic disequilibrium trends ultimately reflect the filtering effects of the disturbance event on community composition (Keddy 1992). For instance, when a drought event filters those species living closer to their climatic tolerance limits, climatic disequilibrium would decrease (Perez-Navarro et al. 2021). By contrast, if the filtering is produced in species living under high climatic suitability (Cavin and Jump 2017; Lloret and Kitzberger 2018), the climatic disequilibrium increases – i.e., a loss of community climatic suitability occurs. Finally, equal values of climatic suitability in the replacing community and the former dominant community (i.e., no change in climatic disequilibrium) would imply high community resilience in terms of community climatic suitability, even if both the initial and the replacing communities are not compositionally equivalent.

Here we study short-term patterns of resilience (engineering resilience) to drought-induced episodes of tree mortality across 48 monospecific forests from Morocco to Slovenia, dominated by 18 different tree species. Resilience estimates were based on plant-by-plant replacement field data. These estimates referred to 1- taxonomic composition (mainly self-replacement), 2- stand structure (gaps, canopy height) and 3- changes in the climatic suitability (estimated from MaxEnt algorithms; Phillips and Dudick 2008) of the replacing community. Stand structural characteristics (basal area, density, woody richness) and management legacy were also recorded in the field.

We analyze short-term resilience of forest taxonomic composition and structure in relation to characteristics of the drought event, the stand characteristics and the climatic suitability of the dominant pre-drought species. A regards the characteristics of the drought event, we hypothesize that resilience overall tends to be lower under high drought intensities (both during and after the drought episode), which will have an impact on both overstory and understory plants from the dominant tree species. With respect to stand characteristics, we hypothesize that self-replacement tends to increase with greater basal area, as a proxy for a population's good performance in a locality, and with higher density, indicating more recruitment of saplings. Gaps will decrease with greater woody richness, because complementarity between species will promote canopy cover, while canopy height will tend to increase with basal area. Milder management (i.e., preserving regeneration) and absence of pests/pathogens will favor overall resilience. As for the climatic suitability of the dominant pre-drought species, we hypothesize that resilience in terms of self-replacement and structural features tends to be greater on sites with a greater historical suitability of the dominant pre-drought species, due to better performance and therefore the existence of surviving recruits and neighboring canopy trees from this species; alternatively, recruits can be equally as affected as adults, or even more affected, thus jeopardizing dominant species' persistence after the event. Furthermore, we address short-term resilience in terms of changes in the climatic suitability of the replacing community relative to the suitability of dominant pre-drought species. We hypothesize a decrease in community climatic suitability and, therefore, a greater climatic disequilibrium following drought, as it is expected that dominant pre-drought species are more suited to historical site conditions than the post-drought replacements.

2. Methods

2.1. Location and description of the study sites

From 2014 to 2019, we surveyed 48 sites distributed across Morocco, Spain, France, Switzerland, Italy and Slovenia (Fig. 1), corresponding to semi-natural forest dominated by single tree species. A total of 2,400 trees were sampled. All sites showed conspicuous standing mortality of the dominant tree species, ranging from 14.5% to 60.6%. Overall, the study sites encompassed 18 different tree species: ten conifers (*Abies*, *Cedrus*, *Juniperus* and *Pinus* genera), and eight belonging to the Fagaceae familiy (*Quercus* genus) (Supplementary Material Table S1). The sites did not show any evidence of recent disturbances (e.g., wildfires, windstorms causing tree fall), planting, or other intensive management practices (pruning, grazing, resin or cork exploitation).

On 28 of the sites (~60%), tree mortality had been explicitly related to drought in previous studies (Supplementary Material Table S1). Moreover, we checked for climatic drought concomitant with tree mortality, according to the Standardized Precipitation-Evapotranspiration Index SPEI (Vicente-Serrano et al. 2010; Begueria et al. 2010). Minimum SPEI values over the ten years before the sampling date were below -1.5 on almost all the studied sites (except for two sites where this value was -1.4) (see below for details on this index) (Supplementary Material Table S1). Overall, these SPEI values correlated positively with the degree of forest die-off across the whole set of sites (Supplementary Material Table S2), endorsing the contribution of drought to forest decay, although other factors, such as pests and pathogens, could also be involved.

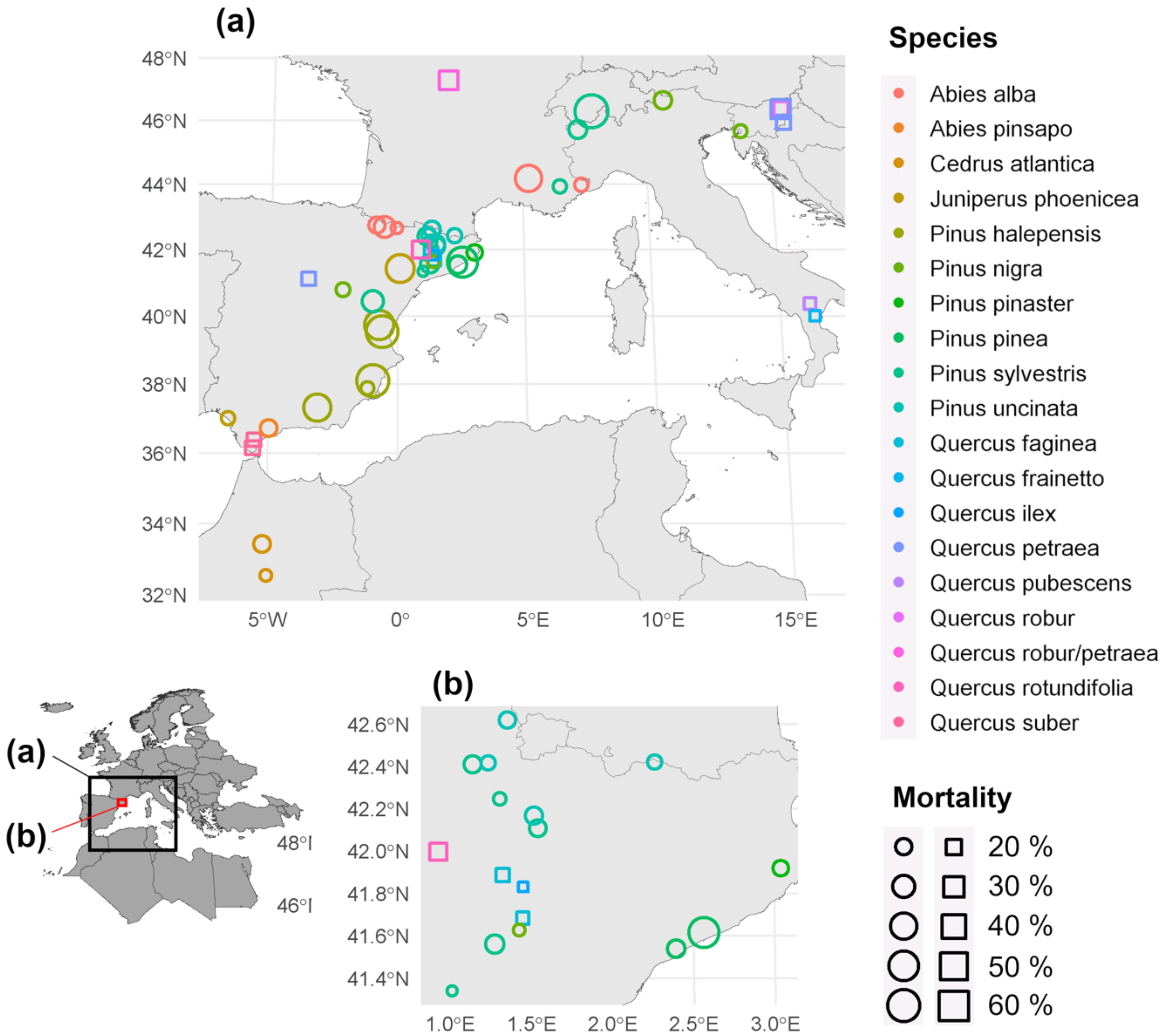

Figure 1. Map of sampled sites in the Western Mediterranean region (a), with detail of locations in Northeastern Spain (b). Sign color identifies the different species: circles correspond to Conifers and squares to Fagaceae. Sign size describes the magnitude of the standing mortality (%) recorded at each site. Additional information for each site is provided in Supplementary Material Table S1.

2.2. Survey description and structural variables

At each site a set of close linear transects (located less than 250 m apart from each other) were randomly selected to include at least 50 adult trees with non-overlapping canopies of the dominant pre-drought species within any of the following die-off categories: (1) dead trees - no green leaves, or in the case of *Quercus*, trees with few leaves on some sprouts, but without the capacity to restore a tree's mid-term viability; (2) defoliated trees - less than 70% of green canopy, and (3) healthy trees - more than 75% of green canopy (Supplementary Material Figures S1, S2). In all cases, sampled trees were part of the forest overstory. An estimate of the standing mortality of the sites' dominant species was obtained from the whole set of recorded trees (Supplementary Material Table S1). For each selected tree, we measured its height (tip of the upper branches) and we identified the tallest woody plants established beneath the canopy. Young seedlings were not considered, while close tree neighbors with canopies occupying the space potentially released by focal trees were included. In order to maintain the same criteria for identifying potential replacers across the three die-off tree categories, we visually estimated the perimeter of the former tree canopy, in case of focal dead trees. When no woody species was present beneath the canopy of the affected trees, no potential replacer was recognized and a "gap" was recorded. The relative height of the canopy of the replacing plants in relation to the former canopy (*Hrel*) was calculated as:

$$Hrel = 100 - \left(\left(\frac{Hdom - Hrep}{Hdom}\right) \times 100\right)$$

where *Hdom* is the height of the selected trees of the dominant species and *Hrep* is the height of the tallest woody plants established beneath the canopy of each selected tree.

Moreover, on each site we estimated the die-off percentage of the dominant species, as well as the total forest density and basal area. To do this, we randomly established 10 to 14 points within 5 m of the transect lines, stratified according to the length of the different transects. At each of these points, two intersecting perpendicular lines were drawn over the ground to demarcate four 90° quadrants. For each quadrant, the distance was measured from the central point to the nearest tree, regardless of its species identity, and the percentage of green canopy and the diameter at breast height (DBH) of all these trees' stems (larger than 2 cm diameter) were measured (Supplementary Material Figure S2). These measures were used to calculate:

- Dominant die-off (% die-off of the dominant tree species in the locality) was calculated as:

$$Dominant\ die-off = \left(\frac{\sum_{i=1}^{k}(ABD_i - (RGC_i \times ABD_i))}{\sum_{i=1}^{k} ABD_i}\right) \times 100$$

where ABD_i is the basal area of all trees (from *i*=1 to *k*) of the dominant species sampled in the 90° quadrants, and RGC_i corresponds to the proportion of each tree's remaining green canopy. This measure can be considered an estimate of drought damage, which is equivalent to the severity of the drought disturbance.

- Density was calculated by considering the inverse of the circular area determined by a radius equal to the distance of the nearest tree, irrespective of species, in each 90° quadrant to the central point (d_i) (Pollard, 1971) as:

$$Density = \left(\frac{4 \times (N-1)}{\pi \sum_{i=1}^{k} d_i^2}\right)$$

where N is the total number of trees (irrespective of species) measured in the 90° quadrants around all central sampling points established on a given site.

- Basal Area (stand basal area) was calculated as the sum of the DBH-derived basal area of all trees, weighted by Density, as:

$$Basal\ Area = \left(\sum_{i=1}^{k} AB_i\right) \times Density$$

where AB_i is the basal area of the nearest tree sampled in each 90° quadrant (from i = 1 to k = 4), irrespective of species.

- Richness, computed as the number of different woody species found as nearest neighbors within the four 90° quadrants around each sampling point.

Furthermore, on each site we recorded information about the management legacy. This information was based on on-site visual evidence of previous planting (e.g., regular spatial and tree size structures), logging (e.g., stumps), pruning, strong grazing (e.g. trampling), resin or cork exploitation, as well as evidence of major pests (Scolytidae, *Mastococcus* sp., processionary moth) or fungal pathogens (*Heterobasidium* sp., *Armillaria* sp., *Phytophtora* sp.). For instance, a legacy of logging or high thinning would correspond to a forest site with abundant stumps. Given the diversity of the studied forests, a one-size-fits-all threshold to define the occurrence of management legacy (e.g., stumps density) is hard to establish and that is why such estimates rely on the authors' observations in the study areas and they result in a qualitative estimation (presence or absence of clear evidence) of such legacy.

2.3. Drought characterization

The drought conditions experienced on each site were characterized using the SPEI index (Vicente-Serrano et al. 2010; Begueria et al. 2010), an index of climatic drought based on the difference between precipitation and potential evapotranspiration. This index has been demonstrated to correlate with other ecological proxies of drought (Vicente-Serrano et al 2013). This multi-scalar index calculates water deficit deviations for a given period in relation to the reference timespan (in our case, 1950-2019), considering different temporal windows of values (encompassing 1 to 48 months, SPEI1 and SPEI48, respectively) (accessed March 2020; https://monitordesequia.csic.es). In our case, drought conditions on each site were estimated from 10-year averages of SPEI24 prior to the sampling date. This wide temporal window is appropriate for exploring the relationships between climate and forest dynamics, since tree growth and mortality responses to climatic variability are often buffered over time and lagged and cumulative responses are common (Tei and Sugimoto 2018). A short temporal window would prevent to correlation of our variables of resilience and climatic suitability changes with the climate conditions that have actually determined the observed patterns of occupancy of the space left by trees damaged by the extreme drought episode. The drought characteristics were then estimated for each site by calculating the following SPEI24-derived variables: (1) minimum SPEI value (drought intensity), (2) total number of months with SPEI<-1.5 (drought frequency), (3) number of consecutive months with SPEI<-1.5 around the minimum SPEI (drought length) and (4) number of months from the sampling date to the minimum SPEI value (time since drought). We opted to use SPEI values under -1.5 as being indicative of drought conditions, as this value appropriately characterizes intense drought in secular climatic series for the considered SPEI window (Vicente-Serrano et al. 2010).

2.4. Estimation of species climatic suitability

We used MaxEnt v3.4.1 (Phillips and Dudik 2008) to compute the climatic suitability of all the dominant pre-drought species and post-drought replacing species (N = 111) on the study sites, based on species occurrence data and six climatic variables: annual isothermality, annual maximum and minimum temperatures, total annual precipitation, precipitation seasonality and aridity. Occurrence data were obtained from GBIF (accessed September 2019; https://doi.org/10.15468/dl.sm1oc0). For each species, we selected occurrence records after 1950 from the original GBIF occurrence records. We retained only one randomly selected occurrence per 1×1 km^2 pixel over the grid defined by the climatic data (detailed below) to obtain a spatially-homogeneous data set, accounting for potential geographical biases in the sampling effort. Subsequently, we used a 95% density distribution kernel to systematically remove outliers in relation to the bulk of each species' occurrence records and we thus removed occurrence points far from the major clusters of the species' distributions. The final number of occurrences ranged from 62 (*Ononis reuteri*) to 67,768

(*Quercus robur*). Finally, the selected occurrences for each species were used to extract the climatic information of the six climatic variables mentioned above. As for aridity, we used an aridity index to quantify precipitation availability over atmospheric water demand, computed as Aridity Index (AI) = MAP / MAE, where: MAP = Mean Annual Precipitation and MAE = Mean Annual Potential Evapo-Transpiration. According to this formulation, the AI index values increase for more humid conditions, and decrease with more arid conditions. Such variables provide a good characterization of the overall precipitation and temperature regime of the study areas. Climatology-type temperature and precipitation data for the period 1970-2000 were obtained at a 1-km^2 spatial resolution from WorldClim 2.0 (Fick and Hijmans 2017) and aridity data were obtained from the CGIAR-CSI Global-Aridity and Global-PET Database (accessed March 2020; http://www.cgiar-csi.org) (Zomer et al. 2007, 2008).

Climatic suitability models for each species were computed on the basis of species occurrence data and pseudo-absences or background points. Background points were randomly located over the geographical area in which each species is present (Acevedo et al. 2012). First, 100 model replicates were fitted with species occurrence data and 1,000 different background points for each species. The models' predictive accuracy was assessed by means of the area under the receiver-operator curve (AUC; mean value for all assessed species 0.989; range 0.938 - 1), which is interpreted as the probability that a randomly chosen species occurrence location has greater suitability than a randomly chosen background point (Merow et al. 2013). Second, species climatic suitability within each study site was computed as the average suitability of the 100 MaxEnt model replicates fitted for each species on the site.

2.5. Analyses

2.5.1. Resilience of forest taxonomic composition and structure

The resilience of taxonomic composition was assessed by checking for each site for differences between the sets of replacing woody species growing under dead, defoliated and healthy trees. For this purpose we performed pair-comparison of species abundance (number of individuals) between such habitats using a Pearson correlation coefficient. Relationships between these R Pearson values and drought characteristics - see above- were explored using Spearman's rank correlation test. We excluded from the analysis seven localities with less than four replacing species. We also checked for differences in species richness (S) and Shannon diversity index (H') between each site's sets of replacing woody species under dead, defoliated and healthy trees by repeated-measures ANOVA (no transformation was needed).

We built different generalized linear mixed models (GLMMs) to evaluate short-term resilience with respect to the persistence of the dominant species (self-replacement) and structural stand characteristics. For each site, these models' response variables, which exhibited normal error distributions, were (1) self-replacement, defined as percentage of cases where dead trees plus trees experiencing die-off presented individuals of the same species beneath its canopy; (2) gaps (%), corresponding to those cases in which the space beneath the tree canopy was exclusively occupied by bare soil, herbs, or scrubs, (3) relative height of the canopy of the replacing plant in relation to the former canopy (Hrel); and (4) a combined estimation of the three previous variables, which corresponded to the coordinates of sites on the first axis of a Principal Component Analysis (PCA) considering self-replacement, gaps and Hrel.

These models' explanatory variables were: climatic suitability of the dominant species, proportion of die-off in dominant species, density, basal area, richness, management legacy (a binomial variable, with presence or absence of evidence), pest/pathogens (a binomial variable, yes/no), taxonomic category of the dominant species (Fagaceae or Pinaceae, Conifers hereafter), and drought characteristics (including the four SPEI-derived variables: minimum SPEI, drought frequency, drought length, time since drought). Dominant pre-drought species were included as a random factor.

2.5.2. Changes in species climatic suitability

Resilience in terms of changes in the forest climatic suitability after drought-induced die-off was estimated by comparing the replacing species' climatic suitability to that of the dominant pre-drought species in each site. We considered different sets of replacing species according to their role in forest structure (1) tree species likely to attain the forest overstory, including the dominant pre-drought species, (2) shrubs that will remain in the understory and (3) all woody species, including the aforementioned trees and shrubs. For the purposes of this comparison, we calculated Relative Climatic Suitability Change (RCSC, hereafter) as:

$$RCSC = \left(\frac{(DomSuit - WSCS)}{DomSuit}\right)$$

where *DomSuit* for a given site was the climatic suitability of the dominant species (Dominant suitability hereafter) and *WSCS* (Weighted Species Climatic Suitability) for a given site was the average climatic suitability of the species belonging to the different forest levels (overstory, understory) weighted by its relative abundance in each set, resulting in several values of RCSC: $RCSC_{over}$ for the overstory, $RCSC_{under}$ for the understory and $RCSC_{woody}$ for the whole set of woody species. Higher positive values of RCSC indicate that the dominant pre-drought species show higher climatic suitability than the replacing community, in relation to the 1970-2000 reference period, evidencing a trend towards a loss of community climatic suitability and an increase in climatic disequilibrium. In contrast, negative values of RCSC indicate that the replacing community has higher climatic suitability than the dominant pre-drought species, pointing to a gain in climatic suitability and a decrease in climatic disequilibrium. The rationale behind using a measure of relative change was to minimize the bias produced by the suitability values of the dominant species, which generally exhibited higher values of climatic suitability than most of the co-existing species, thus largely determining the value of the difference between dominant suitability and WSCS.

We also aimed to incorporate changes in suitability due to the absence of woody species under the canopy of affected trees, i.e. gaps. We thus built a PCA that considered the values of three variables on each site: $RCSC_{over}$, $RCSC_{under}$ and gaps (percentage). Then, we used the first and second PCA axis (PCA1 RCSC and PCA2 RCSC, respectively) as an integrative measure of forest change on each site associated with species climatic suitability.

Finally, we built GLMMs with the variables describing changes in climatic suitability as dependent variables (i.e., $RCSC_{over,}$, $RCSC_{under}$, $RCSC_{woody}$; first and second axis of PCA with

$RCSC_{over}$, $RCSC_{under}$ and gaps) and the same explanatory and random factor variables as in the aforementioned GLMMs exploring self-replacement and structural stand features.

Transformations of data were applied when required to obtain a normal error distribution: arc-sinus to self-replacement, Hrel, richness, drought length, and time since drought, and logarithmic to gaps (ln+1), dominant die-off, basal area and density. In all models, variables were centered and scaled by SD, and then the minimum value of each variable was added to all measures to avoid negative values. We checked in all models for the inflation factor, which always had values under 1.5, and for the percentage of the random factor's contribution to the total variance. We included all explanatory variables and bivariate interactions in full models, and we selected the best fitted model by following a backward procedure and applying the AIC criterion. Calculations were made with JMP10.0.0. (@2012 SAS Institute Inc.), following REML procedure.

A table with the information on all the variables used in these models is provided in Supplementary Material Table S3.

3. Results

3.1. Resilience of taxonomic composition and stand structure

3.1.1. Changes in species composition

The composition of replacing species under the canopy of dead and healthy trees was significantly different on only nine of the 41 sites, thereby endorsing the overall resilience of understory taxonomic composition. Similarly, when comparing dead and defoliated trees, we found differences in only ten cases, and when comparing defoliated and healthy trees we found differences in only seven cases (Supplementary Material Table S1). Three localities (Arenys and Cabrera, both with *Pinus pinea*, and Jimena, with *Quercus suber* as pre-drought dominants) exhibited different compositions of replacing species when comparing the three states of the effect of drought on the dominant species. There was a negative correlation between the R Pearson values of the dead vs defoliated tree comparison of replacing composition and minimum SPEI value (i.e. drought intensity) (Spearman *ro* = -0.359, P = 0.023), this correlation being marginally significant when comparing dead vs healthy trees (Spearman *ro* = -0.280, P = 0.076). These results support our hypothesis that that more intense droughts correlate with less resilience in terms of taxonomic composition, i.e., with taxonomic similarities between the replacing species under dead trees and those under less affected trees. Finally, we did not find any significant differences in the species richness (F ratio = 0.80, P = 0.453) and the H' diversity index (F ratio = 0.25, P = 0.771) of replacing plants under dead, defoliated and healthy trees.

3.1.2. Self-replacement

Self-replacement significantly decreased with a higher proportion of die-off of the dominant species, and it increased with a higher basal area (Figure 2A), supporting our hypotheses. However, contrary to from our expectations, self-replacement was not significantly determined by the climatic suitability of the dominant species or by drought characteristics

(Table 1). The final model also included a positive effect of the interaction between dominant die-off and density, due to the elimination of the negative relationship of dominant die-off with self-replacement when high density occurs (Figure 3). Management legacy also influenced self-replacement, decreasing its value from 38.21% ±6.72SE (no evidence of management legacy) to 17.1% ±3.45SE (management legacy) (Supplementary Material Figure S3A). This finding also supported our hypothesis.

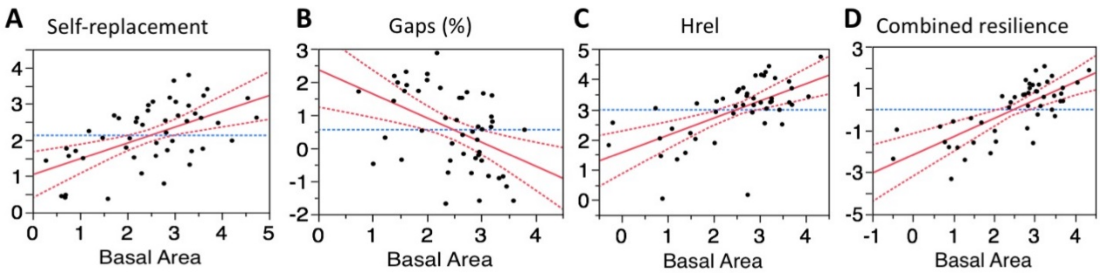

Figure 2. Leverage plot of the effect of stand basal area on several variables describing resilience: self-replacement (A), gaps (B), Hrel (C) and combined resilience (coordinates in the first axis of a PCA considering self-replacement, gaps and Hrel (D). Residuals of the response variable are plotted against the residuals of the respective explanatory variable. Solid line shows least square fit, while dashed lines show 5% confidence bands for the mean. The dashed horizontal blue line represents the mean of the response variable leverage residuals. The slope and P-values correspond to the respective estimate in the model (Table 1). Hrel: relative distance of the canopy of the replacing plant from the former canopy.

Table 1. GLMM results of self-replacement, gaps, Hrel and combined resilience as response variables and dominant suitability and die-off, stand characteristics, drought characteristics, management legacy and taxonomic category of the dominant species as explanatory variables. Combined resilience was calculated as the first axis of a PCA considering, self-replacement, gaps and Hrel. R^2: conditional correlation coefficient. Var ratio: ratio between variance attributed to the random effect (species) and variance attributed to the residual. See Methods for a description of the full model and variable transformations. Hrel: relative distance of the canopy of the replacing plant from the former canopy.

Self-replacement
(R^2 = 0.412, AIC = 135.09, Var ratio = -0.092)

	Estimate (SD)	F ratio	P
Intercept	1.040 (0.357)		
Dominant die-off	-0.344 (0.114)	9.05	0.005
Basal area	0.437 (0.121)	13.10	0.001
Density	-0.403 (0.145)	7.71	0.035
Dominant die-off : Density	0.355 (0.127)	7.87	0.008
Management legacy [Yes]	-0.518 (0.131)	15.76	<0.001

Gaps
(R^2 = 0.496, AIC = 156.51, Var ratio = 0.138)

	Estimate (SD)	F ratio	P
Intercept	1.750 (0.331)		
Basal area	-0.728 (0.205)	12.59	0.003
Richness	-0.526 (0.178)	8.77	0.005

Hrel
(R^2 = 0.370, AIC = 129.92, Var ratio = -0.021)

	Estimate (SD)	F ratio	P
Intercept	1.750 (0.331)		
Basal area	0.567 (0.127)	19.83	<0.001
Taxonomic category [Fagaceae]	0.385 (0.134)	8.27	0.011

Combined resilience
(R^2 = 0.559, AIC = 143.37, Var ratio = -0.035)

	Estimate (SD)	F ratio	P
Intercept	-2.111 (0.421)		
Basal area	0.870 (0.156)	31.09	0.001
Taxonomic category [Fagaceae]	0.577 (0.165)	12.25	0.010
Management legacy [Yes]	-0.363 (0.195)	3.46	0.087

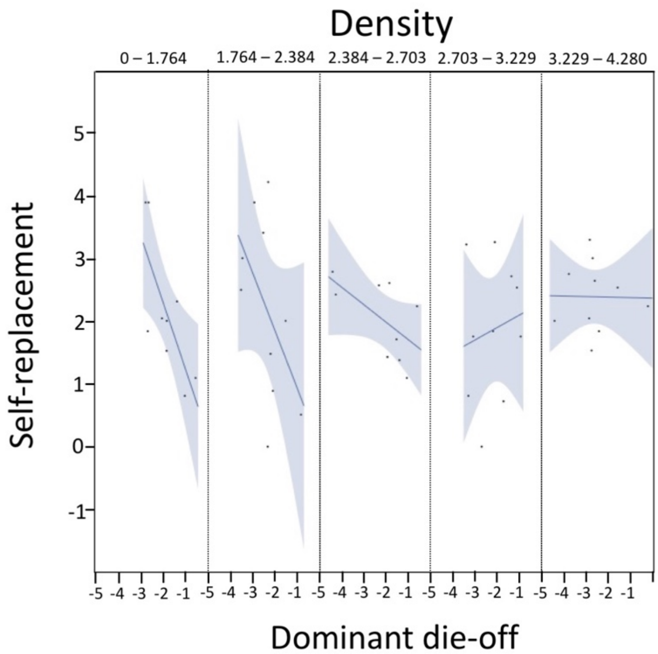

Figure 3. Self-replacement in relation to the affectation of the pre-drought dominant species (Dominant die-off) at different intervals of stand Density. Intervals include similar number of cases, illustrating the significant interaction between Dominant die-off and stand Density, but they did not intervene in the model's calculations. See Methods for scaling and transformation of variables and for a complete description of the model (GLMM). Shadow indicates 95% confidence of fit.

3.1.3. Stand structure

The mean percentage of gaps (no woody species beneath the canopy of the affected trees) appearing after the drought-induced episodes of tree mortality was 10.4% (± 2.5 SE). As expected, gaps became significantly less frequent with increasing richness (Supplementary Material Figure S4) and basal area (Figure 2B) (Table 1), and sites with a greater basal area also had replacing plants with higher Hrel (Figure 2C). In Fagaceae-dominated forests, the replacing plants also grew closer to the remaining canopy (height of replacing plants corresponding to 83.7% ±4.61SE of the height of the former canopy) than in Conifer-dominated forests (66.2% ±4.76SE), as supported by the significant effect of taxonomic category on Hrel (Table 1) (Supplementary Material Figure S3B). Gaps and Hrel were not significantly determined by the climatic suitability of the dominant pre-drought species or drought characteristics.

3.1.4. Combined self-replacement and stand structure

The first axis of the PCA considering self-replacement and resilience of structural characteristics (gaps, Hrel) accounted for 59.6% of the variance (eigenvalue = 1.79) and was mostly related to greater resilience in terms of replacing canopy (Hrel) and, to a lesser extent, to greater self-replacement and less gaps. The second axis of the PCA only accounted for 25.5% of the variance; it roughly correlated with self-replacement and gaps, but the eigenvalue was only 0.76 and we excluded it from further analyses (Supplementary Material Figure S5).

The model explaining the ordination of sites on this first PCA axis - indicating greater short-term resilience in terms of self-replacement and replacing canopy height - showed a significant positive correlation of stand basal area with the first PCA axis (Figure 2D) in keeping with the assumption that greater basal area - as a proxy for a population's good performance in a locality - would be positively related to short-term resilience. Fagaceae-dominated forests also showed significantly higher values than Conifers-dominated ones on this first axis, while management legacy had a marginal effect, resulting in lower values on the first PCA axis (Table 1) (Supplementary Material Figure S3C,D). PCA axes were not significantly determined by the climatic suitability of the dominant pre-drought species or drought characteristics in agreement with previous results on self-replacement and stand structure.

The percentage of variance components corresponding to the random effect (species) was negligible in the models evaluating self-replacement, Hrel and ordination on the first PCA axis combining self-replacement and structural characteristics. In contrast, this percentage had a value of 12.16 in the model with gaps as the dependent variable.

3.2. Changes in species climatic suitability

The mean values of $RCSC_{over}$, $RCSC_{under}$, $RCSC_{woody}$ were 0.004 ± 0.019SE, 0.005 ± 0.021SE and 0.0017 ± 0.0152SE, respectively, representing a range that included gain and loss of climatic suitability of the replacing community in relation to the suitability of the dominant pre-drought species. $RCSC_{over}$ was positively related to dominant suitability, indicating that replacing communities on sites where dominant species live in more suitable conditions tended to reduce their climatic suitability more than the dominant pre-drought species (Table 2), overall supporting our overall hypothesis. This trend tends to disappear under very intense drought conditions, as indicated by the significant interaction between dominant suitability and minimum SPEI (maximal drought intensity) (Figure 4A). Indeed, under stronger drought conditions, $RCSC_{over}$ tended to be higher, as revealed by the marginally negative relationship of $RCSC_{over}$ with minimum SPEI (maximal drought intensity) (Table 2). Loss of climatic suitability in the understory-replacing community (higher values of $RCSC_{under}$) was also positively related to the suitability of the dominant pre-drought species and negatively related to tree density (Supplementary Material Figure S6). Management legacy tended to diminish the climatic suitability of the replacing understory ($RCSC_{under}$ values of 0.006±0.038SE and 0.004±0.025 for managed and unmanaged forest, respectively) (Supplementary Material Figure S3E). Evidence of pests or pathogens reduced $RCSC_{under}$, pointing to an increase in the climatic suitability of the replacing understory relative to that of the pre-drought species ($RCSC_{under}$ values of -0.017±0.035SE and 0.019±0.026SE for forests with and without signs of biotic disturbance, respectively) (Supplementary Material Figure S3F). Finally, the time since drought significantly affected the loss of the replacing understory's climatic suitability (Supplementary Material Figure S6) (Table 2). The $RCSC_{woody}$ model reproduced the results obtained in the $RCSC_{over}$ model (Table 2). The explanation of these variables was greatly affected by the different performances of dominant pre-drought species, since much of the variance (35.5% in the $RCSC_{over}$ model, 77.1% in the $RCSC_{under}$ model, and 45.5% in the $RCSC_{woody}$ model) was attributed to the random effect (species).

The first axis of the PCA considering $RCSC_{over}$, $RCSC_{under}$ and gaps (PCA1 RCSC) accounted for 60.4% of the variance (eigenvalue = 1.82) and was positively related to all three variables, particularly $RCSC_{under}$. The second axis of the PCA (PCA2 RCSC) accounted for 29.8% of the variance (eigenvalue = 0.89) and correlated positively with gaps and negatively with $RCSC_{over}$ (Supplementary Material Figure S7). The model explaining the ordination of sites in PCA1 RCSC - corresponding to higher $RCSC_{over}$ and $RCSC_{under}$ and more gaps - showed a positive relationship with dominant suitability, but this trend was reversed at low stand densities, as indicated by a significant interaction between dominant suitability and stand density (Figure 4B). Also, management legacy correlated positively with this first PCA axis (Supplementary Material Figure S8A) (Table 2). Again, the percentage of the variance component corresponding to the random effect (species) was remarkably high in this model (69.1%). The model explaining the ordination of sites in PCA2 RCSC - with higher values for lower $RCSC_{over}$ and more gaps - showed a significant negative relationship with stand basal area (Supplementary Material Figure S8B) (Table 2); in this model, only 11.8% of the variance was attributed to the random effect (species).

Table 2. GLMM results of relative changes in the climatic suitability (RCSC) of the recruiting community relative to the dominant species' climatic suitability. $RCSC_{over}$: overstory community, $RCSC_{under}$: understory community, $RCSC_{woody}$: all woody species, PCA1 RCSC and PCA2 RCSC: first and second axis of PCA built with $RCSC_{over}$, $RCSC_{under}$ and percentage of gaps (PCA1 was positively related with all three variables, while PCA2 positively correlated with gaps and negatively with $RCSC_{over}$). Explanatory variables included species dominant suitability and die-off, stand features, drought characteristics, signs of pest or pathogens and management legacy. Lower values of Minimum SPEI correspond to higher drought intensity. R^2: conditional correlation coefficient. Var ratio: ratio between variance attributed to the random effect (species) and variance attributed to the residual. See Methods for a description of the full model and variable transformations. SPEI: Standardized Precipitation Evapotranspiration Index.

$RCSC_{over}$
(R^2 = 0.647, AIC = 131.10, Var ratio = 0.550)

	Estimate (SD)	F ratio	P
Intercept	2.949 (0.603)		
Dominant suitability	0.406 (0.125)	10.45	0.002
Minimum SPEI	-0.238 (0.129)	3.38	0.074
Dominant suitability : Minimum SPEI	0.528 (0.161)	10.75	0.002

$RCSC_{under}$
(R^2 = 0.949, AIC = 81.89, Var ratio = 3.375)

	Estimate (SD)	F ratio	P
Intercept	1.589 (0.340)		
Dominant suitability	0.784 (0.083)	87.52	<0.001
Density	-0.426 (0.097)	19.21	<0.001
Management legacy [Yes]	0.361 (0.106)	11.73	0.002
Pest/Pathogens [Yes]	-0.187 (0.068)	7.63	0.011
Time since drought	0.317 (0.076)	17.15	<0.001

$RCSC_{woody}$
(R^2 = 0.707, AIC = 130.67, Var ratio = 0.835)

	Estimate (SD)	F ratio	P
Intercept	2.766 (0.580)		
Dominant suitability	0.439 (0.122)	13.00	<0.001
Minimum SPEI	-0.120 (0.118)	2.87	0.098
Dominant suitability : Minimum SPEI	0.467 (0.158)	8.73	0.005

PCA1 RCSC
(R^2 = 0.909, AIC = 85.03, Var ratio = 2.233)

	Estimate (SD)	F ratio	P
Intercept	1.686 (0.414)		
Dominant suitability	0.702 (0.105)	44.59	<0.001
Density	-0.155 (0.122)	1.65	0.213
Management legacy [Yes]	0.302 (0.137)	4.83	0.035
Dominant suitability : Density	0.971 (0.220)	19.43	<0.001

PCA2 RCSC
(R^2 = 0.357, AIC = 107.95, Var ratio = 0.133)

	Estimate (SD)	F ratio	P
Intercept	2.691 (0.435)		

Basal area	-0.425 (0.173)	6.07	0.024

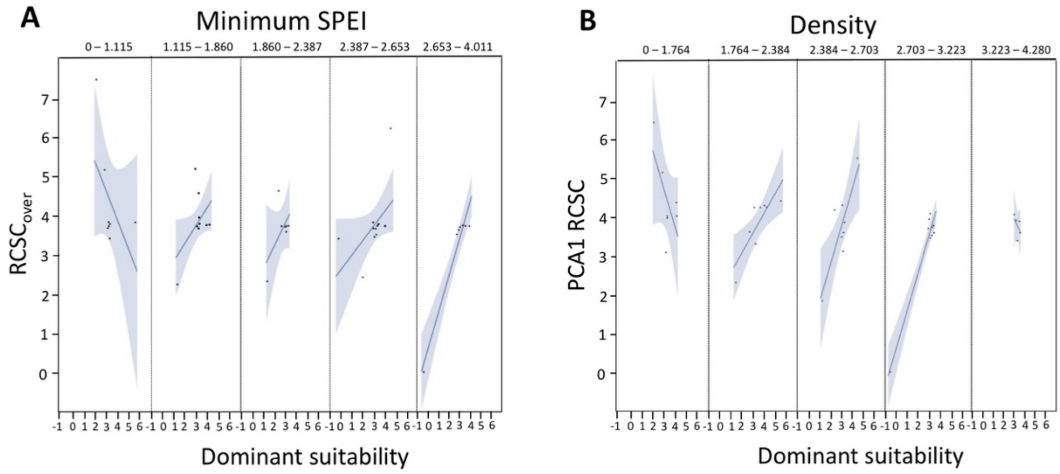

Figure 4. Relative change in the climatic suitability of the overstory recruit community compared to the dominant species' climatic suitability ($RCSC_{over}$), in relation to the climatic suitability of the dominant species (Dominant suitability) at different intervals of maximal drought intensity (minimum SPEI) (A), and first axis of a PCA built with $RCSC_{over}$, $RCSC_{under}$ and percentage of gaps - positively related with all these three variables - (PCA1 RCSC) in relation to the climatic suitability of the dominant species at different intervals of stand Density (B). Intervals include similar number of cases, illustrating significant interaction, but they did not intervene in the model's calculations. See Methods for scaling and transformation of variables and for a complete description of the models (GLMMs). Shadow indicates 95% confidence of fit. SPEI: Standardized Precipitation Evapotranspiration Index.

4. Discussion

4.1. General patterns

Our study shows that, over a broad geographical range and different types of forest, short-term resilience after drought-induced tree mortality is influenced by both the degree of severity of the disturbance experienced in the forest and stand characteristics. These stand features include species diversity, tree density and forest basal area, which reflects management legacy. The impact of drought on the replacing community is shown to be a major mechanism for explaining the relevance of these factors. Interestingly, the relevance of these factors is not affected by the historical climatic suitability of the dominant species on each site. In other words, dominant tree populations living close to their optimal climatic conditions may be vulnerable to these drought episodes. In turn, populations living near the limits of species climatic suitability may exhibit mechanisms that allow them to persist. Nevertheless, our models showed a limited statistical capacity to explain short-term resilience in the studied forests. This may be due to the existence of other unexplored factors, to our low ability to quantify the studied factors (e.g., management legacy), and, especially, to the inherent variability within the types and range of the studied forests, which cover a broad range of biogeographical and land use contexts.

4.2. Resilience of taxonomic composition

Self-replacement constitutes a major mechanism for forest resilience after disturbances (Johnstone et al. 2016). Here, we found that self-replacement was jeopardized by drought damage (% dominant die-off), equivalent to the severity of the drought disturbance. This indicates that recruits from the dominant species, in addition to adults, were likely affected. Previous studies have demonstrated that forest understory can also be impacted in drought-induced mortality episodes (Lloret et al. 2004; Suarez and Kitzberger 2008). In fact higher mortality rates have been reported in juvenile and small individuals than in adults in these episodes (Lloret et al. 2004), as well as in drought experiments (Hanson et al 2001). This suggests that the physiological mechanisms leading to drought-induced mortality (hydraulic failure, carbon starvation, Adams et al. 2017) could operate similarly in adults and juvenile plants (e.g., Sapes et al. 2019). Overall, this sensitivity of recruiting populations is consistent with the common demographic trends of high mortality rates in younger plants and of regeneration climatic niche as subsets of adult niche (Dobrowski et al. 2015).

However, climate variables characterizing drought, together with species climatic suitability derived from SDMs failed to explain self-replacement rates. The above-mentioned limitations inherent to our study may explain this failure. In addition, several mechanisms may mask the relationship between estimates of climatic suitability and demographic processes associated with drought episodes. Moreover, acclimation of populations to specific conditions can be important to understand short-term resilience, and this process is not well considered in SDMs, which assume that species respond homogeneously to climate across their range (Benito Garzon et al. 2011). Populations living close to a species' climatic optimum may have produced a large stock of recruits ready to replace dying trees ("core hypothesis" Lloret and Kitzberger 2018), but these populations may also suffer from extreme climatic conditions due to their acclimation history. They may be less efficient under these extreme conditions (Anderegg et al. 2016), or they may be vulnerable if they have built structures such as stems, branches or leaves that require a significant amount of resources for their maintenance (Jump et al. 2017). In contrast, plants - including recruits - living close to the climatic limits of species suitability (i.e., marginal populations) may have experienced acclimation or selection to extreme conditions (Valladares et al. 2014; Solarik et al. 2018). The balance between sensitivity *vs.* acclimation to extreme conditions may explain similar levels of self-replacement across the broad range of conditions and species suitability assessed here. This is consistent with the reported occurrence of tree die-back and mortality in both core and edge populations (Lloret and Kitzberger 2018; Margalef et al. 2020) and with patterns of forest dynamics after drought-induced mortality (Martinez-Vilalta and Lloret 2016, Batllori et al. 2020).

Self-replacement patterns were also explained by stand characteristics, across a wide range of forests types. A large basal area likely reflects good habitat quality - as determined by soil depth and nutrient availability, for instance -, which should promote tree growth and the existence of saplings and young adults of the dominant species (Vayreda et al. 2013). Moreover, a large basal area also characterizes forests that have not recently experienced extensive disturbances; in these undisturbed forests, recruits are more likely to be found. This is consistent with the negative effect of management legacy on self-replacement, also reflected in the first axis of the PCA-combined estimation of resilience, likely due to its impact on potential recruits. Management is a major contributor to forest dynamics in semi-natural forests, as is the case on most of the studied sites, and it has been reported as determining ecological short-term trajectories after drought-mortality episodes, often leading to increasing prevalence of shrubs (Batllori et al. 2020). The importance of recruits would also be reflected by higher levels of self-replacement in stands with high density, which would likely shelter more recruits. Accordingly, in high density stands the correspondence between high dominant die-off and low self-replacement tends to disappear.

Although the composition of replacing species that grew beneath dead, defoliated and healthy trees was different in some forests, a consistent pattern was not observed. This could be attributable to a level of replication insufficient to capture site variability. However, our sampling was able to distinguish changes in the resemblance of the replacing community under trees with different degrees of die-off in relation to drought intensity. Thus, assuming that the understory was relatively uniform across each site before the episode, and that it was affected by drought, our results suggest that drought impacted the understory to some extent as well. This impact would correspond to a sorting effect caused by environmental stress, as proposed by community assembly theory (White and Jentsch 2004). In this case, drought would be the driver of such community sorting, as has been observed in Mediterranean shrublands close to some of the study sites (Perez-Navarro et al. 2019).

Our appreciation of resilience, particularly of taxonomic composition including self-replacement, corresponds to a short temporal window of forest dynamics whose capacity to predict the long-term fate of forests subjected to extreme drought episodes is clearly limited. Alternatively, pre-established long-term programs of forest inventories have also been able to document tendencies in taxonomical and functional composition likely related to increasing levels of climate dryness (Zhang et al. 2018; Ruiz-Benito et al. 2017), but the monitoring timespan of most of these programs to date has been too short to produce conclusive results, and they find it difficult to capture a sufficient number of plots in areas strongly affected by drought. Our approach has the advantage of focusing on foresst that have experienced such affectation. However, oncoming disturbance regimes, climate change - including further drought episodes -, biotic interactions - pests, exotic species - and management will largely determine the trajectories of the studied forests. Nevertheless, many recent studies highlight the importance of the initial stages after disturbances in forest dynamics (Turner et al. 1998; Seidl et al. 2014; Johnstone et al. 2016), particularly when successional trajectories are not disrupted by any further disturbances or management. Species sorting in these initial stages may be determined by different, non-exclusive mechanisms (White and Jentsch 2004). Species badly adapted to arid conditions can get filtered (Perez-Navarro et al. 2019). Alternatively, gap opening may initiate successional trajectories in accordance with the existing sapling bank and the differential tolerance of species to light and competition (Prach and Walker 2020), causing succession to move back toward earlier stages (Pickett and White 1985). Another possibility is that the death of trees that are dominant in the canopy may accelerate the transition to later stages through species replacement (Rigling et al. 2013). This could be further assessed by an accurate analysis of a species' successional status and plant functional traits in the replacing community (Batllori et al 2020). Although we cannot compare the differences between these stages and those occurring in paired stands of unaffected forests, our individual-based comparison between trees with different degrees of drought disturbance reveals that initial trajectories following drought exhibit noticeable differences from one forest to another.

4.3. Resilience of stand structure

In stands with a larger basal area, recruits and pre-established trees were closer to the canopy level of the damaged trees, and gap occurrence after drought mortality was lower, reflecting better habitat quality or a late successional stage of stands. Interestingly, gap occurrence also diminished in stands with higher richness of woody species, likely indicating the existence of complementarity effects of diversity (Loreau and de Mazancourt 2013). Thus, the overall forest canopy would be more likely to be maintained if the total set of species is able to live in a wide range of climatic conditions - including those occurring during the experienced drought episodes. This hypothesis corresponds with the increasing evidence that tree species richness promotes forest resilience, particularly under strong climatic fluctuations (Lloret et al. 2007; Hutchinson et al. 2018; Sousa-Silva et al. 2018).

Also, Fagaceae-dominated forests tended to be more resilient, especially in terms of canopy height, than Conifer-dominated ones. This higher resilience of Fagaceae-dominated forests is consistent with recent patterns of forest growth in the Iberian Peninsula in response to drought (Vidal-Macua et al. 2017). This pattern can be related with distinct functional characteristics of Fagaceae and Conifers (Carnicer et al. 2013), involving a greater legacy of drought impact on radial growth in Pinaceae than in Fagaceae (Cailleret et al. 2017), higher photosynthetic rates in evergreen angiosperms than in Conifers (Lusk et al. 2003), or a greater ability to maintain NSC pools in deciduous species, which are common among Fagaceae, than in evergreen ones (Piper 2020). Also, Fagaceae species produce larger seeds than Conifers, which eventually confer them with a greater recruiting capacity (Carnicer et al. 2014).

Furthermore, Fagaceae have a greater resprouting capacity - from stumps or epicormic buds - than Conifers (Bond and Midgley 2001; Zeppel et al. 2015). Resprouting is recognized as a key trait for plant recovery after disturbances (Bond and Midgley 2001; Pausas et al. 2016), including drought-induced mortality episodes (Zeppel et al. 2015; Batllori et al. 2020). It has also been proposed that resprouters show a more conservative strategy of water use than non-resprouters (Zeppel et al. 2015), which would give them a particular would confer them advantage during intense drought (Pausas et al. 2016). Moreover, post-disturbance regrowth tends to be faster in species resprouting from surviving plants than in non-resprouting ones, which must recruit new individuals. Overall, resprouter species, such as *Quercus* spp., *Populus* spp., *Eucalyptus* spp., tend to become more prevalent than non-resprouters ones after episodes of drought-induced mortality in temperate and boreal forests (Batllori et al. 2020).

4.4. Changes in species climatic suitability

Changes in the climatic suitability of the replacing community also reflect the resilience of forests affected by drought. Substantial changes in the climatic suitability of the replacing community would indicate that such forests are in the initial stage of a sorting process, in which species turnover results in an altered climatic suitability in relation to the historical climate. The fact that the time since drought tends to increase $RCSC_{under}$ suggests that, in the studied forests, the initial pulses of reduction of climatic suitability are consolidated over the long term, and that the demographic impact of drought on the understory persists for some time (Lloret et al. 2004). The changes observed in replacing communities' climatic suitability were strongly determined by species idiosyncrasy, as shown by the large contribution of the random factor (species) in the models. Considering that the average suitability values of the replacing species on each site were not significantly different from the suitability value of the dominant pre-drought species (t ratio = 0.90, P = 0.372), these changes should mostly be attributed to shifts in the species' relative abundance.

The variability explained by the rest of the models’ fixed variables ($RCSC_{over}$, $RCSC_{under}$, $RCSC_{woody}$, PCA1 RCSC and PCA2 RCSC) shows that the greater the suitability of the dominant pre-drought species, the greater the loss of suitability in the replacing community, and the greater the increase in community climatic disequilibrium. This may be explained by the assumption that dominant species are well suited to a region's climatic conditions (but see Sexton et al. 2009). In fact, when drought intensity was higher, this relationship between both $RCSC_{over}$ and $RSCS_{woody}$ and the historical suitability of the dominant species tended to disappear, probably because of the concomitant impact of drought on other species. Alternatively, in a context of climate change, a sudden short-term reduction of community climatic disequilibrium may also occur as a result of a decrease in those species less adjusted to the harsh climatic conditions concurrent with the disturbance (Perez-Navarro et al. 2021), or a greater abundance of those species better suited to the new conditions. This reflects the widely acknowledged notion that species assemblages match the climatic conditions of the sites on which they occur, and that climatic changes are followed by corresponding changes in species distribution and community composition (Blonder 2015, Svenning and Sandel 2013, Gauzere et al. 2018). Thus, climatic disequilibrium would occur when community composition does not track the climate promptly or accurately (Blonder et al 2015) - in our case, this corresponds to higher RCSC -. Both management and the effects of pests and pathogens on $RCSC_{under}$ may also reflect human-driven modification in understory composition, thus altering any such climate tracking. Nevertheless, the relevance of all these processes should be considered with caution, given the low explanatory power of the model when discounting the contribution of the species (random) effect.

Moreover, the overall failure of climatic suitability in explaining resilience to drought of stand structure and taxonomic composition could also be due to a low capacity in our procedure for quantitative discrimination of climatic suitability across species. The MaxEnt algorithm is recognized as being robust for species comparisons, performing particularly well when occurrences are low across the species distribution area (Pearson et al. 2007). It has also been proved to be useful for explaining differences between species' demographic responses to drought episodes (Sapes et al. 2017, Lloret and Kitzberger 2018), even more than other algorithms (Pérez-Navarro et al. 2019), even though their outputs may be sensitive to the selected climatic variables. In our case, the 10% and 90% percentile values of climatic suitability for pre-drought dominant trees obtained from MaxEnt models were 0.407 and 0.700, respectively. This reduced capacity of the fitted models to discriminate between species likely affected our calculations of changes in climatic suitability before and after drought, and this may have contributed to the low explanatory capacity of our statistical models. Predictions obtained by assembling different algorithms are supposed to be advantageous for predicting populations' suitability (Araujo and New 2007) but these ensembles can be sensitive to the predictive capacity of the selected algorithms. Therefore, the inclusion of models with low predictive accuracy could reduce the performance of consensus predictions in comparison with individual models (Elith and Graham 2009; Hao et al. 2020). A more accurate assessment of community climatic disequilibrium could be achieved in the future via other procedures, such as building the climatic environment's multivariate space, including yearly variability, and then using the distance between the species assemblies and observed climate (Blonder et al. 2015; Perez-Navarro et al. 2020)

5. Conclusions

Our study reveals that the self-replacement of dominant species after drought-induced mortality episodes is not guaranteed. In fact, the percentage of gaps uncovered by woody vegetation may noticeably increase in the short term after a single die-off episode. Regardless of the historical climatic suitability of the affected species, the short-term community dynamics and the recovery of major structural forest features depend on the pre-existing bank of potential replacers - both in the understory and the overstory. This result contrasts with our expectations of higher resilience in terms of self-replacement in those localities with high climatic suitability for the dominant pre-drought species. As hypothesized, other essential drivers of resilience are related to the structural conditions of the forest, such as basal area - likely reflecting habitat quality or successional/maturity stage - stand density and, to a lesser degree, species richness, all of which are closely linked to management legacy. Also, the replacing community is affected by the impact on pre-drought understory species, supporting our hypothesis about the role of drought characteristics in the short-term patterns of resilience. Therefore, drought could exert a filtering effect on community composition in the early stages of the subsequent successional trajectories. To what extent this climatic filtering can alter expected successional pathways remains to be elucidated. A decrease in the climatic suitability of the replacing community, was observed, particularly on sites climatically suitable for dominant species, thus supporting our overall hypothesis of greater climatic disequilibrium following drought. However, our results were largely determined by a highly idiosyncratic performance in which both species composition and the structural state of forests would be determining factors. Therefore, forest management should reinforce resilient trajectories by controlling such parameters.

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