Ecosystem Services 79 (2026) 101858

Contents lists available at ScienceDirect

Ecosystem Services

journal homepage: www.elsevier.com/locate/ecoser

Full Length Article

Assessing ecosystem services resilience to drought and its drivers in mediterranean forests using a counterfactual, process-based modelling approach

Francesco D'Adamo [a,b,*], Miquel De Cáceres [a], Josep Maria Espelta [a], Jose Valentin Roces-Díaz [c,d], Adrià Descals [a], Miriam Selwyn [a], Francisco Lloret [a,e], Jordi Martínez-Vilalta [a,e]

[a] CREAF, Campus de Bellaterra, Cerdanyola del Vallès, Spain
[b] National Institute of Oceanography and Applied Geophysics, Trieste, Italy
[c] Biodiversity Research Institute IMIB, University of Oviedo (CSIC), Mieres, Spain
[d] Department of Organismal and Systems Biology, University of Oviedo, Oviedo, Spain
[e] Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Spain

ARTICLE INFO

Keywords:
Bluewater provision
Climate change
Counterfactual approach
Forest resilience
Forest resistance
Timber volume stock
Trait-enabled forest models

ABSTRACT

Forests cover ca. 30% of land surface, host much of Earth's biodiversity, and provide many ecosystem services to humans. As global environmental change alters ecosystems at fast rates, we still have a limited understanding of how forests and their services may respond to anthropogenic and natural disturbances. The resilience framework represents a powerful approach for assessing forests' ability to withstand pressures and understand how to preserve biodiversity and human well-being. Here we used a process-based model and forest inventory data to estimate five forest ecosystem services (FES) (bluewater provision, erosion mitigation, potential recreational value, timber volume stock, carbon stock) and assess their resistance and resilience to the severe drought that affected Catalonia in 1994. Specifically, we estimated annual FES from 1990 to 2020 under three scenarios, i.e., actual (including 1994 drought), extreme (increasing drought by 50%), and counterfactual (undisturbed), and then quantified resistance and resilience as the log-ratio of FES under the actual or extreme scenario relative to the undisturbed scenario in 1994 and integrated over five years following the drought, respectively. Catalan forests withstood historical drought conditions yet faced substantial damage under the extreme scenario. Resistance and resilience varied among FES, with hydrologically related services showing sharper declines but quicker recoveries than services that directly depend on forest structure and stocks. Local drought intensity was the primary driver of resilience, while forest structure had service-specific effects. These findings underscore the importance of evaluating a broad range of ecosystem services to capture diverse responses to drought and inform management strategies to sustain key forest functions under increasingly extreme climate conditions.

1. Introduction

Forests provide a multitude of ecosystem services essential to human well-being, capturing, for instance, ca. 30% of anthropogenic carbon emissions and providing key habitats for global biodiversity (Mori et al. 2017). However, global environmental change is intensifying disturbances such as droughts (Spinoni et al. 2018), wildfires (van Wees et al. 2021), wind (Patacca et al., 2023), and pest outbreaks (Seidl et al. 2017), leading to forest loss and disruption of key forest processes in many regions (Hartmann et al. 2022), including Europe (Senf et al. 2020; Grünig et al. 2026). Among these disturbances, drought has emerged as a particularly pressing threat, with increasing frequency and severity under ongoing climate change (Brodribb et al. 2020). Considerable uncertainty remains regarding how forest ecosystems will withstand prolonged or recurrent drought events, particularly in terms of their ability to sustain key functions and ecosystem services, as well as the underlying factors that control their dynamics. This uncertainty poses significant challenges for forest strategies aimed at enhancing

* Corresponding author.
E-mail address: f.dadamo@creaf.uab.cat (F. D'Adamo).

https://doi.org/10.1016/j.ecoser.2026.101858
Received 12 September 2025; Received in revised form 10 April 2026; Accepted 18 April 2026
Available online 2 May 2026

resilience in the face of climatic extremes (Groover et al. 2025).

The dynamics of forest ecosystem services (FES) are shaped by an interplay of climatic, ecological, and structural factors, all influencing forests' ability to withstand disturbances. Climate, a major determinant of forest distribution and function, governs services supply from local to global scales (Runting et al. 2017; Roces-Díaz et al. 2018). The relationships between biodiversity, ecological functioning, and FES provision are also well recognised (Felipe-Lucia et al. 2018; Liang et al. 2022). For instance, species richness and functional diversity play a key role in services provision through the control of biomass productivity (Isbell et al. 2015; Oliveira et al. 2022), whereas stand structure and age explain the supply of regulating services (e.g., carbon sequestration, temperature regulation) and cultural services (e.g., plants of cultural value, bird-watching potential) (Felipe-Lucia et al. 2018; Jonsson et al. 2020). Forest management further influences tree species composition and ecosystem structure, leading to variable FES outcomes (Mina et al. 2017). Clear-cutting practices, for instance, can either negatively (Sing et al. 2018) or positively (García-Valdés et al. 2021) affect multiple services, underscoring the context-dependent nature of FES responses (Gutsch et al. 2018; Schwaiger et al. 2019). As services respond differently to drivers and disturbances, it is important to consider the full spectrum of FES categories, from provisioning and regulating services to cultural ones, which are often underrepresented in quantitative studies.

In the Mediterranean basin, forests have been shaped by millennia of human activities and are particularly exposed to global change stressors (Doblas-Miranda et al. 2017; Peñuelas et al. 2017). Over recent decades, reduced forest management, declining timber extraction, and agricultural land abandonment (Ameztegui et al., 2010; Gauquelin et al., 2018) have led to increased carbon stocks, altered growth and mortality patterns, and greater dominance of broadleaved species thanks to their higher competitive ability and greater capacity to cope with most disturbances via resprouting (Vayreda et al. 2016; Anderegg et al. 2020). At the same time, warming and drying trends since the 1990 s have triggered episodes of drought-induced forest mortality, particularly affecting Eurosiberian species such as beech and Scots pine (Martínez-Vilalta and Piñol 2002; Peñuelas and Boada 2003). Drought is the primary limiting factor for Mediterranean forests under current and, even more so, future climate change (Tramblay et al. 2020), as exemplified by the extreme 2021–2024 drought across southern Europe (Toreti et al. 2024). Drought-induced mortality can reduce carbon sequestration as dying forests shift from carbon sinks to sources, alter hydrological fluxes through decreased transpiration and canopy interception, and increase soil erosion following canopy loss (Anderegg et al. 2013), with particularly severe effects expected in Mediterranean areas, where increasing aridity and dense stand structures resulting from management abandonment amplify trade-offs among services (Morán-Ordóñez et al. 2020). However, despite growing evidence of these impacts and our improved understanding of stand-replacing disturbances such as wildfires (Thom and Seidl 2016; Roces-Díaz et al. 2022), knowledge remains limited regarding the effects of drought, which typically results in less severe impacts but operates over longer timescales and larger areas, gradually altering forest structure, composition, and functioning.

Resilience, generally defined as the capacity to absorb or withstand disturbance effects (Holling 1973; Hodgson et al. 2015), has become a valuable framework for studying the impact of global environmental change on terrestrial ecosystems, as it focuses on the intrinsic properties (e.g., resistance, recovery) that shape the responses of complex systems (Nikinmaa et al. 2020). However, quantifying resilience is inherently challenging, much like measuring abstract qualities such as creativity or hard work (Yi and Jackson 2021). When considering specific disturbances, two components of resilience, i.e., resistance and recovery, can be considered (Hodgson et al. 2015). Resistance is defined as the ratio of the property value during the disturbance relative to a pre-disturbance or undisturbed state, and recovery as the ratio of the property value at a given time after the disturbance relative to the value during the disturbance (Lloret et al. 2011; Serra-Maluquer et al. 2018). Resilience can be quantified as the ratio of the property value at a given time after the disturbance relative to a pre-disturbance or undisturbed state (Lloret et al. 2011), or as the time required for attaining pre-disturbance or undisturbed values (Cantarello et al. 2017; Ingrisch and Bahn 2018). In principle, resistance and recovery are negatively related, yet different processes operate on them, i.e., those related with the immediate impact of the disturbance and those operating after the disturbance, respectively. Assessing resilience by referring to a pre-disturbance situation assumes that conditions before and after the disturbance (i.e., during recovery) are similar, which is rarely the case (Lloret et al. 2024). Alternatively, counterfactual approaches explicitly assess what would have happened in the absence of the disturbance under study and use this condition as the reference state (Epstude and Roese 2008; Lloret et al. 2024). That is, they compare the dynamics of the actual variable (during and after the disturbance) with those of a scenario in which the disturbance did not occur, while keeping all other factors constant. The main advantage is that the reference condition becomes dynamic and accounts explicitly for environmental variability, which helps distinguish disturbance-driven changes from background variations, overcoming the limitations of static pre-disturbance baselines (Coetzee and Gaston 2021). While counterfactual thinking is gaining attention in disciplines such as conservation, land system science, and sociology (Jellesmark et al. 2021; Magliocca et al. 2023), its application for empirical estimations of forest resilience is still limited (e.g., Martínez-Vilalta et al. 2012; Schmitt et al. 2020; Zheng et al. 2023; Barrere et al. 2024). This is mostly because effectively producing counterfactuals, i.e., the alternative scenarios to the actual conditions, is inherently complex. However, numerical modelling provides a viable solution, allowing key drivers to be manipulated while keeping other variables constant. In particular, process-based forest models have evolved significantly in recent decades (Bugmann and Seidl 2022), enabling the study of environmental conditions with no historical equivalent and in silico experiments of potential future scenarios across large spatiotemporal scales (Seidl et al. 2016). This is particularly relevant for forest ecosystems, given their slow dynamics and delayed responses to environmental change (Albrich et al. 2020). Additionally, forest models are particularly suitable for predicting FES at the temporal resolution and over the timescale needed to assess resilience, as short-term observations may fail to capture the full trajectory of ecosystem recovery (Pretzsch et al. 2015).

The main objective of this paper is to characterise the main factors that determine the resilience to drought of key FES in Catalonia, Northeastern Spain. We address this objective by focusing on a particularly severe historical drought and using a counterfactual approach that takes advantage of a process-based forest model and extensive data from national forest inventory plots. Specifically, we first evaluated the recent (1990–2020) dynamics of five key FES in Catalonia (i.e., blue-water provision, erosion mitigation, potential recreational value, timber volume stock, and carbon stock) in response to the summer drought of 1994, the most severe during the study period, as well as to a more extreme, climate-change-type drought scenario. We then characterised the resistance (reflecting the immediate drought impact) and resilience (reflecting post-drought dynamics) of FES under each drought scenario, relative to a no-drought, counterfactual scenario. Finally, we applied linear mixed-effects models to evaluate the drivers of resistance and resilience, including topoclimatic factors, structural and compositional stand characteristics, and land-use legacy effects. We hypothesize that (1) stand structure will be a strong driver of FES resilience, with forests with high basal area and low species richness being less resistant and resilient to drought; (2a) climate and forest functional type will also have a strong effect on resilience, with mediterranean-type forests being more resistant and resilient than montane forests dominated by Eurosiberian species that reach the southern limit of their distribution in the study area; (2b) the latter effects will be exacerbated under the extreme drought scenario; and (3) there will be significant differences in resilience between FES, with those services more tightly linked to weather conditions (hydrologically related services) being more responsive in the short term (lower resistance) but more resilient in the long term than services that directly depend on forest structure and stocks.

2. Materials and methods

2.1. Study area

Catalonia covers ca. 32000 km^2 of northeastern Spain. It is an overall mountainous region with marked climate variability due to substantial altitudinal and latitudinal ranges, complex topography, and an intense coastal-inland climate gradient (annual rainfall and mean temperature range from 400 mm per year and 18° C along the southern coast to over 1500 mm per year and 5° C over northern mountainous areas). Some 42% of Catalonia is covered by forests, of which 75% are privately owned. Timber extraction is moderate (ca. 30% of the annual forest growth), with intensive practices (e.g., clear-cutting) occurring in only 5% of the forested area. This is due to limited productivity from dry Mediterranean summers and the prevalence of young, overstocked forests following recent land abandonment (Cervera et al. 2019). The dominant tree species belong to the Pinaceae and Fagaceae families. More specifically, coastal and low-altitude forests are dominated by *Pinus halepensis* Mill. (Aleppo pine), *Quercus faginea* Lam. (Portuguese oak) and *Quercus ilex* L. (Holm oak), middle-altitude forests (800 – 1500 m) by *Pinus sylvestris* L. (Scots pine), *Pinus nigra* J.F. Arnold (Black pine), *Quercus pubescens* Willd. (Downy oak) and *Fagus sylvatica* L. (European beech), while above 1500 m, the main species are *Pinus uncinata* Raymond (Mountain pine) and *Abies alba* Mill. (Silver fir) (Roces-Díaz et al. 2018).

2.2. MEDFATE model

MEDFATE (version 2.9.3) is a mechanistic model that simulates energy, water and carbon balances, and forest dynamics for both tree and shrub species in a forest stand. It is a trait-enabled model, meaning that it accounts for the plant functional diversity through parameters that can be mapped to measured traits, and where similar plants in terms of taxonomy and size are represented as a single cohort with average structural characteristics (De Cáceres et al. 2023).

In MEDFATE, plant transpiration and photosynthesis are calculated using a description of plant hydraulics to estimate stomatal regulation based on the steady-state and profit maximisation approaches (Sperry et al. 1998, 2017). Carbon compartments include leaves, sapwood, and fine roots, while carbon pools are differentiated into structural and labile, both metabolic (i.e., soluble sugars) and storage (i.e., starch) (Dietze et al. 2014). Growth is simulated as changes in leaf, sapwood, and fine root areas using parameters that define maximum daily growth rates relative to sapwood area. Tree leaf and fine root biomass are constrained by allometric equations for leaf biomass, which limit growth to replacing ageing tissues unless changes in forest structure occur. Sapwood growth is primarily determined by maximum relative growth rates, carbon availability, and temperature- and turgor-related limitations (Körner 2015; Cabon et al. 2024). As sapwood formation increases tree diameter, maximum sapwood growth rates determine the growth of leaves and roots and, consequently, the entire plant maximum growth (De Cáceres et al. 2023). Plant mortality occurs at a steady basal rate to account for processes not explicitly represented in the model (e.g., windstorms, biotic attacks). In addition, mortality rates increase once the desiccation and carbon starvation thresholds expected to trigger drought-induced mortality are exceeded (McDowell et al. 2022). In our modelling exercise, we set desiccation to occur when the stem relative water content decreases below 60% (Sapes and Sala 2021) and starvation when the size of the sapwood metabolic carbon pool falls below 40% of its maximum value (Martínez-Vilalta et al. 2016). While we applied these two thresholds independently, starvation and desiccation processes are coupled within the model through the linkage of water and carbon economies. To evaluate the performance of the model at the regional scale, we conducted a spatial and temporal comparison of leaf area index (LAI), a key biophysical variable characterising canopy interactions with light and precipitation as well as biogeochemical fluxes at the biosphere–atmosphere interface (Brown et al. 2024). We compared LAI as simulated by MEDFATE with the Moderate Resolution Imaging Spectroradiometer (MODIS) LAI collection 6 (MCD15A3H) (Myneni et al., 2021) (Appendix A1). An in-depth description of MEDFATE and additional validation exercises against forest inventory data, sapflow, and eddy covariance data are available in De Cáceres et al. (2023, 2021), Saponaro et al. (2025), Veuillen et al. (2026), and at https://emf-creaf.github.io/medfatebook/.

2.2.1. Input data

The primary data sources were the permanent plots from the Spanish National Forest Inventory (NFI), a program of periodic surveys of forest stand characteristics (diameter at breast height, tree height, tree density, species composition) distributed across Spanish forests. NFI plots are distributed on a regular grid with an average density of one plot per 2 km^2. Each plot consists of four concentric subplots (10, 20, 30, and 50 m diameter) where trees are sampled according to their diameter at breast height (DBH). Regeneration (DBH $<$ 2.5 cm) is recorded in categorical abundance classes by species, saplings (2.5–7.5 cm DBH) are counted with mean height recorded, and adult trees (DBH $\geq$ 7.5 cm) are individually measured for species, DBH, and total height across the nested subplots (Alberdi et al. 2016). Here we used only plots in Catalonia that were resampled in all three available NFIs, i.e., NFI2 (1990), NFI3 (2000), and NFI4 (2015) (Roces-Díaz et al. 2021). From these plots (n = 3415), we selected only those with initial stand basal area (BA) greater than 5 m^2 ha^{-1} to exclude very sparse forests as well as forests that had experienced severe, recent disturbances such as fire and logging (García-Valdés et al. 2021). We also excluded plots that failed during the simulations, likely due to uncertainties in secondary species parameterisation or the complexity of simulating competition dynamics. This reduced the number of plots to 2345. As NFI data do not come with information on soils, per-plot soil physical properties such as texture, bulk density, and organic matter content were obtained from the SoilGrids global database (Hengl et al. 2017). The input daily weather data were retrieved via interpolation of weather observations from both the Catalan and Spanish ground station networks at each plot location using the R package meteoland (De Cáceres et al. 2018).

2.2.2. Simulation design

We assessed the resistance and resilience of FES to an intense historical drought episode and a simulated, more extreme scenario representative of future climate-change-induced droughts. To this end, we focused on the summer of 1994, the most severe drought recorded between 1976 and 2020 in the study area (Martínez-Vilalta and Piñol 2002; Altava-Ortiz et al. 2025), and applied a counterfactual approach to compare the value of each ecosystem service under the actual and the extreme drought scenario with those from a simulated, undisturbed scenario (Section 2.4). Accordingly, we ran three sets of simulations, each initialised from the same 2345 NFI plots:

- Actual scenario. Here we run the model using actual weather data from 1990 to 2020.
- Extreme scenario. This scenario was created by increasing the intensity of the 1994 drought by roughly 50%. To do this, we extended the 1994 drought into autumn by using data from the year with the lowest cumulative rainfall for the period September-October-November from 1976 to 2020, which was 1978. We used weather data for this year to replace actual 1994 data starting on the 8th of September. This resulted in a total rainfall value for 1994 in the extreme scenario of 409 mm yr^{-1} (averaged over all the study area), which is approximately 50% of the total annual rainfall for 1994 in the actual scenario (801 mm yr^{-1}).

- Undisturbed scenario. In this scenario, we used weather data as if there had been no drought in 1994. To calculate it, we identified the year with a June-July-August (JJA) cumulative rainfall curve closest to the 75th percentile of the JJA cumulative rainfall curve for 1976–2020. We opted for the 75th threshold to ensure a relatively wet year that maximises differences with 1994, considering that summers in Catalonia are generally dry. The best match, identified using the lowest root mean square error, was the year 1995, which we used to replace actual 1994 data. Specifically, 1995 data were used from the day after the last rainfall event over 10 mm in May to the day before the first rainfall event over 10 mm in September. Therefore, the undisturbed scenario in 1994 combines data from 01 to 01-1994 to 13–05-1994, 14–05-1995 to 19–09-1995, and 20–09-1994 to 31–12-1994 (total annual rainfall of 954 mm yr^{-1}).

While we calculated the undisturbed and extreme scenarios based on rainfall only, the input weather data were created by replacing daily records of all variables (precipitation; mean, minimum, and maximum temperature; mean, minimum, and maximum relative humidity; radiation; wind speed; and potential evapotranspiration), to maintain the covariation structure of weather data (Appendix A2).

2.3. Forest ecosystem services

Our assessment of ecosystem services included bluewater provision, erosion mitigation, potential recreational value, timber volume stock, and carbon stock. These services were calculated annually at the plot level from 1990 to 2020 under the actual, extreme, and undisturbed scenarios by using the relevant MEDFATE outputs either alone or combined with other information (Table 1). The choice of these services reflects their importance in Catalan forests, availability of data, feasibility to capture their dynamics with MEDFATE, ability to represent a wide range of ecosystem services, and potential to exhibit varying responses to drought (Roces-Díaz et al. 2018; Haines-Young et al. 2023).

- Bluewater provision (mm yr^{-1}). It represents the amount of water that flows from the forest stand to the water table. Bluewater corresponds to the sum of the surface runoff and the water that percolates beyond the reach of plant roots. We modelled both runoff and deep drainage at the daily temporal resolution and later summed them into annual values.
- Erosion mitigation (Mg ha^{-1} yr^{-1}). It describes the amount of soil erosion prevented by vegetation. We used the Revised Universal Soil Loss Equation (RUSLE), which estimates soil erosion as K × LS × R × C × P (Guerra et al. 2016). K is the intrinsic soil erodibility of each soil type (Panagos et al. 2014), LS describes the slope length and steepness of the terrain (Panagos et al. 2015), R refers to the physical erosivity of rainfall calculated with the rainfall erosivity model by Diodato and Bellocchi (2010) using daily rainfall data, while C is the mitigation effect due to vegetation, represented here by the fraction of photosynthetically active radiation reaching the ground (P is the conservation practices factor but was not included in our calculations). Erosion mitigation corresponds to the difference between soil erosion calculated without and with the effect of vegetation, i.e., K × LS × R × (1 – C).
- Potential recreational value (0 – 1). We estimated the potential value of forest stands for recreation based on forest structure and composition metrics that have been shown to directly influence potential recreation in European forests (e.g., Gundersen and Frivold 2008; Edwards et al. 2012; De Meo et al. 2015; Chen et al. 2015; Filyushkina et al. 2017; Hegetschweiler et al. 2017, 2020; Agimass et al. 2018) and can be estimated with MEDFATE. These metrics included maximum DBH, coefficient of variation of DBH, tree LAI, total shrub cover (limited to shrubs taller than 15 cm), tree species richness, variation in tree size among nearby stands (defined as the maximum DBH of the target plot divided by the average maximum DBH of plots within a 10 km radius), and non-forest cover (calculated as one minus the proportion of forest cover, i.e., the frequency of plots with basal area > 4 m^2 ha^{-1} and shrub cover > 30% within a 10 km radius of the target plot). We identified the MEDFATE model outputs that best corresponded to each metric, calculated their ranges for Catalan forests, and conducted an expert assessment. For this, we presented a questionnaire to eight experts in Catalan forest ecology to determine the most likely relationships between model outputs and recreational value in the study area. As a result, we obtained a recreational value (from 0 to 1) for each output, which we finally weighted-averaged into an overall potential recreational value (Appendix A3).
- Timber volume stock (m^3 ha^{-1}). It represents the harvestable timber volume for construction and furniture. Timber volume was calculated by applying allometric volume equations obtained within the study area (Alberdi et al. 2016) based on species, DBH, height, and stem form (e.g., uniform cylindrical shape, branching before 4 m, twisted/damaged/highly branched, etc.) for tree stems with DBH greater than 22.5 cm of all species, excluding typical firewood species (i.e., *Quercus ilex, Quercus pubescens, Quercus faginea, Quercus cerrioides, Arbutus unedo,* and *Erica arborea*). Our calculations included bark.
- Carbon stock ($MgCO_2$ ha^{-1}). It quantifies the carbon sequestered by the aboveground and belowground woody components of vegetation. We estimated carbon from tree biomass, a direct indicator of tree carbon stock, by applying species-specific allometric biomass equations (obtained within the study area) based on the height and DBH for each biomass compartment, as in Ruiz-Peinado et al. (2012, 2011). Carbon stock was calculated for trees with DBH greater than 7.5 cm.

Table 1
The five forest ecosystem services included in our analysis. Bluewater provision corresponds to the sum of water runoff and deep drainage as estimated by the model, while the remaining services were derived using model outputs together with other information. FPAR: fraction of photosynthetically active radiation, DBH: diameter at breast height, LAI: leaf area index, RUSLE: revised universal soil loss equation, K: intrinsic soil erodibility, LS: slope length and steepness, R: rainfall erosivity.

Forest ecosystem service	Category	Unit	MEDFATE output	Other information
Bluewater provision	Provisioning	mm yr^{-1}	Runoff, deep drainage	–
Erosion mitigation	Regulating	Mg ha^{-1} yr^{-1}	FPAR	Additional RUSLE parameters (K, LS, R)
Potential recreational value	Cultural	0 – 1	DBH, LAI, number of species, shrub cover	Expert assessment (Appendix A3)
Timber volume stock	Provisioning	m^3 ha^{-1}	Tree species, DBH	Allometric volume equations
Carbon stock	Regulating	$MgCO_2$ ha^{-1}	DBH	Allometric biomass equations

2.4. Data analysis

2.4.1. Resistance and resilience metrics

For each ecosystem service, we estimated resistance as the log-ratio of the actual or extreme scenario to the counterfactual undisturbed scenario in 1994 (Dorheim et al. 2022), while resilience was calculated as the log-ratio of the actual or extreme scenario to the counterfactual undisturbed scenario, integrated over five years after the drought (1995–1999) (Anderegg et al. 2015). Although resistance inherently influences resilience, the two metrics are not necessarily correlated, as resistance is directly linked to drought impact and resilience is also determined by processes operating after the drought, including recovery. To avoid an excessive number of response variables, and given that recovery is already captured by resilience (and tends to have a strong, negative correlation with resistance) (Zheng et al. 2021), we decided not to include it as a separate metric in our analyses. The log-ratio approach standardises comparisons between different variables and scenarios, facilitating the interpretation of whether a service was higher or lower during the actual or extreme drought scenarios, relative to what would have occurred without the drought episode. For instance, a log-ratio of −1 indicates that the ecosystem service is ca. 2.7 times lower (63% reduction), 0 indicates no change, and + 1 indicates a ca. 2.7 times higher (170% increase) relative to the counterfactual value. Finally, Appendix A4 presents a sensitivity analysis of resilience calculated by integrating the log-ratio over one (1995), three (1995–1997), and seven (1995–2001) years after the drought.

2.4.2. Drivers of resistance and resilience

We identified ten potential drivers of resistance and resilience, each calculated at the plot level in 1990 (i.e., the beginning of the study period), except for bioclimatic region, which was derived using data from 1965 to 2000, and the Standardized Precipitation Evapotranspiration Index (SPEI), which was calculated for the summer drought of 1994 relative to the long-term climatic average (i.e., January 1976 to December 1994). Drivers related to forest structure were calculated for trees with DBH greater than 7.5 cm only. Spatial maps for each driver are shown in Appendix A5.

- Dominant functional type (categorical). The relative abundance of broadleaved and needleleaved species may affect resilience because of the differences in structural, physiological, and ecological traits (Pardos et al. 2021). To account for this, we used basal area to classify plots according to the dominant tree functional type among broadleaved deciduous, broadleaved evergreen, and needleleaved species.
- Bioclimatic region (categorical). To assess the role of climate on forest resilience, plots were classified according to the Bioclimatic Classification for Continental Spain, which uses the thermicity index calculated for the period 1965–2000 (i.e., the sum of the mean annual temperature, mean temperature of the lowest values of the coldest month, and the mean temperature of the highest values of the warmest month, expressed in tenths of degrees) to represent long-term climate and, ultimately, potential vegetation types. Here we considered mediterranean (including coniferous, sclerophyllous, and mixed), supramediterranean (including coniferous, semi-deciduous, sclerophyllous, and mixed), and montane (including coniferous and mixed coniferous-deciduous) forests (Selwyn et al. 2024). We chose this approach because it represented a more general (and largely independent) climate driver, distinct from the daily climate data we used as input for MEDFATE.
- SPEI (unitless). The level of dryness during the summer drought of 1994 relative to the long-term mean is a measure of disturbance intensity, and it likely affects both resistance and resilience. Thus, we included SPEI as a driver, calculated for May-August 1994 (time window of 6 months) using the R package SPEI (Beguería and Vicente-Serrano 2023).
- Basal area (m^2 ha^{-1}). We included basal area as a driver because it is a key metric for characterising forest structure, stand development, and potential competition for water resources.
- Coefficient of variation of DBH (unitless). As an additional forest structure metric, we evaluated the potential effects of the relative variability of DBH as a measure of structural complexity.
- Tree richness (unitless). Forests with higher species richness are generally more resilient (Ibáñez et al. 2019). We therefore included richness as a driver, calculated by counting the number of unique tree species in the NFI2 plots.
- Slope (degrees) and aspect (categorical). We included topographic drivers such as slope and aspect to account for their effect on local hydrology, soils, and exposure to solar radiation. Aspect was classified as North (greater than 315° and less than 45°), South (greater than 135° and less than 225°), West (greater than 225° and less than 315°), and East (greater than 45° and less than 135°).
- Past forest management (categorical). Forest management that occurred before 1990 may influence the ability of forest stands to withstand and respond to disturbances. Therefore, we included past forest management as a presence/absence driver, based on evidence recorded in the NFI2 data.
- Land-use history (categorical). We defined land-use history by overlaying the position of each forest plot with orthoimages from the 1956 American Flight B series over Spain. This exercise allowed us to classify plots into either long-existing forests, which were already present in 1956, or recent forests, established in croplands or pasturelands after 1956 following rural abandonment. The year 1956 predates the significant forest expansion that occurred in the second half of the 20th century, making it an effective baseline for distinguishing between older and newer forests (Cervera et al. 2019). We consider this classification a meaningful driver of resistance and resilience based on previous studies showing significant differences in both the functioning and structure between these two forest types (Alfaro-Sánchez et al. 2019; Espelta et al. 2020).

2.4.3. Statistical modelling

To assess the drivers of resistance and resilience, linear mixed-effects models (LMMs) were fitted using the lmer function from the lme4 (Bates et al. 2024) and lmerTest packages (Kuznetsova et al. 2022). We scaled continuous variables using the standardised parameters function from the effectsize package (Ben-Shachar et al. 2024). Both the resistance and resilience of each ecosystem service in the actual and extreme scenarios were used as response variable, resulting in 20 LMMs. We used the same set of drivers as predictors for both resistance and resilience and included county ($n = 41$) as a random effect to account for potential non-independence among nearby plots (Harrison et al. 2018). We did not consider interactions due to the high number of drivers included in our analysis, and because preliminary analyses indicated that including interactions generally had a negligible impact on model results. For each model, we applied the stepAIC function from the MASS package (Ripley and Venables 2024) to find the most parsimonious model that best balances goodness of fit with model complexity, as indicated by the Akaike Information Criteria (AIC). Further, we used the r.squaredGLMM function from the MuMIn package (Bartoń, 2024) to derive the proportion of variance explained by fixed effects alone (R^2m) and by both fixed and random effects (R^2c). No collinearity was observed among the drivers, as indicated by low variance inflation factors (Appendix A6). Our methodological workflow is summarised in Fig. 1. All analyses were performed within the R environment, version 4.2.1 (Posit team 2025).

3. Results

3.1. Changes in forest ecosystem services

Annual values of the five FES from 1990 to 2000 averaged by bioclimatic region are shown in Fig. 2 (the complete time series covering 1990–2020 is provided in Appendix A7). Bluewater provision and erosion mitigation showed an increase in the drought year for the actual scenario with respect to 1993, as autumn 1994 was particularly wet. Potential recreational value, timber volume stock, and carbon stock appeared relatively unaffected. The simulated extreme drought significantly decreased bluewater provision and erosion mitigation, left the potential recreational value unaltered, and had modest effects on timber volume and carbon stock. Under the counterfactual undisturbed

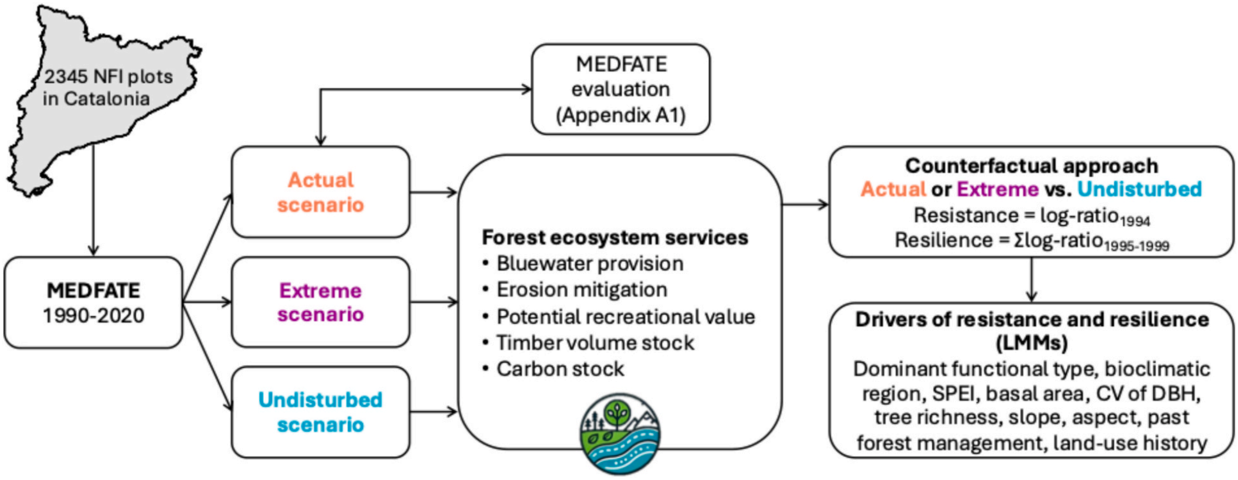

Fig. 1. Schematic overview of our methodological workflow. We used a process-based forest model (MEDFATE) to run three sets of simulations (actual, extreme, and undisturbed scenarios) on 2345 plots of the Spanish National Forest Inventory (NFI) program in Catalonia. From these simulations, we retrieved five relevant forest ecosystem services, for which we calculated the resistance and resilience to drought using a counterfactual approach. Linear mixed-effect models (LMMs) were fitted to identify the drivers of resistance and resilience. We evaluated MEDFATE performance by comparing simulated leaf area index (LAI) from the actual scenario against MODIS LAI.

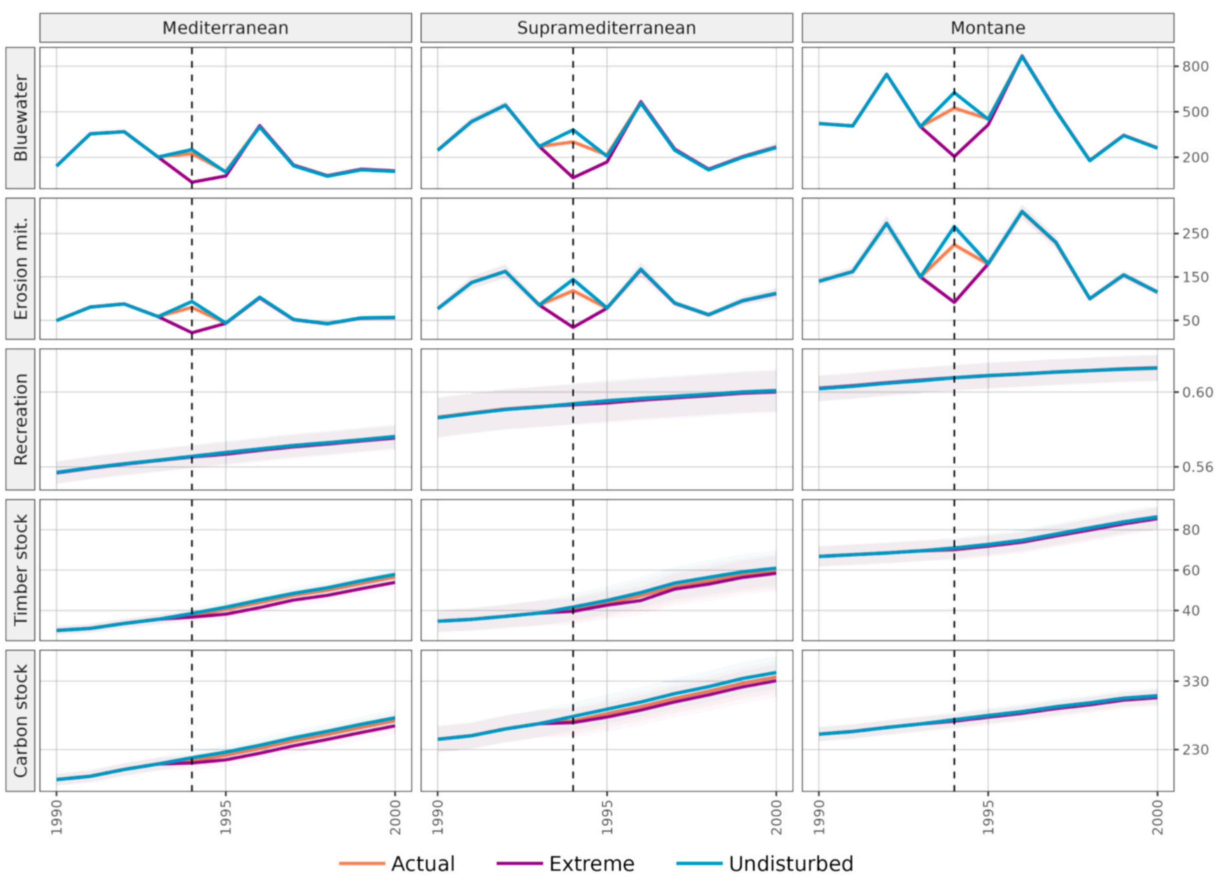

Fig. 2. Annual average values with 95% confidence intervals of the five forest ecosystem services by scenario and bioclimatic region for 1990–2000. Vertical dashed lines indicate year 1994. Bluewater: bluewater provision (mm yr^{-1}), Erosion mit.: erosion mitigation (Mg ha^{-1} yr^{-1}), Recreation: potential recreational value (0 – 1), Timber stock: timber volume stock (m^3 ha^{-1}), Carbon stock: carbon stock ($MgCO_2$ ha^{-1}).

scenario, patterns did reflect a no-drought condition. Noticeably, while bluewater provision and erosion mitigation returned to pre-drought levels within a year across the three bioclimatic regions, the extreme scenario in the mediterranean and supramediterranean regions delayed the return to pre-drought levels for timber and carbon stocks.

3.2. Forest ecosystem services resistance and resilience

In the actual scenario, resistance clustered around zero (i.e., small drought impact) for all FES, except for hydrologically related services (i.e., bluewater provision and erosion mitigation), which exhibited negative values (Fig. 3a). In the extreme scenario (Fig. 3b), negative responses were amplified for these services (median resistance below –1), while potential recreational value, timber volume stock, and carbon stock remained generally resistant. Resilience showed greater variability than resistance and, importantly, all services decreased when transitioning from the actual (Fig. 3c) to the extreme (Fig. 3d) scenario (except for potential recreational value), indicating lower resilience under harsher drought conditions. The montane region appeared to be more resilient than the Mediterranean and supramediterranean regions, as reflected by less negative log-ratio values and smaller interquartile ranges.

3.3. Drivers of forest ecosystem services resistance and resilience

Bioclimatic region, SPEI, and basal area emerged as key drivers of resistance across most FES (Fig. 4). Montane and supramediterranean forests tended to show lower resistance of hydrologically related services (i.e., bluewater provision and erosion mitigation) under the actual scenario. For the other services and for the extreme scenario overall, montane forests tended to generally exhibit higher resistance than mediterranean ones, particularly under extreme drought, while supramediterranean ones showed similar responses to the mediterranean. As expected, SPEI consistently showed a strong positive effect on the resistance of most services across both scenarios, underscoring the role of drought intensity in shaping ecosystem-level impacts (higher SPEI denotes lower drought intensity, and vice versa). The role of basal area was less consistent, showing negative effects on bluewater provision only in the extreme scenario, but positive effects on timber volume and carbon stocks in the extreme scenario. In stands dominated by resprouting needleleaved evergreen species, resistance was lower for bluewater provision across both scenarios, and for erosion mitigation in the extreme scenario. Other drivers played a relatively minor role (Fig. 4).

Bioclimatic region, SPEI, and basal area emerged as the most significant drivers also for resilience (Fig. 5). Specifically, SPEI had a positive effect on the resilience of most services, except for bluewater provision under both scenarios. Basal area effects were significant only in the extreme scenario, where it decreased the resilience of bluewater provision, while increasing the resilience of erosion mitigation, timber volume and carbon stocks. In addition, needleleaved evergreen forests, which negatively affected resistance, showed a positive effect on resilience for bluewater provision (both scenarios), suggesting lower resistance but a greater ability to recover compared to broadleaved deciduous forests. More clearly than for resistance, montane forests displayed higher resilience than mediterranean forests across most services, particularly in the extreme scenario. Other significant effects included aspect (positive for timber volume stock in the actual scenario) and coefficient of variation of DBH (negative for potential recreational value under both scenarios).

4. Discussion

Our counterfactual modelling approach enabled us to isolate the effects of drought from other drivers of forest resilience dynamics by comparing actual and extreme drought scenarios against an undisturbed baseline. This provided a consistent framework for evaluating patterns of resistance and resilience to drought for a range of FES.

Our first hypothesis was only partially supported, as the effects of forest structure and tree richness on FES resistance and resilience were generally limited and outweighed by climate-related drivers (Figs. 4 and 5). These results contrast with previous assessments, such as Roces-Díaz et al. (2021), which identified structural characteristics as the primary driver of recent FES dynamics in Catalonia. However, that study focused on general trends and spatiotemporal patterns in service provision at a decadal timescale, whereas our analysis estimates resilience to a specific drought event. Considered together, our results and those of Roces-Díaz et al. (2021) may indicate that (i) long-term FES dynamics are shaped by stand structure and succession, but (ii) responses to specific drought events are primarily climate-driven, as indicated by SPEI effects (Appendix A8). As expected, the effect of SPEI was positive in nearly all cases, indicating that less severe drought promoted FES resistance and resilience. These results are consistent with the key role of negative

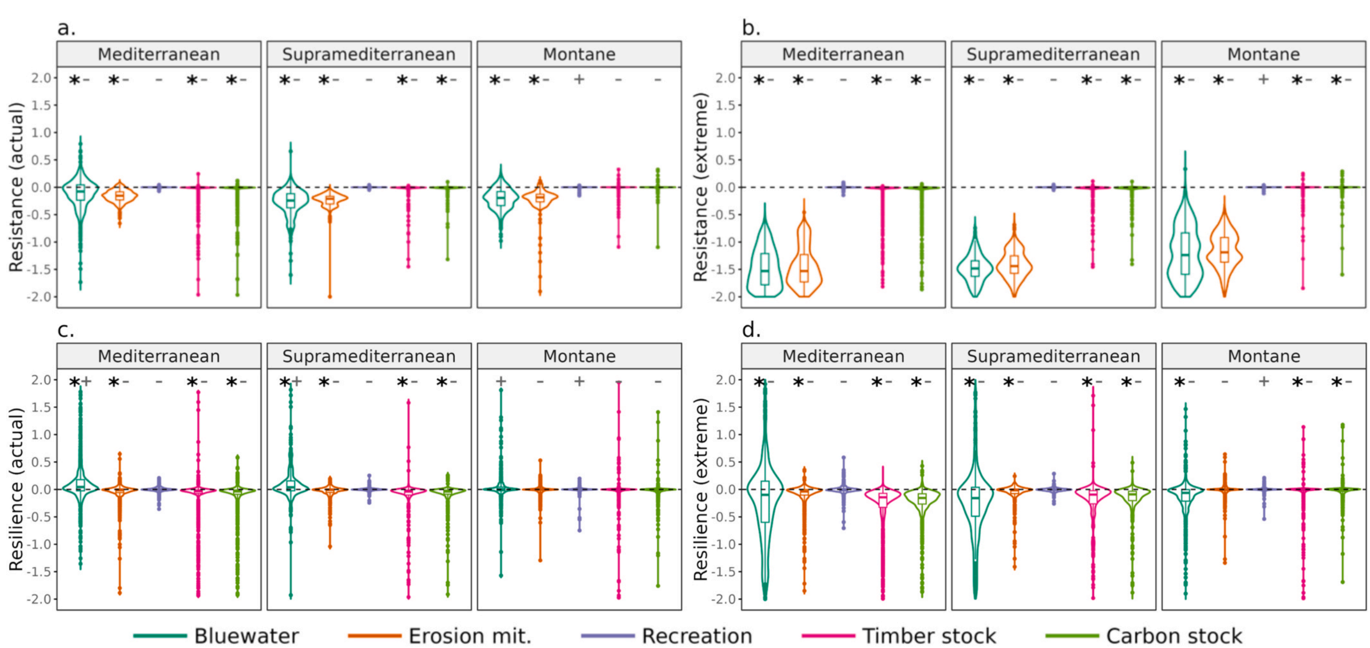

Fig. 3. Resistance, calculated as the log-ratio of actual (a) or extreme (b) to undisturbed in 1994, and resilience, calculated as the log-ratio of actual (c) or extreme (d) to undisturbed integrated during 1995–1999, for the five forest ecosystem services. Asterisks indicate significant ($p < 0.001$) departure from zero based on one-sample t-tests computed within each scenario. Gray signs indicate whether the median is positive (+) or negative (–). For clarity, y-axes are capped between –2 and 2. Bluewater: bluewater provision, Erosion mit.: erosion mitigation, Recreation: potential recreational value, Timber stock: timber volume stock, Carbon stock: carbon stock.

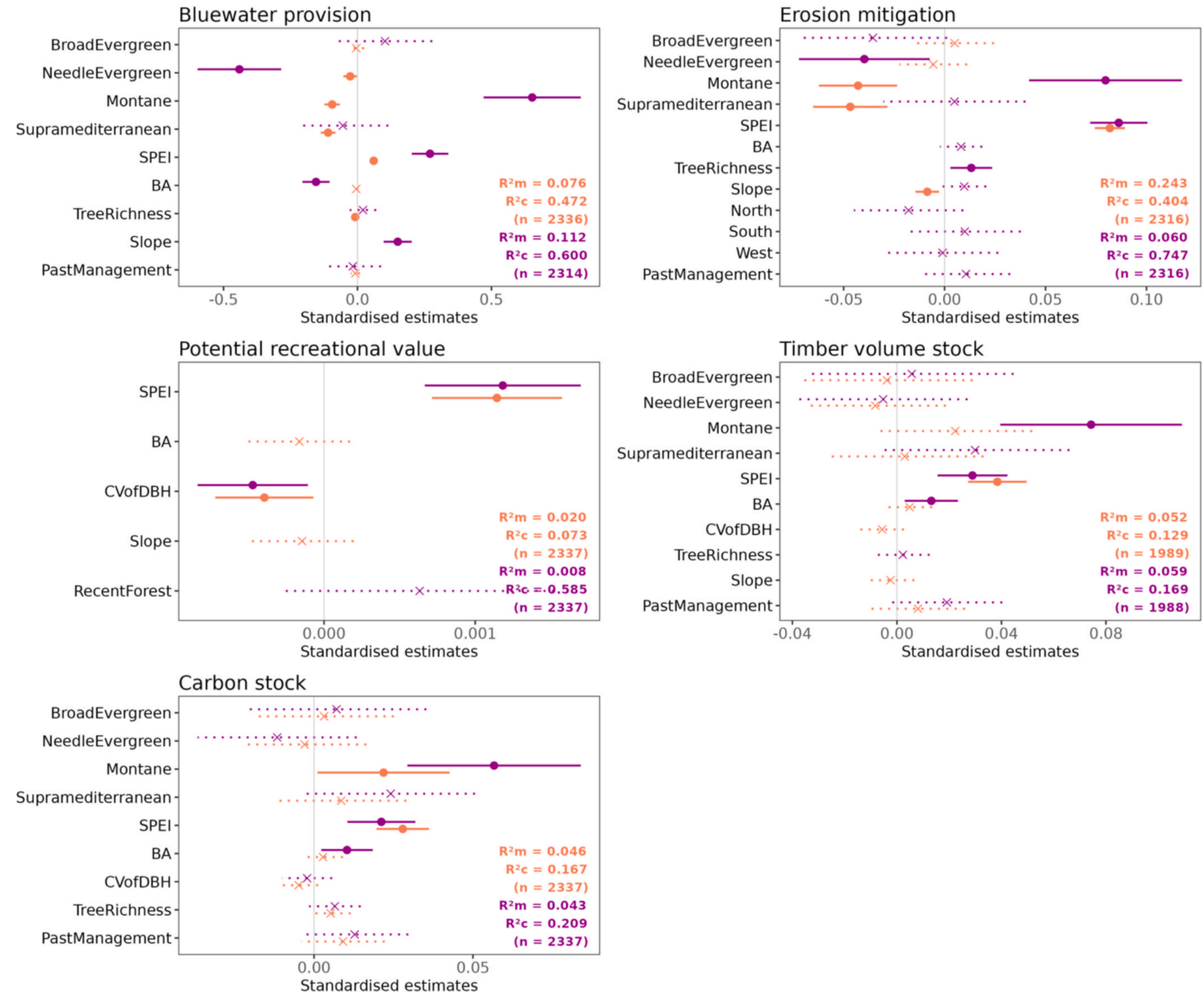

Fig. 4. Standardised estimates of the best LMMs explaining the effects of drivers of resistance of the five forest ecosystem services. The reference level for dominant functional type is broadleaved deciduous, for bioclimatic region is mediterranean, for aspect is East, for past forest management is absence of past management, and for land-use history is long-lasting forest. Orange indicates the actual scenario, purple indicates the extreme scenario, solid lines and dots are significant estimates ($p < 0.05$), dashed lines and crosses are non-significant estimates ($p > 0.05$). R^2m: marginal R^2, R^2c: conditional R^2, (n): number of plots in each LMM (this is not necessarily 2345 due to some missing soil erodibility data, the exclusion of unrealistic plots with no annual rainfall, and the fact that not all plots met the conditions required to produce timber). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

rainfall anomalies in promoting drought-induced forest decline in the study area (Chaparro et al. 2017). Basal area emerged as the most influential structural attribute, exhibiting negative effects on the resistance and resilience of hydrologically related services, as higher basal area intensified competition for water, exacerbating the effects of climatic drought on soil water availability and hydrological output. In contrast, basal area had positive effects on stock-based services, particularly under extreme drought conditions, where larger basal area implied greater initial stocks, thereby reducing the relative impact of mortality rates with similar absolute magnitude (and resulting in smaller log-ratio). This evidence supports long-lasting knowledge that denser stands increase plant competition for light, water, and nutrients (Haberstroh and Werner 2022), leading to faster resource depletion and, consequently, lower resilience of water and carbon fluxes (Giuggiola et al. 2013, 2018. However, biomass reductions during drought were proportionately lower in forests with higher basal area, implying a greater capacity to maintain timber and carbon stocks over time. These findings underscore trade-offs between enhancing the resilience of hydrologically related services (and services representing rates such as timber volume increment and carbon sequestration rate; Appendix A9) and maintaining stock-based ones, particularly in water-limited regions such as the Mediterranean Basin (Roces-Díaz et al. 2021). This has important management implications, as reducing stand density may help alleviate competition and improve drought resilience of water provision, but high extraction rates might negatively affect the capacity to sustain timber volume and carbon stocks in the mid-term (Ameztegui et al. 2017; Bottero et al. 2017). These results contribute to the evidence showing the complexity of stand development and thinning effects on forest responses to drought, even when focusing solely on water-related services (Bachofen et al. 2023).

Tree species richness did not emerge as a dominant driver of both resistance and resilience as generally understood (Mori et al. 2013; Oliver et al. 2015), but this does not refute the possibility that more nuanced measures of taxonomic or functional diversity may play a more

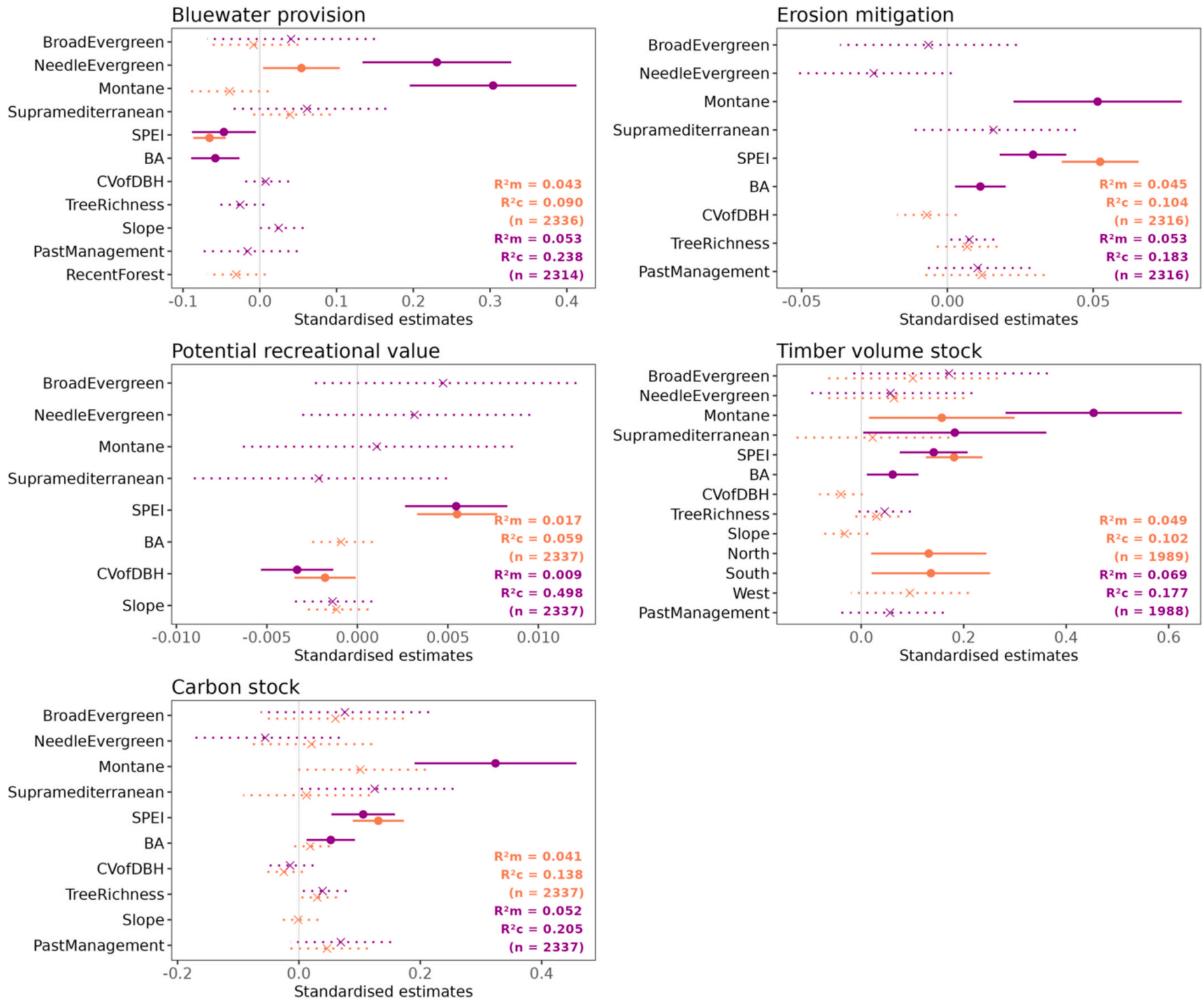

Fig. 5. Standardised estimates of the best LMMs explaining the effects of the drivers of resilience of the five forest ecosystem services. The reference levels are the same as in Fig. 4. Orange indicates the actual scenario, purple indicates the extreme scenario, solid lines and dots are significant estimates ($p < 0.05$), dashed lines and crosses are non-significant estimates ($p > 0.05$). R^2m: marginal R^2, R^2c: conditional R^2, (n): number of plots in each LMM. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

important role in driving resilience to drought than just the absolute number of species (García-Valdés et al. 2021). The small effect of tree richness may reflect the extensive erosion of tree species diversity in mediterranean-type forests after a long history of intensive management, as indicated by the limited variation in richness and forest structure observed in 1990 across the study region (Appendix A5) (Sánchez De Dios et al. 2023). Thus, we cannot discard that more functional measures of tree diversity (e.g., García-Valdés et al. 2021; Ouyang et al. 2023) would have shown a stronger impact on FES resilience. Long-existing forests and recent forests showed similar resistance and resilience, possibly because they are very similar, on average, in terms of species composition and stand structure (Appendix A5). Indeed, previous studies conducted in the region have indicated that species colonisation credits in recent forests are relatively quickly cancelled (after ca. 40 years) and, therefore, they exhibit a similar tree species composition and basal area to long-existing ones (Espelta et al. 2020; Cruz-Alonso et al. 2021). Ultimately, the minimal influence of past management and land-use history on resistance and resilience suggests that current forest conditions may be more important for drought response than legacy effects. This implies that management decisions could primarily focus on present-day forest characteristics, potentially simplifying planning and intervention.

Mediterranean forests were not the most resistant or resilient, and our second hypothesis was therefore not supported. Instead, montane regions, despite being dominated by species with relatively lower drought tolerance, exhibited higher resistance and resilience across most ecosystem services, particularly under the extreme drought scenario (Figs. 3-5), and also returned to pre-drought levels faster (Fig. 2) (similar patterns were observed for timber volume increment and carbon sequestration rate, Appendix A9). This may be attributed to the lower drought severity experienced in this region, as indicated by SPEI values (Appendix A8), and the inherently wetter climate, which on the one hand determines less extreme absolute drought metrics for a given SPEI and, on the other, facilitates faster soil moisture replenishment once the drought episode is over. These results align with observations of drought-induced forest decline in the study area, where both mediterranean and montane forests have been affected, suggesting that spatial patterns cannot be explained solely by species' historical climatic affiliations (Margalef-Marrase et al. 2020; Hartmann et al. 2022). Ultimately, mediterranean forests emerged as vulnerable to extreme drought conditions (Figs. 2 and 3), underscoring the need for targeted management interventions to enhance their resilience and ensure the continued provision of ecosystem services in the future.

As expected, and consistent with our third hypothesis, the extreme scenario showed a marked decline in resistance followed by a rapid return to pre-drought levels of hydrologically related services, highlighting the strong dependence of these services on precipitation patterns. Under the actual scenario, however, this pattern was less apparent, as the exceptionally wet autumn of 1994 offset the summer water deficit and led to relatively high annual rainfall, ultimately enhancing both resistance and resilience (Figs. 2 and 3a and c, and Appendix A2). These findings highlighted the overall marked sensitivity of hydrologically related services to precipitation, with sharp declines during drought conditions and the capacity to recover once moisture availability improves. This response is particularly relevant when interpreting differences between mediterranean and more humid montane systems. From a purely hydrological perspective, changes in precipitation in drier forests primarily affect evapotranspiration, with minimal influence on runoff, whereas in more humid forests, precipitation changes more directly influence blue water availability (Piñol et al. 1991). This framework helps explain why bluewater provision was less affected by the actual 1994 drought in mediterranean forests compared to montane ones (Fig. 2). However, the stronger decline in bluewater provision under the extreme scenario suggests that additional mechanisms (e.g., changes in forest structure) may also be contributing. It is also worth noting that annual precipitation totals may obscure seasonal extremes, emphasising the importance of considering intra-annual dynamics when evaluating ecosystem responses. In the study area, water provision depends largely on spring and autumn precipitation rather than on summer rainfall, which is typically insufficient to meet evaporative demand (De Cáceres et al. 2015). Whether the impacts on hydrologically related services would differ under a multi-year drought rather than a single, intense event remains an open research question. Finally, FES more related to forest structure (timber volume and carbon stocks, and potential recreational value) showed higher resistance compared to hydrologically related services, reflecting their dependence on slower-changing forest attributes. Specifically, timber volume and carbon stocks exhibited modest declines under the extreme scenario with a corresponding decrease in resilience, while potential recreational value remained unaffected across scenarios and regions (Figs. 2 and 3). Such limited impact on structural services is consistent with the fact that droughts do not typically lead to abrupt, widespread stand loss at regional scale. Whether this will still be the case under future climatic regimes characterised by longer and hotter droughts is yet to be understood (Allen et al., 2010; Hartmann et al., 2022). That said, the low sensitivity of potential recreational value to drought could also reflect methodological limitations in the way it was estimated in this study (Section 4.1).

4.1. Limitations

A limitation of our study lies in how our forest model represents demographic dynamics after drought. Resprouting, for instance, particularly relevant for broadleaf species with strong regenerative capacity, was not included in version 2.9.3 of the model, potentially leading to underestimations of resilience in services sensitive to post-disturbance regrowth (Martínez-Vilalta and Lloret 2016). This is a common limitation in forest modelling, as most models do not account for resprouting mechanisms, thereby hampering the ability to simulate post-disturbance dynamics (Hanbury-Brown et al. 2022). However, this artefact is unlikely to significantly affect our results, as resprouter-dominated plots represent a similar, moderate fraction of the study plots (around one third) in the three bioclimatic regions (Appendix A10). In addition, resprouting is generally higher following disturbances such as clear-cutting or fire than after drought-induced mortality. As we excluded plots with signs of logging or fire, the underestimation of drought-induced resprouting may be less pronounced than in post-harvest scenarios. Further, the model's limited temporal accuracy, likely due to uncertainty in soil water holding capacity or misrepresented defoliation thresholds (Appendix A1), may further influence how post-disturbance trajectories of services are simulated over time and, hence, their interpretation (Cabon et al. 2018). Soil data from SoilGrids, a product with known limitations, especially with respect to rock content, may affect the accuracy of drought stress predictions and post-drought dynamics. This represents yet another common challenge in forest modelling (Dukes et al. 2026), as precise soil hydraulic properties are rarely available at the regional scale. Given that uncertainties in soil water holding capacity can lead to underestimation of drought severity, our simulated post-drought trajectories may be faster than in reality, potentially inflating resilience estimates. Nonetheless, the model reproduced observed empirical patterns and provided coherent simulations of actual, extreme, and undisturbed drought conditions, as evidenced by consistent temporal dynamics and patterns of resistance and resilience across scenarios, suggesting its overall suitability for comparative resilience assessments.

Finally, the selection of ecosystem services was guided by the outputs that MEDFATE can provide. Process-based forest models simulate biophysical processes but are not designed to capture cultural ecosystem services, which depend on social and behavioural factors. Empirical data on recreational use of forests are also spatially fragmented and temporally inconsistent, further limiting their integration with model outputs. To address this, we developed a first expert-based scoring approach to estimate the potential recreational value within a process-based modelling framework, combining structural model outputs with expert judgement. While this provided a usable proxy, the resulting index is largely driven by slowly changing structural attributes, which may limit its responsiveness and help explain the observed low sensitivity to drought. The provisioning services could also be expanded in future work. For instance, the yield of edible mushrooms is an important forest product in Mediterranean forests and their relevance as a key provisioning service has been previously modelled and assessed in the study area (de-Miguel et al. 2014; Roces-Díaz et al. 2021), but empirical equations are currently available for pine-dominated forests only, which would have excluded all broadleaved-dominated plots from our assessment.

5. Conclusions

The different responses of the five FES underscore the need to assess resistance and resilience across multiple ecological functions. Hydrologically related services, for instance, exhibited much sharper declines and quicker recoveries compared to structural services such as timber volume and carbon stocks. These differences reflect inherent variations in service dynamics, emphasising the value of spatiotemporal, multifunctional approaches to capture the full spectrum of ecosystem responses to disturbances (Mori et al. 2017; Himes et al. 2020). Overall, we show that while Catalan forests demonstrated relatively high resilience to the 1994 summer drought, they may not withstand more extreme events expected under future climate change scenarios, particularly in the Mediterranean region. Climate (including local drought intensity during the event) was the dominant driver of resistance and resilience to drought, while structural attributes such as basal area played a secondary but, importantly, service-specific role (e.g., enhancing stock-based services while undermining resilience of hydrologically related services). Species richness, past forest management, and land-use history had marginal effects, likely due to the relative structural and biodiversity homogeneity observed across the region and the variability within categories describing recent forest dynamics (Appendix A5).

CRediT authorship contribution statement

Francesco D'Adamo: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Miquel De Cáceres:** Writing – review & editing, Software, Methodology, Investigation, Conceptualization. **Josep Maria Espelta:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Conceptualization. **Jose Valentin Roces-Díaz:** Writing – review & editing, Methodology. **Adrià Descals:** Writing – review & editing, Data curation. **Miriam Selwyn:** Writing – review & editing, Methodology. **Francisco Lloret:** Writing – review & editing. **Jordi Martínez-Vilalta:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Conceptualization.

Declaration of competing interest

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

Acknowledgements

This project was supported by funding from the RESONATE (EU H2020-RUR-2020-2, grant no. 101000574), BOMFORES (MCIN/AEI, grant no. PID2021–126679OB-I00), and IMPROMED (MCIN/AEI, grant no. PID2023-152644NB-I00) projects. We thank Víctor Granda García for his assistance with Linux and R programming.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoser.2026.101858.

Data availability

Data will be made available on request.

References

Agimass, F., Lundhede, T., Panduro, T.E., Jacobsen, J.B., 2018. The choice of forest site for recreation: a revealed preference analysis using spatial data. Ecosyst. Serv. 31, 445–454. https://doi.org/10.1016/j.ecoser.2017.11.016.

Alberdi, I., Sandoval, V., Condes, S., et al., 2016. The Spanish National Forest Inventory, a tool for the knowledge, management and conservation of forest ecosystems. Ecosistemas 25, 88–97. https://doi.org/10.7818/ECOS.2016.25-3.10.

Albrich, K., Rammer, W., Turner, M.G., et al., 2020. Simulating forest resilience: a review. Glob. Ecol. Biogeogr. 29, 2082–2096. https://doi.org/10.1111/geb.13197.

Alfaro-Sánchez, R., Jump, A.S., Pino, J., et al., 2019. Land use legacies drive higher growth, lower wood density and enhanced climatic sensitivity in recently established forests. Agric. For. Meteorol. 276–277, 107630. https://doi.org/10.1016/j.agrformet.2019.107630.

Allen, C.D., Macalady, A.K., Chenchouni, H., et al., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manag 259, 660–684. https://doi.org/10.1016/j.foreco.2009.09.001.

Altava-Ortiz V, Barrera-Escoda A, Barnolas M, et al (2025) Anàlisi I Context Climàtic de La Sequera 2021-2024.

Ameztegui, A., Brotons, L., Coll, L., 2010. Land-use changes as major drivers of mountain pine (Pinus uncinata Ram.) expansion in the Pyrenees. Glob. Ecol. Biogeogr. 19, 632–641. https://doi.org/10.1111/j.1466-8238.2010.00550.x.

Ameztegui, A., Cabon, A., De Cáceres, M., Coll, L., 2017. Managing stand density to enhance the adaptability of Scots pine stands to climate change: a modelling approach. Ecol. Model. 356, 141–150. https://doi.org/10.1016/j.ecolmodel.2017.04.006.

Anderegg, W.R.L., Kane, J.M., Anderegg, L.D.L., 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. Nat. Clim. Chang. 3, 30–36. https://doi.org/10.1038/nclimate1635.

Anderegg, W.R.L., Schwalm, C., Biondi, F., et al., 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. Science 349, 528–532. https://doi.org/10.1126/science.aab1833.

Anderegg, W.R.L., Trugman, A.T., Badgley, G., et al., 2020. Divergent forest sensitivity to repeated extreme droughts. Nat. Clim. Chang. 10, 1091–1095. https://doi.org/10.1038/s41558-020-00919-1.

Bachofen, C., Poyatos, R., Flo, V., et al., 2023. Stand structure of central European forests matters more than climate for transpiration sensitivity to VPD. J. Appl. Ecol. 60, 886–897. https://doi.org/10.1111/1365-2664.14383.

Barrere, J., Reineking, B., Jaunatre, M., Kunstler, G., 2024. Forest storm resilience depends on the interplay between functional composition and climate—Insights from European-scale simulations. Funct. Ecol. 38, 500–516. https://doi.org/10.1111/1365-2435.14489.

Kamil Bartoń (2024) MuMIn: Multi-Model Inference. 1.47.5.

Bates D, Maechler M, Bolker B, Walker S (2024) lme4: Linear Mixed-Effects Models using "Eigen" and S4. 1.1-35.5.

Beguería S, Vicente-Serrano SM (2023) SPEI: Calculation of the Standardized Precipitation-Evapotranspiration Index. 1.8.1.

Ben-Shachar, M.S., Makowski, D., Lüdecke, D., et al., 2024. effectsize. Indices of Effect Size. 0.8.9.

Bottero, A., D'Amato, A.W., Palik, B.J., et al., 2017. Density-dependent vulnerability of forest ecosystems to drought. J. Appl. Ecol. 54, 1605–1614. https://doi.org/10.1111/1365-2664.12847.

Brodribb, T.J., Powers, J., Cochard, H., Choat, B., 2020. Hanging by a thread? Forests and drought. Science 368, 261–266. https://doi.org/10.1126/science.aat7631.

Brown, L.A., Morris, H., MacLachlan, A., et al., 2024. Hyperspectral leaf area index and chlorophyll retrieval over forest and row-structured vineyard canopies. Remote Sens 16, 2066. https://doi.org/10.3390/rs16122066.

Bugmann, H., Seidl, R., 2022. The evolution, complexity and diversity of models of long-term forest dynamics. J. Ecol. 110, 2288–2307. https://doi.org/10.1111/1365-2745.13989.

Cabon, A., Martínez-Vilalta, J., Martínez De Aragón, J., et al., 2018. Applying the eco-hydrological equilibrium hypothesis to model root distribution in water-limited forests. Ecohydrology 11, e2015.

Cabon, A., Ameztegui, A., Anderegg, W.R.L., et al., 2024. Probing the interplay of biophysical constraints and photosynthesis to model tree growth. Agric. For. Meteorol. 345, 109852. https://doi.org/10.1016/j.agrformet.2023.109852.

Cantarello, E., Newton, A.C., Martin, P.A., et al., 2017. Quantifying resilience of multiple ecosystem services and biodiversity in a temperate forest landscape. Ecol. Evol. 7, 9661–9675. https://doi.org/10.1002/ece3.3491.

Cervera, T., Pino, J., Marull, J., et al., 2019. Understanding the long-term dynamics of forest transition: from deforestation to afforestation in a Mediterranean landscape (Catalonia, 1868–2005). Land Use Policy 80, 318–331. https://doi.org/10.1016/j.landusepol.2016.10.006.

Chaparro, D., Vayreda, J., Vall-llossera, M., et al., 2017. The role of climatic anomalies and soil moisture in the decline of drought-prone forests. IEEE J. Sel. Top. Appl. Earth Obs. Remote Sens. 10, 503–514. https://doi.org/10.1109/JSTARS.2016.2585505.

Chen, Y., Sun, B., Liao, S., et al., 2015. Landscape perception based on personal attributes in determining the scenic beauty of in-stand natural secondary forests. Ann. For. Res. 59, 1. https://doi.org/10.15287/afr.2015.440.

Coetzee, B.W.T., Gaston, K.J., 2021. An appeal for more rigorous use of counterfactual thinking in biological conservation. Conserv. Sci. Pract. 3, e409.

Cruz-Alonso, V., Espelta, J.M., Pino, J., 2021. Woody species richness and turnover in expanding Mediterranean forests: a story of landscape legacies influenced by climatic aridity. Landsc. Ecol. 36, 1787–1800. https://doi.org/10.1007/s10980-021-01249-z.

De Cáceres, M.D., Martínez-Vilalta, J., Coll, L., et al., 2015. Coupling a water balance model with forest inventory data to predict drought stress: the role of forest structural changes vs. climate changes. Agric. For. Meteorol. 213, 77–90. https://doi.org/10.1016/j.agrformet.2015.06.012.

De Cáceres, M., Martin-StPaul, N., Turco, M., et al., 2018. Estimating daily meteorological data and downscaling climate models over landscapes. Environ Model Softw. 108, 186–196. https://doi.org/10.1016/j.envsoft.2018.08.003.

De Cáceres, M., Mencuccini, M., Martin-StPaul, N., et al., 2021. Unravelling the effect of species mixing on water use and drought stress in Mediterranean forests: a modelling approach. Agric. For. Meteorol. 296, 108233. https://doi.org/10.1016/j.agrformet.2020.108233.

De Cáceres, M., Molowny-Horas, R., Cabon, A., et al., 2023. MEDFATE 2.9.3: a trait-enabled model to simulate Mediterranean forest function and dynamics at regional scales. Geosci. Model Dev. 16, 3165–3201. https://doi.org/10.5194/gmd-16-3165-2023.

De Meo, I., Paletto, A., Cantiani, M.G., 2015. The attractiveness of forests: preferences and perceptions in a mountain community in Italy. Ann. For. Res. 58, 1. https://doi.org/10.15287/afr.2015.308.

de-Miguel, S., Bonet, J.A., Pukkala, T., Martínez De Aragón, J., 2014. Impact of forest management intensity on landscape-level mushroom productivity: a regional model-based scenario analysis. For Ecol Manag 330, 218–227. https://doi.org/10.1016/j.foreco.2014.07.014.

Dietze, M.C., Sala, A., Carbone, M.S., et al., 2014. Nonstructural carbon in woody plants. Annu. Rev. Plant Biol. 667–687.

Diodato, N., Bellocchi, G., 2010. MedREM, a rainfall erosivity model for the Mediterranean region. J. Hydrol. 387, 119–127. https://doi.org/10.1016/j.jhydrol.2010.04.003.

Doblas-Miranda, E., Alonso, R., Arnan, X., et al., 2017. A review of the combination among global change factors in forests, shrublands and pastures of the mediterranean region: beyond drought effects. Glob Planet Change 148, 42–54. https://doi.org/10.1016/j.gloplacha.2016.11.012.

Dorheim, K., Gough, C.M., Haber, L.T., et al., 2022. Climate drives modeled forest carbon cycling resistance and resilience in the upper great lakes region, USA. J Geophys Res Biogeosciences 127, e2021JG006587. https://doi.org/10.1029/2021JG006587.

Dukes, J.S., Xu, C., Liao, C., et al., 2026. Improving the representation of plant water stress and water use in Earth System Models. New Phytol. 249, 39–55. https://doi.org/10.1111/nph.70687.

Edwards DM, Jay M, Jensen FS, et al (2012) Public Preferences Across Europe for Different Forest Stand Types as Sites for Recreation. Ecol Soc 17:art27. https://doi.org/10.5751/ES-04520-170127.

Epstude, K., Roese, N.J., 2008. The functional theory of counterfactual thinking. Personal. Soc. Psychol. Rev. 12, 168–192. https://doi.org/10.1177/1088868308316091.

Espelta, J.M., Cruz-Alonso, V., Alfaro-Sánchez, R., et al., 2020. Functional diversity enhances tree growth and reduces herbivory damage in secondary broadleaf forests, but does not influence resilience to drought. J. Appl. Ecol. 57, 2362–2372. https://doi.org/10.1111/1365-2664.13728.

Felipe-Lucia, M.R., Soliveres, S., Penone, C., et al., 2018. Multiple forest attributes underpin the supply of multiple ecosystem services. Nat. Commun. 9, 4839. https://doi.org/10.1038/s41467-018-07082-4.

Filyushkina, A., Agimass, F., Lundhede, T., et al., 2017. Preferences for variation in forest characteristics: does diversity between stands matter? Ecol. Econ. 140, 22–29. https://doi.org/10.1016/j.ecolecon.2017.04.010.

García-Valdés, R., Vayreda, J., Retana, J., Martínez-Vilalta, J., 2021. Low forest productivity associated with increasing drought-tolerant species is compensated by an increase in drought-tolerance richness. Glob. Chang. Biol. 27, 2113–2127. https://doi.org/10.1111/gcb.15529.

Gauquelin, T., Michon, G., Joffre, R., et al., 2018. Mediterranean forests, land use and climate change: a social-ecological perspective. Reg. Environ. Chang. 18, 623–636. https://doi.org/10.1007/s10113-016-0994-3.

Giuggiola, A., Bugmann, H., Zingg, A., et al., 2013. Reduction of stand density increases drought resistance in xeric Scots pine forests. For Ecol Manag 310, 827–835. https://doi.org/10.1016/j.foreco.2013.09.030.

Giuggiola, A., Zweifel, R., Feichtinger, L.M., et al., 2018. Competition for water in a xeric forest ecosystem – Effects of understory removal on soil micro-climate, growth and physiology of dominant Scots pine trees. For Ecol Manag 409, 241–249. https://doi.org/10.1016/j.foreco.2017.11.002.

Groover, A., Holbrook, N.M., Polle, A., et al., 2025. Tree drought physiology: critical research questions and strategies for mitigating climate change effects on forests. New Phytol. 245, 1817–1832. https://doi.org/10.1111/nph.20326.

Grünig, M., Rammer, W., Senf, C., et al., 2026. Climate change will increase forest disturbances in Europe throughout the 21st century. Science 391, eadx6329. https://doi.org/10.1126/science.adx6329.

Guerra, C.A., Maes, J., Geijzendorffer, I., Metzger, M.J., 2016. An assessment of soil erosion prevention by vegetation in Mediterranean Europe: current trends of ecosystem service provision. Ecol. Ind. 60, 213–222. https://doi.org/10.1016/j.ecolind.2015.06.043.

Gundersen, V.S., Frivold, L.H., 2008. Public preferences for forest structures: a review of quantitative surveys from Finland, Norway and Sweden. Urban For. Urban Green. 7, 241–258. https://doi.org/10.1016/j.ufug.2008.05.001.

Gutsch, M., Lasch-Born, P., Kollas, C., et al., 2018. Balancing trade-offs between ecosystem services in Germany's forests under climate change. Environ. Res. Lett. 13, 045012. https://doi.org/10.1088/1748-9326/aab4e5.

Haberstroh, S., Werner, C., 2022. The role of species interactions for forest resilience to drought. Plant Biol. 24, 1098–1107. https://doi.org/10.1111/plb.13415.

Haines-Young R, Consul F (2023) Common International Classification of Ecosystem Services (CICES) V5.2 Guidance on the Application of the Revised Structure.

Hanbury-Brown, A.R., Ward, R.E., Kueppers, L.M., 2022. Forest regeneration within Earth system models: current process representations and ways forward. New Phytol. 235, 20–40. https://doi.org/10.1111/nph.18131.

Harrison, X.A., Donaldson, L., Correa-Cano, M.E., et al., 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ 2018, 1–32. https://doi.org/10.7717/peerj.4794.

Hartmann, H., Bastos, A., Das, A.J., et al., 2022. Climate change risks to global forest health: emergence of unexpected events of elevated tree mortality worldwide. Annu. Rev. Plant Biol. 73, 673–702. https://doi.org/10.1146/annurev-arplant-102820-012804.

Hegetschweiler, K.T., Plum, C., Fischer, C., et al., 2017. Towards a comprehensive social and natural scientific forest-recreation monitoring instrument—A prototypical approach. Landsc. Urban Plan. 167, 84–97. https://doi.org/10.1016/j.landurbplan.2017.06.002.

Hegetschweiler, K.T., Fischer, C., Moretti, M., Hunziker, M., 2020. Integrating data from National Forest Inventories into socio-cultural forest monitoring – a new approach. Scand. J. For. Res. 35, 274–285. https://doi.org/10.1080/02827581.2020.1799066.

Hengl, T., Mendes De Jesus, J., Heuvelink, G.B.M., et al., 2017. SoilGrids250m: global gridded soil information based on machine learning. PLoS One 12, e0169748. https://doi.org/10.1371/journal.pone.0169748.

Himes, A., Puettmann, K., Muraca, B., 2020. Trade-offs between ecosystem services along gradients of tree species diversity and values. Ecosyst. Serv. 44, 101133. https://doi.org/10.1016/j.ecoser.2020.101133.

Hodgson, D., McDonald, J.L., Hosken, D.J., 2015. What do you mean, 'resilient'? Trends Ecol. Evol. 30, 503–506. https://doi.org/10.1016/j.tree.2015.06.010.

Holling, C.S., 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. 4 (1), 1–23.

Ibáñez, I., Acharya, K., Juno, E., et al., 2019. Forest resilience under global environmental change: do we have the information we need? a systematic review. PLoS One 14, 1–17. https://doi.org/10.1371/journal.pone.0222207.

Ingrisch, J., Bahn, M., 2018. Towards a Comparable Quantification of Resilience. Trends Ecol. Evol. 33, 251–259. https://doi.org/10.1016/j.tree.2018.01.013.

Isbell, F., Craven, D., Connolly, J., et al., 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. Nature 526, 574–577. https://doi.org/10.1038/nature15374.

Jellesmark, S., Ausden, M., Blackburn, T.M., et al., 2021. A counterfactual approach to measure the impact of wet grassland conservation on U.K. breeding bird populations. Conserv. Biol. 35, 1575–1585. https://doi.org/10.1111/cobi.13692.

Jonsson, M., Bengtsson, J., Moen, J., et al., 2020. Stand age and climate influence forest ecosystem service delivery and multifunctionality. Environ. Res. Lett. 15, 0940a8. https://doi.org/10.1088/1748-9326/abaf1c.

Körner, C., 2015. Paradigm shift in plant growth control. Curr. Opin. Plant Biol. 25, 107–114. https://doi.org/10.1016/j.pbi.2015.05.003.

Kuznetsova A, Bruun Brockhoff P, Haubo Bojesen Christensen R (2022) lmerTest: Tests in Linear Mixed Effects Models. 3.1-3.

Liang, M., Baiser, B., Hallett, L.M., et al., 2022. Consistent stabilizing effects of plant diversity across spatial scales and climatic gradients. Nat. Ecol. Evol. 6, 1669–1675. https://doi.org/10.1038/s41559-022-01868-y.

Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. Oikos 120, 1909–1920. https://doi.org/10.1111/j.1600-0706.2011.19372.x.

Lloret, F., Hurtado, P., Espelta, J.M., et al., 2024. ORF, an operational framework to measure resilience in social–ecological systems: the forest case study. Sustain. Sci. 19, 1579–1593. https://doi.org/10.1007/s11625-024-01518-1.

Magliocca, N.R., Dhungana, P., Sink, C.D., 2023. Review of counterfactual land change modeling for causal inference in land system science. J. Land Use Sci. 18, 1–24. https://doi.org/10.1080/1747423X.2023.2173325.

Margalef-Marrase, J., Pérez-Navarro, M.Á., Lloret, F., 2020. Relationship between heatwave-induced forest die-off and climatic suitability in multiple tree species. Glob. Chang. Biol. 26, 3134–3146. https://doi.org/10.1111/gcb.15042.

Martínez-Vilalta, J., Lloret, F., 2016. Drought-induced vegetation shifts in terrestrial ecosystems: the key role of regeneration dynamics. Glob Planet Change 144, 94–108. https://doi.org/10.1016/j.gloplacha.2016.07.009.

Martínez-Vilalta, J., López, B.C., Loepfe, L., Lloret, F., 2012. Stand- and tree-level determinants of the drought response of Scots pine radial growth. Oecologia 168, 877–888. https://doi.org/10.1007/s00442-011-2132-8.

Martínez-Vilalta, J., Sala, A., Asensio, D., et al., 2016. Dynamics of non-structural carbohydrates in terrestrial plants: a global synthesis. Ecol. Monogr. 86, 495–516. https://doi.org/10.1002/ecm.1231.

Martínez-Vilalta, J., Piñol, J., 2002. Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. For Ecol Manag 161, 247–256. https://doi.org/10.1016/S0378-1127(01)00495-9.

McDowell, N.G., Sapes, G., Pivovaroff, A., et al., 2022. Mechanisms of woody-plant mortality under rising drought, CO2 and vapour pressure deficit. Nat. Rev. Earth Environ. 3, 294–308. https://doi.org/10.1038/s43017-022-00272-1.

Mina, M., Bugmann, H., Cordonnier, T., et al., 2017. Future ecosystem services from European mountain forests under climate change. J. Appl. Ecol. 54, 389–401. https://doi.org/10.1111/1365-2664.12772.

Morán-Ordóñez, A., Ameztegui, A., De Cáceres, M., et al., 2020. Future trade-offs and synergies among ecosystem services in Mediterranean forests under global change scenarios. Ecosyst. Serv. 45, 101174. https://doi.org/10.1016/j.ecoser.2020.101174.

Mori, A.S., Furukawa, T., Sasaki, T., 2013. Response diversity determines the resilience of ecosystems to environmental change. Biol. Rev. 88, 349–364. https://doi.org/10.1111/brv.12004.

Mori, A.S., Lertzman, K.P., Gustafsson, L., 2017. Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. J. Appl. Ecol. 54, 12–27. https://doi.org/10.1111/1365-2664.12669.

Myneni, R., Knyazikhin, Y., & Park, T. (2021). *MODIS/Terra+Aqua Leaf Area Index/FPAR 4-Day L4 Global 500m SIN Grid V061* [Data set]. NASA Land Processes Distributed Active Archive Center. https://doi.org/10.5067/MODIS/MCD15A3H.061 Date Accessed: 2024-03-17.

Nikinmaa, L., Lindner, M., Cantarello, E., et al., 2020. Reviewing the use of resilience concepts in forest sciences. Curr. For. Rep. 6, 61–80. https://doi.org/10.1007/s40725-020-00110-x.

Oliveira, B.F., Moore, F.C., Dong, X., 2022. Biodiversity mediates ecosystem sensitivity to climate variability. Commun. Biol. 5, 628. https://doi.org/10.1038/s42003-022-03573-9.

Oliver, T.H., Heard, M.S., Isaac, N.J.B., et al., 2015. Biodiversity and resilience of ecosystem functions. Trends Ecol. Evol. 30, 673–684. https://doi.org/10.1016/j.tree.2015.08.009.

Ouyang, S., Gou, M., Lei, P., et al., 2023. Plant functional trait diversity and structural diversity co-underpin ecosystem multifunctionality in subtropical forests. For. Ecosyst. 10, 100093. https://doi.org/10.1016/j.fecs.2023.100093.

Panagos, P., Meusburger, K., Ballabio, C., et al., 2014. Soil erodibility in Europe: a high-resolution dataset based on LUCAS. Sci. Total Environ. 479–480, 189–200. https://doi.org/10.1016/j.scitotenv.2014.02.010.

Panagos, P., Borrelli, P., Meusburger, K., 2015. A new european slope length and steepness factor (LS-Factor) for modeling soil erosion by water. Geosciences 5, 117–126. https://doi.org/10.3390/geosciences5020117.

Pardos, M., Del Río, M., Pretzsch, H., et al., 2021. The greater resilience of mixed forests to drought mainly depends on their composition: Analysis along a climate gradient across Europe. For Ecol Manag 481, 118687. https://doi.org/10.1016/j.foreco.2020.118687.

Patacca, M., Lindner, M., Lucas-Borja, M.E., Cordonnier, T., Fidej, G., Gardiner, B., Hauf, Y., Jasinevičius, G., Labonne, S., Linkevičius, E., Mahnken, M., Milanovic, S., Nabuurs, G.-J., Nagel, T.A., Nikinmaa, L., Panyatov, M., Bercak, R., Seidl, R., Ostrogović Sever, Jaroslaw Socha, Dominik Thom, Dijana Vuletic, Zudin, Sergey, Mart-Jan Schelhaas, 2023. Significant increase in natural disturbance impacts on European forests since 1950. Global Change Biology 29, 1359–1376. https://doi.org/10.1111/gcb.16531.

Peñuelas, J., Boada, M., 2003. A global change-induced biome shift in the Montseny mountains (NE Spain). Glob. Chang. Biol. 9, 131–140. https://doi.org/10.1046/j.1365-2486.2003.00566.x.

Peñuelas, J., Sardans, J., Filella, I., et al., 2017. Impacts of global change on mediterranean forests and their services. Forests 8, 463. https://doi.org/10.3390/f8120463.

Piñol, J., Lledó, M.J., Escarré, A., 1991. Hydrological balance of two Mediterranean forested catchments (Prades, northeast Spain). Hydrol. Sci. J. 36, 95–107. https://doi.org/10.1080/02626669109492492.

Posit team (2025). RStudio: Integrated Development Environment for R. Posit Software, PBC, Boston, MA. URL http://www.posit.co/.

Pretzsch, H., Forrester, D.I., Rötzer, T., 2015. Representation of species mixing in forest growth models. A Review and Perspective. Ecol Model 313, 276–292. https://doi.org/10.1016/j.ecolmodel.2015.06.044.

Ripley B, Venables B (2024) MASS: Support Functions and Datasets for Venables and Ripley's MASS. 7.3-61.

Roces-Díaz, J.V., Vayreda, J., Banqué-Casanovas, M., et al., 2018. Assessing the distribution of forest ecosystem services in a highly populated Mediterranean region. Ecol. Ind. 93, 986–997. https://doi.org/10.1016/j.ecolind.2018.05.076.

Roces-Díaz, J.V., Vayreda, J., De Cáceres, M., et al., 2021. Temporal changes in Mediterranean forest ecosystem services are driven by stand development, rather than by climate-related disturbances. For Ecol Manag 480, 118623. https://doi.org/10.1016/j.foreco.2020.118623.

Roces-Díaz, J.V., Santín, C., Martínez-Vilalta, J., Doerr, S.H., 2022. A global synthesis of fire effects on ecosystem services of forests and woodlands. Front. Ecol. Environ. 20, 170–178. https://doi.org/10.1002/fee.2349.

Ruiz-Peinado, R., Del Rio, M., Montero, G., 2011. New models for estimating the carbon sink capacity of spanish softwood species. For. Syst. 20, 176–188. https://doi.org/10.5424/fs/2011201-11643.

Ruiz-Peinado, R., Montero, G., Del Rio, M., 2012. Biomass models to estimate carbon stocks for hardwood tree species. For. Syst. 21, 42–52. https://doi.org/10.5424/fs/2112211-02193.

Runting, R.K., Bryan, B.A., Dee, L.E., et al., 2017. Incorporating climate change into ecosystem service assessments and decisions: a review. Glob. Chang. Biol. 23, 28–41. https://doi.org/10.1111/gcb.13457.

Sánchez De Dios, R., DeSoto, L., Cortón, B., Hernández, L., 2023. The renaissance of mixed forests? New insights into shifts in tree dominance and composition following centuries of human-induced simplification of iberian forests. Ecosystems 26, 1159–1172. https://doi.org/10.1007/s10021-023-00823-7.

Sapes, G., Sala, A., 2021. Relative water content consistently predicts drought mortality risk in seedling populations with different morphology, physiology and times to death. Plant Cell Environ. 44, 3322–3335. https://doi.org/10.1111/pce.14149.

Saponaro, V., De Cáceres, M., Dalmonech, D., et al., 2025. Assessing the combined effects of forest management and climate change on carbon and water fluxes in European beech forests. For. Ecosyst. 12, 100290. https://doi.org/10.1016/j.fecs.2024.100290.

Schmitt, S., Maréchaux, I., Chave, J., et al., 2020. Functional diversity improves tropical forest resilience: insights from a long-term virtual experiment. J. Ecol. 108, 831–843. https://doi.org/10.1111/1365-2745.13320.

Schwaiger, F., Poschenrieder, W., Biber, P., Pretzsch, H., 2019. Ecosystem service trade-offs for adaptive forest management. Ecosyst. Serv. 39, 100993. https://doi.org/10.1016/j.ecoser.2019.100993.

Seidl, R., Spies, T.A., Peterson, D.L., et al., 2016. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. J. Appl. Ecol. 53, 120–129. https://doi.org/10.1111/1365-2664.12511.

Seidl, R., Thom, D., Kautz, M., et al., 2017. Forest disturbances under climate change. Nat. Clim. Chang. 7, 395–402. https://doi.org/10.1038/nclimate3303.

Selwyn, M., Pino, J., Espelta, J.M., 2024. Recent tree diversity increase in NE Iberian forests following intense management release: a task for animal-dispersed and drought-tolerant species. J. Appl. Ecol. 61, 1029–1040. https://doi.org/10.1111/1365-2664.14609.

Senf, C., Buras, A., Zang, C.S., et al., 2020. Excess forest mortality is consistently linked to drought across Europe. Nat. Commun. 11, 6200. https://doi.org/10.1038/s41467-020-19924-1.

Serra-Maluquer, X., Mencuccini, M., Martínez-Vilalta, J., 2018. Changes in tree resistance, recovery and resilience across three successive extreme droughts in the northeast Iberian Peninsula. Oecologia 187, 343–354. https://doi.org/10.1007/s00442-018-4118-2.

Sing, L., Metzger, M.J., Paterson, J.S., Ray, D., 2018. A review of the effects of forest management intensity on ecosystem services for northern European temperate forests with a focus on the UK. For Int J for Res 91, 151–164. https://doi.org/10.1093/forestry/cpx042.

Sperry, J.S., Adler, F.R., Campbell, G.S., Comstock, J.P., 1998. Limitation of plant water use by rhizosphere and xylem conductance: results from a model. Plant Cell Environ. 21, 347–359. https://doi.org/10.1046/j.1365-3040.1998.00287.x.

Sperry, J.S., Venturas, M.D., Anderegg, W.R.L., et al., 2017. Predicting stomatal responses to the environment from the optimization of photosynthetic gain and hydraulic cost. Plant Cell Environ. 40, 816–830. https://doi.org/10.1111/pce.12852.

Spinoni, J., Vogt;, J.V., Naumann, G., et al., 2018. Will drought events become more frequent and severe in Europe? Int. J. Climatol. 38, 1718–1736. https://doi.org/10.1002/joc.5291.

Thom, D., Seidl, R., 2016. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. Biol. Rev. 91, 760–781. https://doi.org/10.1111/brv.12193.

Toreti, A., Bavera, D., Acosta Navarro, J., Acquafresca, L., Azas, K., Barbosa, P., de Jager, A., Ficchì, A., Fioravanti, G., Grimaldi, S., Hrast Essenfelder, A., Magni, D., Mazzeschi, M., McCormick, N., Salamon, P., Santos Nunes, S., Volpi, D., 2024. Drought in Europe: July 2024: GDO analytical repor. Publications Office, LU.

Tramblay, Y., Koutroulis, A., Samaniego, L., et al., 2020. Challenges for drought assessment in the Mediterranean region under future climate scenarios. Earth Sci. Rev. 210, 103348. https://doi.org/10.1016/j.earscirev.2020.103348.

van Wees, D., Van Der Werf, G.R., Randerson, J.T., et al., 2021. The role of fire in global forest loss dynamics. Glob. Chang. Biol. 27, 2377–2391. https://doi.org/10.1111/gcb.15591.

Vayreda, J., Martinez-Vilalta, J., Gracia, M., et al., 2016. Anthropogenic-driven rapid shifts in tree distribution lead to increased dominance of broadleaf species. Glob. Chang. Biol. 22, 3984–3995. https://doi.org/10.1111/gcb.13394.

Veuillen, L., Simioni, G., De Cáceres, M., et al., 2026. Thinning enhances hydraulic safety but not growth resistance to drought in Atlas cedar on the long-term. Agric. For. Meteorol. 378, 111019. https://doi.org/10.1016/j.agrformet.2026.111019.

Yi, C., Jackson, N., 2021. A review of measuring ecosystem resilience to disturbance. Environ. Res. Lett. 16, 053008. https://doi.org/10.1088/1748-9326/abdf09.

Zheng, T., Martínez-Vilalta, J., García-Valdés, R., et al., 2021. Disentangling biology from mathematical necessity in twentieth-century gymnosperm resilience trends. Nat. Ecol. Evol. 5, 733–735. https://doi.org/10.1038/s41559-021-01436-w.

Zheng, T., Martínez-Vilalta, J., García-Valdés, R., et al., 2023. Growth plasticity of conifers did not avoid declining resilience to soil and atmospheric droughts during the 20th century. For. Ecosyst. 10, 100107. https://doi.org/10.1016/j.fecs.2023.100107.