Drought, fire and grazing precursors to large-scale pine forest decline

Simon E Connor, João Araújo, Tomasz Boski, Ana Gomes, Sandra D Gomes, Manel Leira, Maria da Conceição Freitas, Cesar Andrade, César Morales-molino, Fátima Franco-múgica, et al.

Received: 4 October 2020 | Revised: 25 January 2021 | Accepted: 4 February 2021

DOI: 10.1111/ddi.13261

BIODIVERSITY RESEARCH

Diversity and Distributions WILEY

Drought, fire and grazing precursors to large-scale pine forest decline

Simon E. Connor[1,2,3] | João Araújo[4] | Tomasz Boski[1] | Ana Gomes[1,5] | Sandra D. Gomes[6,7] | Manel Leira[8] | Maria da Conceição Freitas[8] | Cesar Andrade[8] | César Morales-Molino[9] | Fátima Franco-Múgica[10] | Rufus B. Akindola[11] | Boris Vannière[2,12]

[1]Centro de Investigaçao Marinha e Ambiental (CIMA), Universidade do Algarve, Faro, Portugal

[2]MSHE Ledoux, CNRS, Université Bourgogne Franche-Comté, Besançon, France

[3]School of Culture, History and Language, College of Asia and the Pacific, Australian National University, Canberra, ACT, Australia

[4]Instituto Português do Mar e da Atmosfera (IPMA), Estação Piloto de Piscicultura de Olhão, Olhão, Portugal

[5]Interdisciplinary Centre for Archaeology and Evolution of Human Behaviour (ICArEHB), Universidade do Algarve, Faro, Portugal

[6]Quaternary Environments and Geoarchaeology, Department of Geography, School of Environment, Education and Development, The University of Manchester, Manchester, UK

[7]Divisão de Geologia Marinha (DivGM), Portuguese Institute for Sea and Atmosphere (IPMA), Lisbon, Portugal

[8]Faculdade de Ciências, Instituto Dom Luiz (IDL), Universidade de Lisboa, Lisboa, Portugal

[9]Institute of Plant Sciences and Oeschger Centre for Climate Change Research, University of Bern, Bern, Switzerland

[10]Departamento de Ecología, Facultad de Ciencias, Universidad Autónoma de Madrid, Madrid, Spain

[11]Faculty of Social Sciences, Federal University Oye-Ekiti, Oye, Nigeria

[12]CNRS, Chrono-environnement UMR 6249, MSHE USR 3124, Université Bourgogne Franche-Comté, Besançon, France

Correspondence
Simon E. Connor, School of Culture, History and Language, College of Asia and the Pacific, Australian National University, Canberra, ACT, Australia.
Email: Simon.Connor@anu.edu.au

Funding information
This work was performed for Project SWIRL (PTDC/AAC-CLI/108518/2008), funded by the Portuguese Science Foundation (FCT), with additional support from the Région Bourgogne Franche-Comté and the MSHE Claude-Nicolas Ledoux.

Editor: José Brito

Abstract

Aim: Temperate forests are currently facing multiple stresses due to climate change, biological invasions, habitat fragmentation and fire regime change. How these stressors interact with each other influences how, when and whether ecosystems recover, or whether they adapt or transition to a different ecological state. Because forest recovery or collapse may take longer than a human lifetime, predicting the outcomes of different stressor combinations remains difficult. A clearer vision of future forest trajectories in a changing world may be gained by examining collapses of forests in the past. Here, we use long-term ecological data to conduct a *post-mortem* examination of the decline of maritime pine forests (*Pinus pinaster* Ait.) on the SW Iberian Peninsula 7000–6500 years ago.

Location: Portugal and Spain.

Methods: We compared four palaeoecological records—two with pine declines and two without—using a multiproxy approach. Bioclimatic differences between the four sites were explored. Proxies for past vegetation and disturbance (fire and grazing)

were compared with independent palaeoclimatic records. We performed functional traits analysis and used phase plots to examine the causes of pine decline.

Results: The pine decline represents a critical transition in SW Iberia, which lies close to maritime pine's bioclimatic limits. Prolonged drought likely killed trees and suppressed the fires that normally stimulate pine germination and pinewood recovery. Increased grazing pressure facilitated the rapid spread of resprouter shrubs. These competed with pine trees and ultimately replaced them. Our data highlight complex interactions between climate, fire, grazing and forest resilience.

Main Conclusions: The pine decline occurred at least a century after post-fire resprouters overtook obligate seeders in the vegetation, constituting an early-warning signal of forest loss. Fire suppression, resprouter encroachment and grazing may threaten the persistence of Mediterranean forests as droughts become more frequent and extreme.

KEYWORDS

fire regime change, forest dynamics, functional traits analysis, palaeoecology, phase plots, tipping point

1 | INTRODUCTION

In the current era of rapid environmental change, ecosystems are under stress on various fronts. Climate change, biological invasions, habitat fragmentation and fire regime change are among the most critical stressors (Slingsby et al., 2017; Trumbore et al., 2015; Turco et al., 2018). Ecological outcomes of multiple interacting stressors are challenging to predict, as these may be greater, less or equal to the sum of the effects (Batllori et al., 2017; Côté et al., 2016; Enright et al., 2014; Foster et al., 2016). Adding to this challenge are the long-term legacies of multiple stressors—those whose ecological effects are only realized decades to millennia later (Essl et al., 2015; Kelly et al., 2011). Observations over short time series may only tell part of the story, especially concerning forest ecosystems in which long-lived species play key functional roles and recovery times are slow (Gonzalez et al., 2016; Taranu et al., 2018; Trumbore et al., 2015; Willis et al., 2018).

Ecological disturbances in forests can precipitate permanent state shifts to shrublands (Enright et al., 2015; Karavani et al., 2018; Willis et al., 2010). Fire-induced deforestation is of particular concern for conifer forests, given their high flammability and their economic and cultural values as global carbon sinks and sources of timber, resins and edible fungi (Abad Viñas et al., 2016; Whitman et al., 2019). In the Mediterranean region, pine forests may permanently shift to shrublands when (a) damage to trees and seedbanks is fatal, (b) no mature trees are present nearby to initiate recovery and (c) replacement resprouting tree species are absent (Karavani et al., 2018). Fire and drought are considered the two most critical disturbance agents driving this process, both having strong selective effects on plant traits (Batllori et al., 2017; Berdugo et al., 2020; Karavani et al., 2018; Seidl et al., 2017). Interactions between fire and drought are complex. Drought tends to increase the probability of fire in high-biomass vegetation, while it reduces fire probability in low-biomass systems (Frejaville & Curt, 2015; Pausas & Paula, 2012; Pausas & Ribeiro, 2013).

Post-fire vegetation recovery is influenced by plant functional traits and the prevailing weather conditions. Drought conditions following a fire may delay recovery where the species pool is composed of obligate seeders, but even resprouters may suffer exhaustion under such conditions (Karavani et al., 2018; Parra & Moreno, 2018). Soil type, grazing, pathogens and seed predation further complicate recovery trajectories (Baeza et al., 2007; Foster et al., 2016; Pausas, 2004; Vega et al., 2011).

The complexity of these interactions requires multiple-stressor models to forecast ecosystem responses to environmental change. Validation of these models is a major challenge, as observational records tend to encompass shorter time frames than the fire- and drought-frequency parameters currently being modelled (Barros et al., 2018; Batllori et al., 2017; Mouillot et al., 2002). Without empirical validation, models may be difficult to apply to real-world conservation and management problems (Côté et al., 2016).

In this paper, we analyse multiple stressors acting on the long-lived tree species *Pinus pinaster* Ait. (maritime pine). *P. pinaster* is the most widespread conifer on the Iberian Peninsula and of major economic importance (Prieto-Recio et al., 2015; Torres et al., 2016). It possesses traits linked to frequent fire occurrence, including thick bark, high rates of post-fire seedling emergence and production of serotinous cones (Tapias et al., 2004; Tavşanoğlu & Pausas, 2018). These traits are traded off in different populations, with resistance traits (thick bark) characteristic of the Western or Atlantic populations, and recovery (serotiny) and resilience (drought tolerance) traits prominent in the Eastern or Mediterranean populations (Tapias

et al., 2004; Zas et al., 2020). *P. pinaster* distribution ranges from sea level to 2,100 m along a rainfall gradient from 350 to 1,400 mm p.a. (Alía & Martín, 2003).

Many *P. pinaster* populations are suffering from drought- and fire-induced stress and, in some cases, mortality (Bravo-Oviedo et al., 2006; Garcia-Gonzalo et al., 2011; Navarro-Cerrillo et al., 2018; Prieto-Recio et al., 2015; Vega et al., 2011). Maritime pine ecosystems require specific fire regimes to maintain ecological health and secure them from extreme fires (Fernandes & Rigolot, 2007). However, increasingly frequent and extreme fires in maritime pine forests have prompted concern about their long-term viability and ecological functioning (Fernandes et al., 2010, 2016; Maia et al., 2012; Mouillot et al., 2002; Torres et al., 2016).

Maritime pine is a good candidate for assessing the impact of multiple stressors over long time-scales, as its distribution was much greater in the past (Carrión et al., 2000; Figueiral, 1995; García-Amorena et al., 2007; Morales-Molino et al., 2012; Salvador et al., 2000). The mid-Holocene "pine decline" (Mateus, 1992) represents an abrupt tipping point in maritime pine's historical abundance and range. The replacement of pine forests by heathlands and other vegetation types is replicated in numerous palaeorecords across SW Iberia, representing hundreds of kilometres of coastline and several major river valleys (Figure 1, see Appendix S1.1; Mateus, 1992, Mateus & Queiroz, 1993, Queiroz, 1999, Santos & Sánchez Goñi, 2003, Queiroz & Mateus, 2004, Vis, 2009, Schneider et al., 2016). The timing of this event centres on 7000–6500 cal. years BP (Before Present, relative to 1950 AD). Pine decline led to structural and functional shifts in vegetation, with heathlands and maquis vegetation substituting forests, often permanently (Queiroz & Mateus, 2004; Santos & Sánchez Goñi, 2003).

The pine decline is a critical transition in the Holocene vegetation history of the Western Mediterranean, yet its drivers are debated. In Portugal, pine decline is linked to progressive aridification (Mateus, 1992; Mateus & Queiroz, 1993; Queiroz, 1999; Santos & Sánchez Goñi, 2003; Schneider et al., 2016; Vis, 2009), coastline retreat (Mateus, 1992) and human impacts (Daveau, 1988; Mateus, 1992; Schneider et al., 2016). In SE Spain, pine declines are attributed to ecological threshold responses to interspecific competition, with extrinsic drivers such as climate considered of secondary importance (Carrión et al., 2001, 2003, 2010). Most palaeoecological studies to date have been unable to interrogate the roles of fire, grazing, drought and interspecific competition, due to a lack of proxies for these key processes in Mediterranean pine forest dynamics (Batllori et al., 2017; Fernandes & Rigolot, 2007; Karavani et al., 2018).

Here, we re-examine the causes of pine decline in the light of robust indicators for fire, grazing, drought and plant functional traits. We hypothesize that interactions between functional traits and disturbance regimes govern long-term forest resilience and recovery. Major changes to disturbance regimes and/or community-level functional trait assemblages could lead to a loss of forest resilience and permanent state shifts from forest to heathland. To test this, we compare a new multiproxy record with three previous sequences that reflect stand-scale dynamics to reconstruct functional traits and their interactions with disturbance regimes at contrasting sites. We also predict that the ecological impacts of disturbance regime change are mitigated by local bioclimate. To assess this, we analyse pine trajectories and climatic variables to find differences between pine decline sites and areas of pine forest continuity. This study contributes to an understanding of multiple-stressor combinations that herald forest collapse and discusses how such collapses may be avoided.

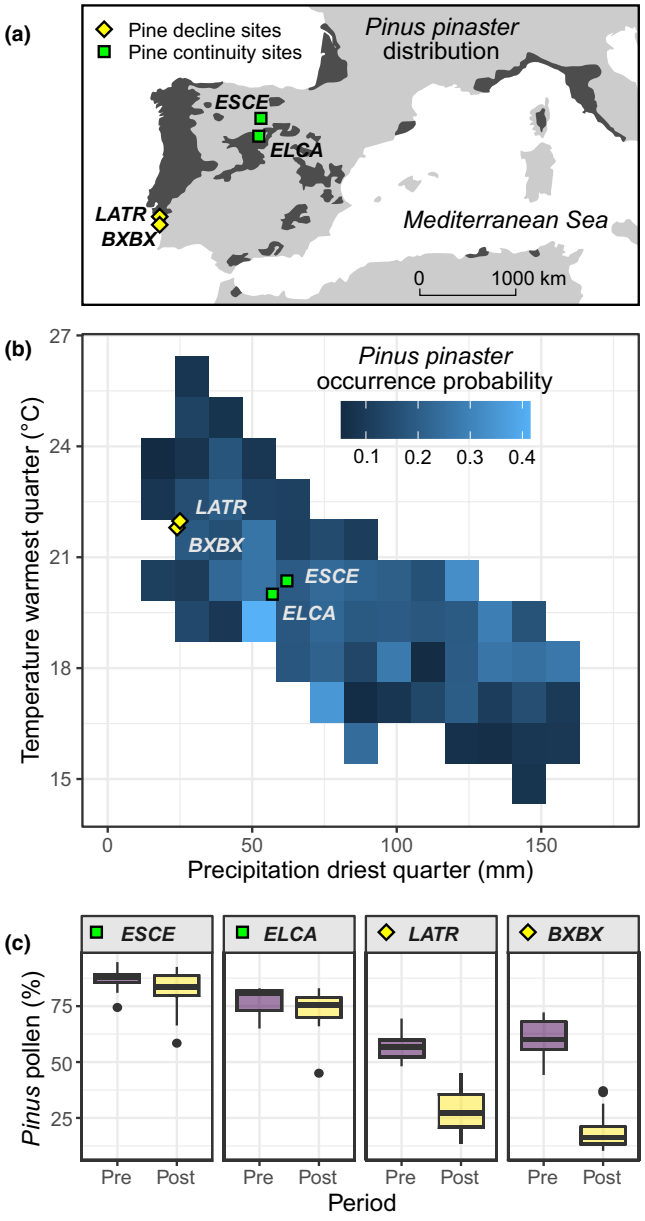

FIGURE 1 (a) Map of *Pinus pinaster's* distribution (shaded) and the study sites mentioned in the text (ESCE—Espinosa de Cerrato; ELCA—El Carrizal; LATR—Lagoa Travessa; BXBX—Barbaroxa de Baixo); (b) bioclimate of *P. pinaster* on the Iberian Peninsula (Abad Viñas et al., 2016; Appendix S1.1), showing the position of the four study sites in relation to dry season precipitation and warm season temperatures; (c) *Pinus* pollen percentages in the four palaeoecological records before and after the greatest decrease in pine pollen during the mid-Holocene

2 | METHODS

2.1 | Study area

We selected four study sites for comparison—two sites with pine continuity and two with evidence of pine decline during the mid-Holocene (8,200–4,200 cal. yr BP, Figure 1a). The continuity sites are Espinosa de Cerrato (ESCE) and El Carrizal (ELCA), located in the Spanish Northern Meseta (Franco Múgica et al., 2001, Franco-Múgica et al., 2005; Morales-Molino et al., 2012, 2017). *Pinus pinaster* was once dominant at ELCA and present among *P. nigra*-dominated vegetation at ESCE (Morales-Molino et al., 2017). The two pine decline sites are Lagoa Travessa (LATR, Mateus, 1992) and a new site, Barbaroxa de Baixo (BXBX, 38.0790N, 8.8098W), both located on the Alentejo coast south of Lisbon (see Appendices S1.1–3). The four sites were selected with attention to factors that influence the source and fidelity of proxy data (Jacobson & Bradshaw, 1981; Whitlock & Larsen, 2001). To address the aim, the sites had to: (a) be small enough to record ecosystem dynamics at a local to extra-local (stand) scale; (b) have minimal stream inflow and slope run-off that could introduce material from beyond the local area; (c) contain sediments that have accumulated continuously and rapidly to ensure an unbroken record with complete fossilization.

2.2 | Bioclimatic analysis

To contextualize pine decline versus continuity sites in terms of *P. pinaster's* bioclimatic envelope on the Iberian Peninsula, we extracted key bioclimatic variables from the WorldClim dataset (Fick & Hijmans, 2017, Appendix S1.3) using a *P. pinaster* occurrence probability map (Abad Viñas et al., 2016, Appendix S1.1). These analyses were performed using the "rgdal" and "raster" packages in R (Bivand et al., 2019; Hijmans, 2020; R Core Team, 2020).

2.3 | Sample collection and analysis

Sedimentary records from wetlands were used to reconstruct mid-Holocene environmental change. Sediment cores were retrieved using a Russian corer (ESCE, ELCA), a Dachnowsky corer (LATR) and a Livingstone corer (BXBX). The cores were dated radiometrically to develop absolute chronologies. Dates were obtained from macrofossils (ESCE, BXBX) or bulk sediment (ELCA, LATR). Age–depth models were based on accelerator mass spectrometer (AMS) dates for three of the sites (ESCE, ELCA and BXBX). The BXBX age–depth model was constructed in OxCal 4.1.7 using Markov chain Monte Carlo modelling (Bronk Ramsey, 2009). Further details are given in Mateus (1989), Franco Múgica et al., (2001), Franco-Múgica et al., (2005), Morales-Molino et al., (2017) and Appendices S1.4–6.

Pollen, an indicator of past vegetation, was extracted from the sediments using standard acetolysis-based techniques (Moore et al., 1991). Pollen was identified using regional guides (listed in Appendix S1.3). Particular attention was paid to the identification of Ericaceae and Cistaceae pollen, following morphological criteria developed by Queiroz (1999) and Mateus (1989).

Disturbance indicators help to improve interpretation of vegetation change. Changes in grazing pressure are based on coprophilous fungal spores (i.e. *Apiosordaria*, *Cercophora*, *Coniochaeta*, *Podospora*, *Sordaria*, *Sporormiella*: van Geel & Aptroot, 2006). Fire history is based on charcoal particles. A local-scale fire history based on macroscopic charcoal (particles > 150 μm) was developed at BXBX, with contiguous samples extracted by sieving (Whitlock & Larsen, 2001). Microscopic charcoal sequences are also available for three of the sites (ESCE, ELCA and BXBX), quantified following Finsinger and Tinner (2005). Charcoal records are considered robust indicators of biomass burned and fire episode frequency (Ali et al., 2012). Methods to reconstruct other key aspects of fire regimes (intensity, severity and seasonality) from charcoal are still under development.

2.4 | Numerical analyses

To reconstruct a mid-Holocene fire history for BXBX, charcoal accumulation rates (CHAR) were calculated and normalized to z-scores following Power et al., (2008). For the macroscopic charcoal record, fire peaks related to local fire episodes were separated from the "background" using a 500-year lowess smoother in CharAnalysis (Higuera et al., 2009). Background charcoal reflects long-term changes in charcoal production and dispersal (Whitlock & Larsen, 2001) and approximates the amount of biomass that has been burned over time (Vannière et al., 2016).

Possible drivers of fire activity were examined by comparing the BXBX charcoal record with regional palaeoclimatic records (Cacho et al., 1999, 2001; Rodrigues et al., 2009; Thatcher et al., 2020), local changes in geochemistry and diatom assemblages (Cruces, 2015, Leira et al., 2019), and lake level variations at BXBX. The latter were derived from detrended correspondence analysis of aquatic and wetland indicators, classified as deep-water limnic, shallow-water telmatic and semi-terrestrial taxa based on modern analogues (Queiroz, 1999).

Functional traits are key to understanding ecosystem resilience and responses to multiple stressors (Batllori et al., 2017; Enright et al., 2014). Integration of plant functional traits and palaeoecological data provides unique long-term insights into vegetation–disturbance interactions (Brussel et al., 2018). We assigned trait scores to pollen taxa to permit interpretation of the pollen sequences in terms of plant functional traits (Barboni et al., 2004; Brussel et al., 2018). Trait scores were derived from Iberian records in the BROT2 database (Tavşanoğlu & Pausas, 2018). Selected traits were growth form, post-fire regeneration strategy, spinescence and taxonomic class, representing a range of adaptations to fire, drought and grazing (Brussel et al., 2018; Hanley et al., 2007; Tavşanoğlu & Pausas, 2018). Taxa were included if they were: (a) easily determined to species or genus level and attributable to one/few plant species; (b) sufficiently abundant in the pollen record to represent population

dynamics; (c) representative of plants in the site's vicinity (in the case of well-dispersed *Pinus* and *Juniperus* pollen, conifer stomata or macrofossils are reliable indicators of local presence: Ammann et al., 2014); and (d) unambiguously associated with terrestrial vegetation. Observed traits were compared with 1,000 null models in which traits were randomly assigned to each of the pollen taxa (Brussel et al., 2018).

Resilience indicators were examined in each of the four records to understand whether the pine decline represents a critical transition. Standard deviation is considered an appropriate resilience indicator for palaeoecological data with uneven temporal sampling (Stegner et al., 2019). The standard deviation of pine pollen sequences was analysed in R using code provided in Stegner et al., (2019) and assessed with Kendall's tau, a nonparametric correlation statistic (Dakos et al., 2010).

Phase plots illustrate interactions between a system's ecological state and environmental drivers (Davies et al., 2018; Willis et al., 2010). Here, we used phase plots to examine the causes of pine decline, comparing *Pinus* pollen percentages with rates of change, climate, fire and grazing proxies.

3 | RESULTS

3.1 | Pinus pinaster bioclimate

Analysis of *P. pinaster* distribution compared with bioclimatic variables shows that the two pine decline sites, LATR and BXBX, occupy the lower limit of the species' current range in terms of dry season precipitation (Figure 1b). This contrasts with the more central position of ELCA and ESCE sites within or near the Spanish *Tierra de Pinares*, where pollen and macrofossil data indicate pine forest continued uninterrupted through the mid-Holocene (Franco Múgica et al., 2001; Franco-Múgica et al., 2005; Morales-Molino et al., 2012, 2017).

3.2 | Chronology

Organic sedimentation in BXBX began around 7,250 cal. BP and accumulated at approximately 1 mm/year until 5,350 cal. BP (Appendix S1.5). Thereafter, sediment accumulation is affected by a regional phenomenon, the Lagoa Travessa hiatus, which represents the desiccation of Portuguese interdunal lakes approx. 4000–3000 cal. year BP (Leira et al., 2019; Mateus, 1992; Queiroz & Mateus, 2004). Our analysis therefore focusses on the pre-hiatus period of the mid-Holocene.

3.3 | Pollen (vegetation)

The most prominent feature of the pine decline sites is the pine decline itself (Figure 1c) and subsequent expansion of shrub taxa

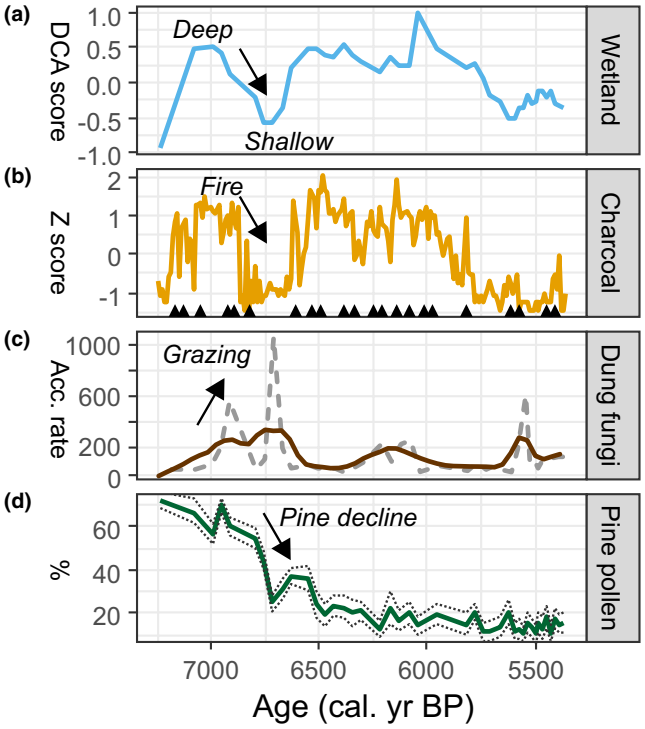

FIGURE 2 Temporal trends in principal proxies of the BXBX palaeoecological record: (a) wetland taxa ordination scores (DCA axis 1); (b) macroscopic charcoal abundance expressed as z-scores (line) and significant charcoal peaks (triangles, see Appendix S1.10); (c) combined abundance of grazing indicators (*Apiosordaria*, *Cercophora*, *Coniochaeta*, *Podospora*, *Sordaria*, *Sporormiella*) shown as fungal spore accumulation rates (spores/cm^2/year) for raw (dashed line) and lowess-smoothed data (solid line); (d) pine pollen percentages with 95% confidence intervals. See Appendices S1.7–9 for complete pollen, spore and charcoal records

(*Erica scoparia*, *Corema album* and *Juniperus*—see Appendix S1.7). At BXBX, the better dated of the two pine decline sites, pine pollen percentages decreased from 60% to 25% in the 200 years between 6,915 and 6,715 cal. BP (Figure 2). Pine pollen accumulation rates declined from 2040 to 850 grains cm^{-2} year^{-1}. A comparable decline occurs at LATR between 7,000 and 6,000 cal. yr BP, whereas no significant change in median *Pinus* values occurs at the other sites (Figure 1c).

Pine's local presence prior to the pine decline is attested by well-preserved pine needles with stomatal structure characteristic of *P. pinaster* (Salvia García Álvarez pers. comm., Álvarez et al., 2009) in BXBX sediments dated 7,240—6,940 cal. BP (photograph in Appendix S1.6), along with conifer stomata at various depths (see Appendix S1.9). Pine pollen is a robust proxy for pine plant abundance in the landscape (Appendices S1.3, 12, 13).

3.4 | Disturbance indicators (grazing, fire)

At BXBX, fungal indicators of grazing (van Geel and Aptroot, 2006) increase around 7,000 cal. BP and reach their maximum around 6,700 cal. BP before declining (Figure 2).

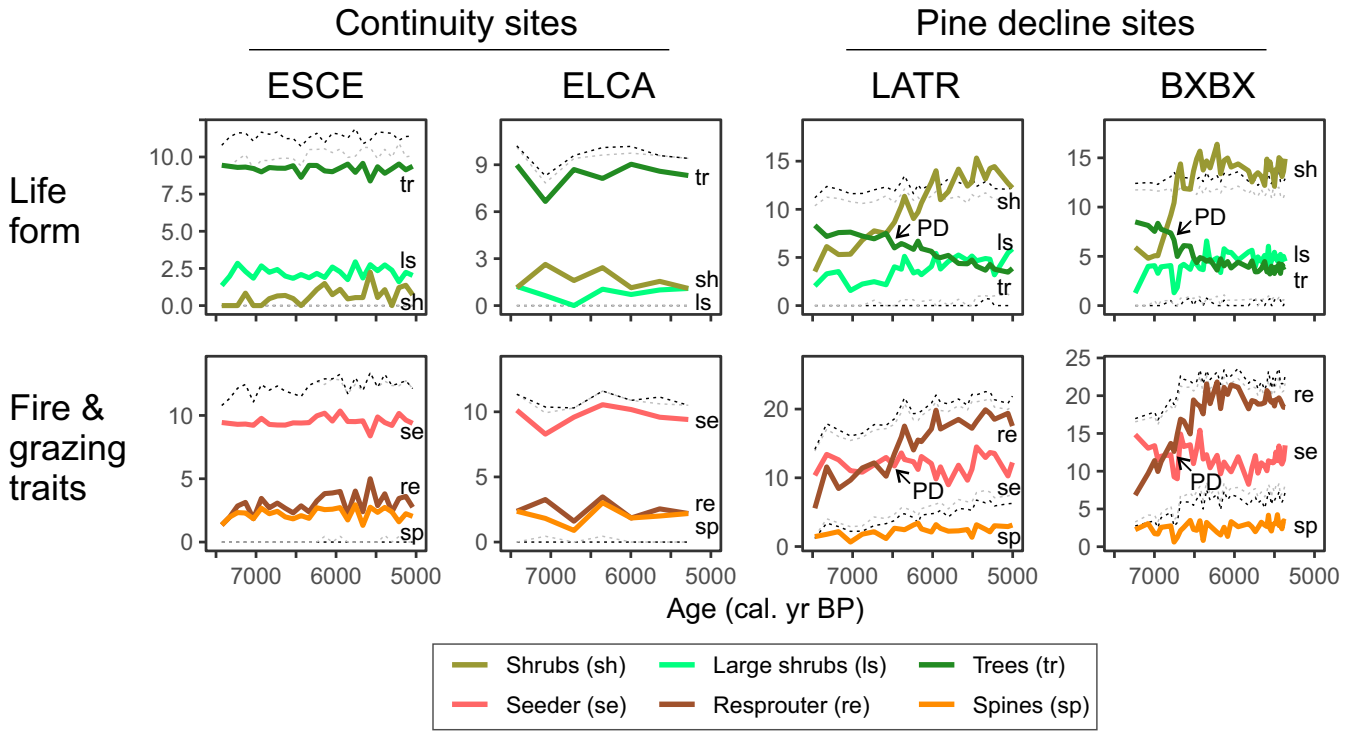

FIGURE 3 Traits analysis of the palaeoecological records with 90% and 95% confidence intervals derived from bootstrapping (dotted lines; see Brussel et al., 2018). Upper panels: life-form (plant height). Lower panel: post-fire regeneration strategy (ability to resprout or re-emerge as seedlings after fire) and spinescence. PD: pine decline

The local fire proxy, macroscopic charcoal, has an average sampling resolution of 10 years and is the most abundant during two phases: 7180–6825 and 6615–5825 cal. BP (Figure 2). Peak analysis of macroscopic charcoal yielded an average fire return interval of approximately 80 years in the early part of the record, with a decreasing frequency after 6,300 cal. BP. The longest fire-free interval was approx. 210 years (6825–6615 cal. BP) and the shortest 30 years (6925–6895 cal. BP; Figure 2). Extended fire-free intervals after 6,000 cal. BP are accompanied by the highest representation of fire-sensitive *Juniperus* (Appendix S1.7). Longer fire-free intervals in the late Holocene are not considered here (see Appendix S1.7).

Detrended correspondence analysis (DCA) of BXBX wetland indicators (Appendix S1.8) weighted limnic taxa positively on axis 1 (e.g. *Pediastrum* algae and *Nymphaea alba* pollen) and semi-aquatic and telmatic taxa negatively (e.g. *Hydrocotyle*, Cyperaceae, *Hypericum elodes*). The DCA trend shows strong affinities with regional precipitation changes in isotopic records, local hydrological changes and fire history (Figure 2, Appendix S1.11). The latter is highly correlated with the DCA result (Spearman's rho: 0.73, $p < .001$).

3.5 | Trait scores

Reconstructed functional trait scores for the four sites appear in Figure 3. Life-form traits showed strong non-random selection at the two pine decline sites, with shrub abundance exceeding 95% confidence intervals (CIs) of the null models after the pine decline. No evidence of non-random selection is apparent at the pine continuity sites. Pine declines occurred after resprouters became more abundant than obligate seeders at BXBX and Lagoa Travessa (Figure 3). Spinescence also exhibited non-random selection at LATR and BXBX, particularly after the pine decline.

3.6 | Resilience analyses

Pine decline is associated with a significant change in resilience statistics at both BXBX and LATR (Kendall's τ: >0.50, $p < .0001$; Table 1). No significant change is recorded at the pine continuity sites.

Pine decline sites experienced rapid rates of change during the decline compared with continuity sites (Figure 4a). Precursors of the pine decline include a temporary reduction in regional precipitation, a decrease in local fire activity and an increase in grazing indicators (Figure 4b–d).

TABLE 1 Testing for a critical transition in each of the palaeorecords around 6,750 cal. yr BP. Sites listed in N–S order

	Pine continuity sites		Pine decline sites	
Site code	**ESCE**	**ELCA**	**LATR**	**BXBX**
Kendall's tau	−0.05	−0.15	0.51	0.59
p-value	.4687	.2263	**<.0001**	**<.0001**

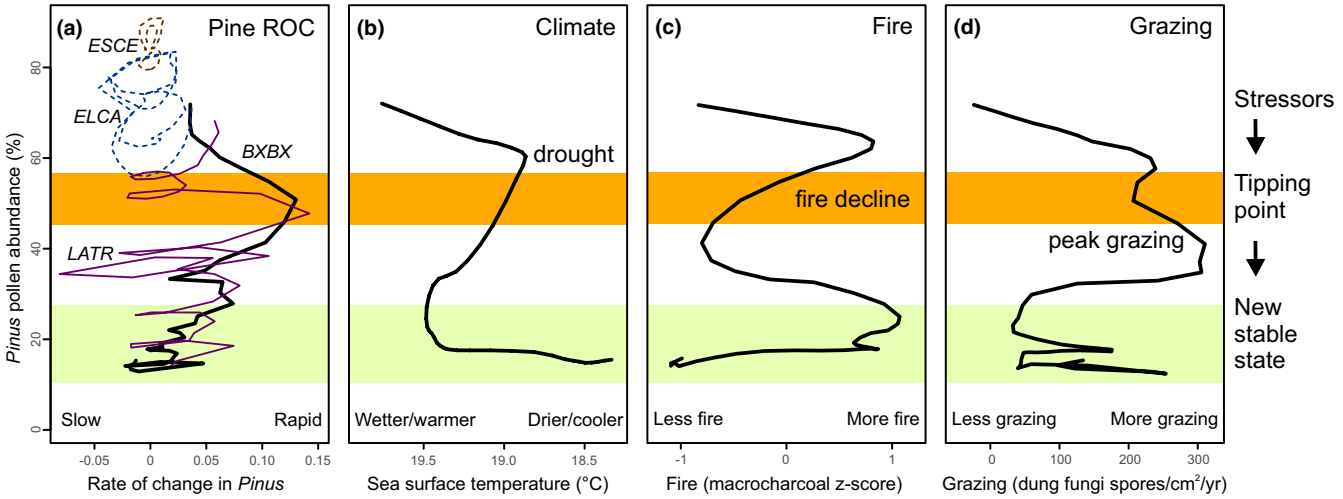

FIGURE 4 Phase plots showing (a) pine rate of change (ROC) with the rapid decline of *Pinus* pollen at pine decline sites (solid lines) compared with pine continuity sites (dashed lines); (b–d) driver–response relationships in the BXBX record (smoothed curves). Sea-surface temperatures from Rodrigues et al., (2009)

4 | DISCUSSION

4.1 | Causes of the pine decline

Pine decline represents a critical transition in the ecological history of the Western Mediterranean (Table 1). A combination of drought, fire suppression, interspecific competition and the expansion of grazing appears to have driven pine decline in SW Iberia during the mid-Holocene. These drivers had greater effect in SW Iberia as this location lies close to the bioclimatic limits for *Pinus pinaster* compared with the Spanish Northern Meseta (Figure 1). It is probable that the SW Iberian populations were also more drought sensitive than the Spanish populations (Zas et al., 2020).

4.2 | Drought

Drought stress is regarded as a key predictor of mortality in Iberian *P. pinaster* stands in the present day (Navarro-Cerrillo et al., 2018; Prieto-Recio et al., 2015). Droughts cause stem contraction in *P. pinaster*, and the trees enter a quiescent state (Vieira et al., 2013). In this state, prolonged and/or severe droughts lead to carbon starvation, increased susceptibility to pathogen attack, and eventually hydraulic failure and tree mortality (McDowell et al., 2008). In SW Iberia during the mid-Holocene, a multidecadal drought is clearly registered in marine and terrestrial isotopic records between 7,000 and 6,500 cal. BP (Appendix S1.11, Cacho et al., 1999, 2001, Rodrigues et al., 2009, Thatcher et al., 2020), including strong indications of low water levels at BXBX (Figure 2, Cruces, 2015, Leira et al., 2019). We suggest that this drought was sufficient to kill pines at the climatically sensitive limits of their range.

Our hypothesis that multidecadal drought drove pine decline, rather than a long-term aridification trend, contrasts with previous interpretations (Jalut et al., 2000). Aridification, coastal retreat, human impacts and estuarine dynamics have been invoked as extrinsic drivers of the mid-Holocene pine decline in Portugal (Mateus, 1992; Queiroz, 1999; Santos & Sánchez Goñi, 2003; Schneider et al., 2016; Vis, 2009). However, interpretations that rely on coastal processes are difficult to uphold as mid-Holocene pine declines are also recorded in Portugal's hinterlands and uplands (Connor et al., 2012; van der Knaap & van Leeuwen, 1995; Vis, 2009). Mid-Holocene pine declines in SE Spain, involving several *Pinus* species, have been explained by intrinsic processes: threshold ecological responses to fire regime changes and interspecific competition (Carrión et al., 2001, 2003, 2010; Carrión & van Geel, 1999).

4.3 | Fire regime change

The failure of SW Iberian *P. pinaster* populations to recover after the end of the drought suggests that fire and competition factors came into play. Ecological models conceptualize fire as a key driver of deforestation in the Mediterranean region (Baeza et al., 2007; Batllori et al., 2017; Karavani et al., 2018; Mouillot et al., 2002) and in Mediterranean-type ecosystems globally (Bowman et al., 2013; Enright et al., 2015). Fire-induced deforestation is also implicated in the creation and persistence of many European heathlands (van der Knaap & van Leeuwen, 1995; Loidi et al., 2010; López-Merino et al., 2012; Odgaard, 1992; Odgaard & Rasmussen, 2000). Our data provide another possibility-that fire deprivation or suppression can lead, under conditions of environmental stress for pines, to a state shift from pine forest to heathland.

The regular occurrence of fires prior to the pine decline (Figure 2) shows the pine forests were resilient to fire return intervals as low as 30 years (cf. Garcia-Gonzalo et al., 2011, Leys et al., 2014, Mouillot et al., 2002). Pine decline occurred during two centuries of local fire absence, the longest fire-free interval of the mid-Holocene at BXBX. Pine decline in SE Spain also occurred during a period of low

fire activity (Carrión et al., 2001). *Pinus pinaster* tolerates a variable or mixed fire regime (Fernandes & Rigolot, 2007), yet pine seedling emergence rates decrease rapidly with time since fire (Pausas et al., 2008). This is perhaps due to the short life span of *P. pinaster* seeds once released from the cones (Ferrandis et al., 1996). A 200-year absence of fires is likely to have had detrimental effects on pine regeneration depending on levels of serotiny in the population.

However, fire's absence cannot explain the inability of pine populations to recover after the pine decline, given that regular fires returned after the drought phase (Figure 2) and pines in Western Iberia typically produce no or few serotinous cones (Tapias et al., 2004). Competition and grazing thus emerge as probable explanations for poor pine recovery.

4.4 | Interspecific competition

Interspecific competition at the pine decline sites is indicated by the switch in dominance from seeders to resprouters in Figure 3. This dominance shift occurs before the pine decline and may represent an early-warning signal for pine decline. Ecological studies indicate that shrubby resprouters are quicker to recover from drought than obligate seeders (Parra & Moreno, 2018; Zeppel et al., 2016) and often outcompete pine trees in post-fire recovery (Calvo et al., 2008; Nuñez et al., 2003; Taboada et al., 2017). *Pinus pinaster* seedlings are shade-intolerant and often outcompeted by resprouters (Batllori et al., 2017; Calvo et al., 2008; Torres et al., 2016), which also compete with Mediterranean pine forests for moisture, promoting drought stress (Karavani et al., 2018). Our data suggest that pine decline was the result of both abiotic stress (multidecadal drought) and biotic interactions (competition) in the context of fire regime change (Carrión et al., 2001, 2003, 2010).

Our observations suggest that obligate seeder trees may be replaced by shrublands in the absence of fire (Figure 4). Ecological models that simulate the effects of drought–fire interactions in Mediterranean vegetation provide little indication of this potential outcome (Batllori et al., 2017; Mouillot et al., 2002). This may be because the duration of mid-Holocene drought in SW Iberia was longer than those simulated in models (e.g. 15 years in Batllori et al., 2017). It may also reflect the additional effect of grazing pressure, which has received less attention in regional modelling simulations, but is regarded as a critical top-down control on woody plant populations (Archibald & Hempson, 2016; Bond, 2005; Midgley et al., 2010).

4.5 | Grazing

Grazing is a disturbance that persisted long after the drought ended in SW Iberia (Figure 4). *Erica scoparia*, the main resprouter that replaced pine at LATR and BXBX, is promoted by grazing (Bartolomé et al., 2005). The increase in grazing indicators (Figures 2 and 4) prior to pine decline indicates that herbivory may have played a role in triggering and maintaining the state shift.

Grazing reduces biomass, impacting on fire regimes (Archibald & Hempson, 2016). In the south-western USA, when European farmers introduced livestock to pine forests in the 19th century, grazing prevented surface fires that had previously been a regular occurrence (Swetnam et al., 1999). This grazing-induced change in fire regime allowed pine competitors to proliferate (Fulé et al., 1997; Savage & Swetnam, 1990; Swetnam et al., 1999). A review by Richardson et al., (2007) describes numerous examples of grazing impacts on pine forests worldwide.

As SW Iberia was colonized by Neolithic farmers, we suggest that the domestic livestock suppressed fire and altered pine recruitment, accelerating pine decline. Native herbivores have been shown to have significantly different effects on seedling establishment, plant diversity and vegetation structure compared with introduced livestock (Perea et al., 2016). Common pre-Neolithic herbivores in SW Iberia included red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), auroch (*Bos primigenius*), wild horse (*Equus ferus*) and roe deer (*Capreolus capreolus*). Domestic sheep, goats, cattle and pigs largely replaced these taxa in Neolithic archaeological assemblages from SW Iberia (Carvalho, 2002; Soares, 1995, 1996).

Intense grazing in the absence of fire strongly favours *Erica scoparia* (Bartolomé et al., 2005), the taxon that expands most rapidly before and during the pine decline. Bartolomé et al., (2005) suggest that fire puts downward pressure on *E. scoparia* recruitment by depleting seedbanks, whereas grazing facilitates rapid spread. The decline in spinescent shrubs (Figure 3) may also relate to overgrazing. Spinescence is a trait regarded as an early evolutionary defence against vertebrate herbivory (Charles-Dominque et al., 2016; Hanley et al., 2007) and is often ineffective against grazers in Mediterranean shrublands during drought (Kohl et al., 2014; Papachristou et al., 2005; Rogosic et al., 2006).

4.6 | Integrating drought, fire and grazing stressors

The relative importance of herbivory and fire in biomass consumption is strongly dependent on rainfall gradients. Fire activity in Mediterranean zones can be "switched on" when climate-controlled thresholds are crossed and fuel loads/connectivity increase (Pausas & Paula, 2012). In the African context, herbivory is the primary consumer in low rainfall zones, but fire takes over as rainfall increases (Archibald & Hempson, 2016). This threshold is lower on nutrient-poor soils. Hence, biomass consumption in drought phases (such as the pine decline) may be dominated by herbivory (Figure 2). Grazing's potential impact on fire spread is integrated into Pausas and Paula's (2012) aridity/productivity gradient in Figure 5, along with a conceptual model of ecological succession in maritime pine forests that compares grazing and drought conditions to fire-led succession.

Given the prediction of more severe droughts in the future (Batllori et al., 2013; Turco et al., 2018), there are suggestions that resilience of Mediterranean forests could be improved by artificially introducing resprouters into the understorey (see Gavinet et al., 2016; Karavani et al., 2018; Moreno-Fernández et al., 2018).

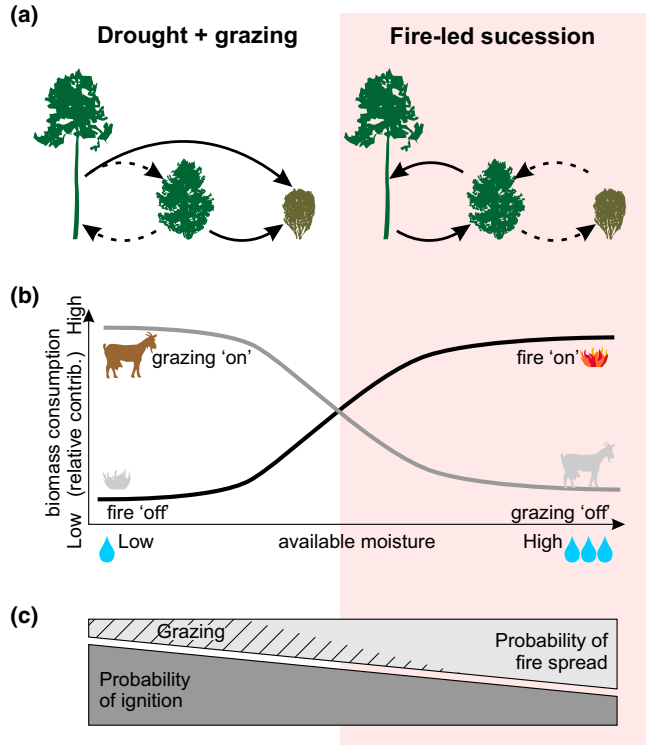

FIGURE 5 A conceptual model for fire- versus drought/grazing-modulated vegetation dynamics, inferred from the palaeorecord: (a) schematic showing the main directions of vegetation change (solid arrows) and subsidiary pathways (dotted arrows) between mature pines, juvenile pines and resprouter shrubs in relation to fire and drought/grazing; (b) the relative effects of grazing and fire in consuming biomass along a gradient of available moisture (adapted from Archibald & Hempson, 2016); and (c) the main drivers of fire in relation to available moisture, showing the hypothesized effect of grazing in reducing the probability of fire spread under fuel-limited conditions (adapted from Pausas & Paula, 2012). Plant images courtesy of *Gobius Comunicação e Ciência*

Our data suggest that such a strategy could push maritime pine forests closer to a tipping point where forest loss could be expected under drought conditions, grazing pressure or as a result of interspecific competition (Calvo et al., 2008; Prieto-Recio et al., 2015). Addition of resprouters may increase moisture stress (Karavani et al., 2018) and fuel connectivity in a way that encourages severe, mortality-inducing canopy fires (Botequim et al., 2017). Greater impacts might be expected among pine populations with few recovery and resilience traits (Zas et al., 2020). As grazing also favours shrubby resprouters, management cannot rely on vertebrate herbivores to replace fire's ecological functions (Bartolomé et al., 2005; Hean & Ward, 2012).

5 | CONCLUSIONS

The aim of this paper was to analyse a critical transition from Mediterranean forest to shrubland. The palaeorecord provides strong evidence of threshold responses in vegetation and fire regime in response to drought and grazing pressures at the bioclimatic limit of *Pinus pinaster's* range. Our data support the theory that relatively frequent fire (30–130-year return interval) gave mid-Holocene *P. pinaster* an advantage over competitors. These competitors showed early-warning signals of overtaking pine, manifested as a dominance switch from obligate seeders to post-fire resprouters at least a century before pine decline. We find a good agreement between the trajectory of the pine decline and ecological models involving multiple stressors, which provide more convincing mechanisms for the pine decline than an aridification trend or human impact. However, current models require improvements to predict forest-to-shrubland transitions where drought and grazing interact to suppress fire and thus limit recruitment in obligate seeders.

The most important implication of our research is that management decisions made now (in relation to grazing, fire and resprouter establishment) will determine how future ecosystems respond to climate change.

ACKNOWLEDGEMENTS

We thank Ana Vidal (Instituto de Conservação da Natureza e da Biodiversidade) and the RNLSAS staff for their support of our research; Salvia García Álvarez for identifying *Pinus pinaster* macrofossils; Margarida Ramires, Óscar Ferreira, Paulo Santana and Paulo Fernandes for laboratory and field support; Pedro Correia, the Blasques family and the Associação de Produtores Florestais da Serra do Caldeirão for accommodating our pollen traps; and Paula Queiroz, José Mateus, Jacqueline van Leeuwen and Pim van der Knaap for guidance.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13261.

DATA AVAILABILITY STATEMENT

Original data are available in the Neotoma Paleoecology Database via the following DOIs: https://dx.doi.org/10.21233/2D56-1A18 (BXBX pollen); https://dx.doi.org/10.21233/JWFE-2H38 (BXBX charcoal); https://dx.doi.org/10.21233/dcqy-3516 (LATR pollen); https://dx.doi.org/10.21233/ZWNY-YK04 (ELCA pollen & charcoal); https://dx.doi.org/10.21233/VBG8-BW42 (ESCE pollen); https://dx.doi.org/10.21233/JVHB-ZM88 (ESCE charcoal).

ORCID

Simon E. Connor https://orcid.org/0000-0001-5685-2390
César Morales-Molino https://orcid.org/0000-0002-9464-862X

REFERENCES

Abad Viñas, R., Caudullo, G., Oliveira, S., & de Rigo, D. (2016). *Pinus pinaster* in Europe: distribution, habitat, usage and threats. In J. San-Miguel-Ayanz, J. D. de Rigo, G. Caudullo, T. Houston Durrant, & A.

Mauri (Eds.), *European Atlas of Forest Tree Species* (pp. e012d59+). Publ. Off. EU.

Ali, A., Blarquez, O., Girardin, M., Hély, C., Tinquaut, F., El Guellab, A., Valsecchi, V., Terrier, A., Bremond, L., Genries, A., Gauthier, S., & Bergeron, Y. (2012). Control of the multimillennial wildfire size in boreal North America by spring climatic conditions. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 20966–20970. https://doi.org/10.1073/pnas.1203467109

Alía, R., & Martín, S. (2003). *EUFORGEN technical guidelines for genetic conservation and use for Maritime pine (*Pinus pinaster*)*. International Plant Genetic Resources Institute.

Álvarez, S. G., García-Amorena, I., Rubiales, J. M., & Morla, C. (2009). The value of leaf cuticle characteristics in the identification and classification of Iberian Mediterranean members of the genus *Pinus*. *Botanical Journal of the Linnean Society*, *161*, 436–448.

Ammann, B., van der Knaap, W. O., Lang, G., Gaillard, M. J., Kaltenrieder, P., Rösch, M., Finsinger, W., Wright, H. E., & Tinner, W. (2014). The potential of stomata analysis in conifers to estimate presence of conifer trees: Examples from the Alps. *Vegetation History and Archaeobotany*, *23*, 249–264. https://doi.org/10.1007/s00334-014-0431-9

Archibald, S., & Hempson, G. P. (2016). Competing consumers: Contrasting the patterns and impacts of fire and mammalian herbivory in Africa. *Philosophical Transactions of the Royal Society, B*, *371*, 20150309. https://doi.org/10.1098/rstb.2015.0309

Baeza, M. J., Valdecantos, A., Alloza, J. A., & Vallejo, V. R. (2007). Human disturbance and environmental factors as drivers of long-term post-fire regeneration patterns in Mediterranean forests. *Journal of Vegetation Science*, *18*, 243–252. https://doi.org/10.1111/j.1654-1103.2007.tb02535.x

Barboni, D., Harrison, S. P., Bartlein, P. J., Jalut, G., New, M., Prentice, I. C., Sanchez-Goñi, M. F., Spessa, A., Davis, B., & Stevenson, A. C. (2004). Relationships between plant traits and climate in the Mediterranean region: A pollen data analysis. *Journal of Vegetation Science*, *15*, 635–646. https://doi.org/10.1111/j.1654-1103.2004.tb02305.x

Barros, A. M. G., Ager, A. A., Day, M. A., Krawchuk, M. A., & Spies, T. A. (2018). Wildfires managed for restoration enhance ecological resilience. *Ecosphere*, *9*, e02161. https://doi.org/10.1002/ecs2.2161

Bartolomé, J., López, Z. G., Broncano, M. J., & Plaixats, J. (2005). Grassland colonization by *Erica scoparia* (L.) in the Montseny Biosphere Reserve (Spain) after land-use changes. *Agriculture, Ecosystems and Environment*, *11*, 253–260.

Batllori, E., De Cáceres, M., Brotons, L., Ackerly, D. D., Moritz, M. A., & Lloret, F. (2017). Cumulative effects of fire and drought in Mediterranean ecosystems. *Ecosphere*, *8*, e01906. https://doi.org/10.1002/ecs2.1906

Batllori, E., Parisien, M.-A., Krawchuk, M. A., & Moritz, M. A. (2013). Climate change-induced shifts in fire for Mediterranean ecosystems. *Global Ecology and Biogeography*, *22*, 1118–1129. https://doi.org/10.1111/geb.12065

Berdugo, M., Delgado-Baquerizo, M., Soliveres, S., Hernández-Clemente, R., Zhao, Y., Gaitán, J. J., Gross, N., Saiz, H., Maire, V., Lehmann, A., Rillig, M. C., Solé, R., & Maestre, F. T. (2020). Global ecosystem thresholds driven by aridity. *Science*, *367*, 787–790. https://doi.org/10.1126/science.aay5958

Bivand, R., Keitt, T., & Rowlingson, B. (2019). *rgdal: Bindings for the 'Geospatial' Data Abstraction Library*. R package version 1.4-8. Retrieved from https://CRAN.R-project.org/package=rgdal

Bond, W. J. (2005). Large parts of the world are brown or black: A different view on the 'Green World' hypothesis. *Journal of Vegetation Science*, *16*, 261–266.10.1658/1100-9233(2005)016[0261:LPOTWA]2.0.CO;2

Botequim, B., Fernandes, P. M., Garcia-Gonzalo, J., Silva, A., & Borges, J. G. (2017). Coupling fire behaviour modelling and stand characteristics to assess and mitigate fire hazard in a maritime pine landscape in Portugal. *European Journal of Forest Research*, *136*, 527–542. https://doi.org/10.1007/s10342-017-1050-7

Bowman, D. M. J. S., Murphy, B. P., Boer, M. M., Bradstock, R. A., Cary, G., Cochrane, M. A., Fensham, R. J., Krawchuk, M. A., Price, O. F., & Williams, R. J. (2013). Forest fire management, climate change, and the risk of catastrophic carbon losses. *Frontiers in Ecology and Evolution*, *11*, 66–67. https://doi.org/10.1890/13.WB.005

Bravo-Oviedo, A., Sterba, H., del Río, M., & Bravo, F. (2006). Competition-induced mortality for Mediterranean *Pinus pinaster* Ait. and *P. sylvestris* L. *Forest Ecology and Management*, *222*, 88–98.

Bronk Ramsey, C. (2009). Bayesian analysis of radiocarbon dates. *Radiocarbon*, *51*, 337–360. https://doi.org/10.1017/S0033822200033865

Brussel, T., Minckley, T. A., Brewer, S. C., & Long, C. (2018). Community-level functional interactions with fire track long-term structural development and fire adaptation. *Journal of Vegetation Science*, *29*, 450–458. https://doi.org/10.1111/jvs.12654

Cacho, I., Grimalt, J. O., Canals, M., Sbaffi, L., Shackleton, N., Schönfeld, J., & Zahn, R. (2001). Variability of the western Mediterranean Sea surface temperature during the last 25,000 years and its connection with the Northern Hemisphere climatic changes. *Paleoceanography*, *16*, 40–52. https://doi.org/10.1029/2000PA000502

Cacho, I., Grimalt, J. O., Pelejero, C., Canals, M., Sierro, F. J., Flores, J. A., & Shackleton, N. J. (1999). Dansgaard-Oeschger and Heinrich event imprints in Alboran Sea temperatures. *Paleoceanography*, *14*, 698–705.

Calvo, L., Santalla, S., Valbuena, L., Marcos, E., Tárrega, R., & Luis-Calabuig, E. (2008). Post-fire natural regeneration of a *Pinus pinaster* forest in NW Spain. *Plant Ecology*, *197*, 81–90. https://doi.org/10.1007/s11258-007-9362-1

Carrión, J. S., Andrade, A., Bennett, K. D., Navarro, C., & Munuera, M. (2001). Crossing forest thresholds: Inertia and collapse in a Holocene sequence from south-central Spain. *The Holocene*, *11*, 635–653. https://doi.org/10.1191/09596830195672

Carrión, J. S., Fernández, S., González-Sampériz, P., Gil-Romera, G., Badal, E., Carrión-Marco, Y., López-Merino, L., López-Sáez, J. A., Fierro, E., & Burjachs, F. (2010). Expected trends and surprises in the Lateglacial and Holocene vegetation history of the Iberian Peninsula and Balearic Islands. *Review of Palaeobotany and Palynology*, *162*, 458–475. https://doi.org/10.1016/j.revpalbo.2009.12.007

Carrión, J. S., Navarro, C., Navarro, J., & Munuera, M. (2000). The distribution of cluster pine (*Pinus pinaster*) in Spain as derived from palaeoecological data: Relationships with phytosociological classification. *The Holocene*, *10*, 243–252. https://doi.org/10.1191/095968300676937462

Carrión, J. S., Sánchez-Gómez, P., Mota, J. F., Yll, R., & Chaín, C. (2003). Holocene vegetation dynamics, fire and grazing from the Sierra de Gádor, southern Spain. *The Holocene*, *13*, 839–849.

Carrión, J. S., & van Geel, B. (1999). Fine-resolution Upper Weichselian and Holocene palynological record from Navarrés (Valencia, Spain) and a discussion about factors of Mediterranean forest succession. *Review of Palaeobotany and Palynology*, *106*, 209–236. https://doi.org/10.1016/S0034-6667(99)00009-3

Carvalho, A. F. (2002). Current perspectives on the transition from the Mesolithic to the Neolithic in Portugal. *Saguntum*, *5*, 235–250.

Charles-Dominque, T., Davies, T. J., Hempson, G. P., Bezeng, B. S., Daru, B. H., Kabongo, R. M., Maurin, O., Muasya, A. M., van der Bank, M., & Bond, W. J. (2016). Spiny plants, mammal browsers, and the origin of African savannas. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, E5572–E5579. https://doi.org/10.1073/pnas.1607493113

Connor, S. E., Araújo, J., van der Knaap, W. O., & van Leeuwen, J. F. N. (2012) A long-term perspective on biomass burning in the Serra da Estrela, Portugal. *Quaternary Science Reviews*, *55*, 114–124.

Côté, I., Darling, E. S., & Brown, C. J. (2016). Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society, B*, *283*, 20152592. https://doi.org/10.1098/rspb.2015.2592

Cruces, A. G. (2015). Caracterização de Ambientes de Transição do SW Alentejano a distintas escalas temporais. PhD thesis. Lisboa: Dept. Geologia, Universidade de Lisboa.

Dakos, V., van Nes, E. H., Donangelo, R., Fort, H., & Scheffer, M. (2010). Spatial correlation as leading indicator of catastrophic shifts. *Theoretical Ecology*, *3*, 163–174. https://doi.org/10.1007/s12080-009-0060-6

Daveau, S. (1988). Progressos recentes no conhecimento da evolução holocénica da cobertura vegetal, em Portugal e nas regiões vizinhas. *Finisterra*, *23*, 101–152.

Davies, A. L., Streeter, R., Lawson, I. T., Roucoux, K. H., & Hiles, W. (2018). The application of resilience concepts in palaeoecology. *The Holocene*, *28*, 1523–1534. https://doi.org/10.1177/0959683618777077

Enright, N. J., Fontaine, J. B., Bowman, D. M. J. S., Bradstock, R. A., & Williams, R. J. (2015). Interval squeeze: Altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Frontiers in Ecology and Environment*, *13*, 265–272. https://doi.org/10.1890/140231

Enright, N. J., Fontaine, J. B., Lamont, B. B., Miller, B. P., & Westcott, V. C. (2014). Resistance and resilience to changing climate and fire regime depend on plant functional traits. *Journal of Ecology*, *102*, 1572–1581. https://doi.org/10.1111/1365-2745.12306

Essl, F., Dullinger, S., Rabitsch, W., Hulme, P. E., Pyšek, P., Wilson, J. R. U., & Richardson, D. M. (2015). Historical legacies accumulate to shape future biodiversity in an era of rapid global change. *Diversity and Distributions*, *21*, 534–547. https://doi.org/10.1111/ddi.12312

Fernandes, P. M., Barros, A. M. G., Pinto, A., & Santos, J. M. (2016). Characteristics and controls of extremely large wildfires in the western Mediterranean Basin. *Journal of Geophysical Research: Biogeosciences*, *121*, 2141–2157. https://doi.org/10.1002/2016JG003389

Fernandes, P. M., Luz, A., & Loureiro, C. (2010). Changes in wildfire severity from maritime pine woodland to contiguous forest types in the mountains of northwestern Portugal. *Forest Ecology and Management*, *260*, 883–892. https://doi.org/10.1016/j.foreco.2010.06.008

Fernandes, P. M., & Rigolot, E. (2007). The fire ecology and management of maritime pine (*Pinus pinaster* Ait.). *Forest Ecology and Management*, *241*, 1–13. https://doi.org/10.1016/j.foreco.2007.01.010

Ferrandis, P., Herranz, J. M., & Martínez-Sánchez, J. J. (1996). The role of soil seed bank in the early stages of plant recovery after fire in a *Pinus pinaster* forest in SE Spain. *International Journal of Wildland Fire*, *6*, 31–35. https://doi.org/10.1071/WF9960031

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*, 4302–4315. https://doi.org/10.1002/joc.5086

Fiigueiral, I. (1995). Charcoal analysis and the history of *Pinus pinaster* (cluster pine) in Portugal. *Review of Palaeobotany and Palynology*, *89*, 441–454. https://doi.org/10.1016/0034-6667(95)00013-3

Finsinger, W., & Tinner, W. (2005). Minimum count sums for charcoal-concentration estimates in pollen slides: Accuracy and potential errors. *The Holocene*, *15*, 293–297. https://doi.org/10.1191/0959683605hl808rr

Foster, C. N., Sato, C. F., Lindenmayer, D. B., & Barton, P. S. (2016). Integrating theory into disturbance interaction experiments to better inform ecosystem management. *Global Change Biology*, *22*, 1325–1335. https://doi.org/10.1111/gcb.13155

Franco Múgica, F., García Antón, M., Maldonado Ruiz, J., Morla Juaristi, C., & Sainz Ollero, H. (2001). The Holocene history of *Pinus* forests in the Spanish Northern Meseta. *The Holocene*, *11*, 343–358.

Franco-Múgica, F., García-Antón, M., Maldonado-Ruiz, J., Morla-Juaristi, C., & Sainz-Ollero, H. (2005). Ancient pine forest on inland dunes in the Spanish northern meseta. *Quaternary Research*, *63*, 1–14. https://doi.org/10.1016/j.yqres.2004.08.004

Frejaville, T., & Curt, T. (2015). Spatiotemporal patterns of changes in fire regime and climate: Defining the pyroclimates of south-eastern France (Mediterranean Basin). *Climatic Change*, *129*, 239–251. https://doi.org/10.1007/s10584-015-1332-3

Fulé, P. Z., Covington, W. W., & Moore, M. M. (1997). Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecological Applications*, *7*, 895–908.10.1890/1051-0761(1997)007[0895:DRCFEM]2.0.CO;2

García-Amorena, I., Gómez Manzaneque, F., Rubiales, J. M., Granja, H. M., Carvalho, G. S., & Morla, C. (2007). The Late Quaternary coastal forests of western Iberia: A study of their macroremains. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *254*, 448–461. https://doi.org/10.1016/j.palaeo.2007.07.003

Garcia-Gonzalo, J., Marques, S., Borges, J. G., Botequim, B., Oliveira, M. M., Tomé, J., & Tomé, M. (2011). A three-step approach to post-fire mortality modelling in maritime pine (*Pinus pinaster* Ait) stands for enhanced forest planning in Portugal. *Forestry*, *84*, 197–206.

Gavinet, J., Prévosto, B., & Fernandez, C. (2016). Introducing resprouters to enhance Mediterranean forest resilience: Importance of functional traits to select species according to a gradient of pine density. *Journal of Applied Ecology*, *53*, 1735–1745. https://doi.org/10.1111/1365-2664.12716

Gonzalez, A., Cardinale, B. J., Allington, G. R. H., Byrnes, J., Endsley, K. A., Brown, D. G., Hooper, D. U., Isbell, F., O'Connor, M. I., & Loreau, M. (2016). Estimating local biodiversity change: A critique of papers claiming no net loss of local diversity. *Ecology*, *97*, 1949–1960. https://doi.org/10.1890/15-1759.1

Hanley, M. E., Lamont, B. B., Fairbanks, M. M., & Rafferty, C. M. (2007). Plant structural traits and their role in anti-herbivore defence. *Perspectives in Plant Ecology, Evolution and Systematics*, *8*, 157–178. https://doi.org/10.1016/j.ppees.2007.01.001

Hean, J. W., & Ward, D. (2012). Fire and herbivory are not substitutable: Evidence from regrowth patterns and changes in physical and chemical defences in *Acacia* seedlings. *Journal of Vegetation Science*, *23*, 13–23. https://doi.org/10.1111/j.1654-1103.2011.01330.x

Higuera, P. E., Brubaker, L. B., Anderson, P. M., Hu, F. S., & Brown, T. A. (2009). Vegetation mediated the impacts of postglacial climatic change on fire regimes in the south-central Brooks Range, Alaska. *Ecological Monographs*, *79*, 201–219.

Hijmans, R. J. (2020). *raster: Geographic Data Analysis and Modeling*. R package version 3.0-12. Retrieved from https://CRAN.R-project.org/package=raster

Jacobson, G. L., & Bradshaw, R. H. W. (1981). The selection of sites for paleovegetational studies. *Quaternary Research*, *16*, 80–96. https://doi.org/10.1016/0033-5894(81)90129-0

Jalut, G., Amat, A. E., Bonnet, L., Gauquelin, T., & Fontugne, M. (2000). Holocene climatic changes in the Western Mediterranean, from south-east France to south-east Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *160*, 255–290. https://doi.org/10.1016/S0031-0182(00)00075-4

Karavani, A., Boer, M. A., Baudena, M., Colinas, C., Díaz-Sierra, R., Pemán, J., de Luis, M., Enríquez-de-Salamanca, Á., & Resco de Dios, V. (2018). Fire-induced deforestation in drought-prone Mediterranean forests: Drivers and unknowns from leaves to communities. *Ecological Monographs*, *88*, 141–169. https://doi.org/10.1002/ecm.1285

Kelly, L. T., Nimmo, D. G., Spence-Bailey, L. M., Haslem, A., Watson, S. J., Clarke, M. F., & Bennett, A. F. (2011). Influence of fire history on small mammal distributions: Insights from a 100-year post-fire chronosequence. *Diversity and Distributions*, *17*, 462–473. https://doi.org/10.1111/j.1472-4642.2011.00754.x

Kohl, K. D., Miller, A. W., & Dearing, M. D. (2014). Evolutionary irony: Evidence that 'defensive' plant spines act as a proximate cue to attract a mammalian herbivore. *Oikos*, *124*, 835–841. https://doi.org/10.1111/oik.02004

Leira, M., Freitas, M. C., Ferreira, T., Cruces, A., Connor, S., Andrade, C., Lopes, V., & Bao, R. (2019). Holocene sea level and climate interactions on wet dune slack evolution in SW Portugal: A model for future scenarios? *The Holocene*, *29*, 26–44. https://doi.org/10.1177/0959683618804633

Leys, B., Finsinger, W., & Carcaillet, C. (2014). Historical range of fire frequency is not the Achilles' heel of the Corsican black pine ecosystem. *Journal of Ecology*, *102*, 381–395. https://doi.org/10.1111/1365-2745.12207

Loidi, J., Biurrun, I., Campos, J. A., García-Mijangos, I., & Herrera, M. (2010). A biogeographical analysis of the European Atlantic lowland heathlands. *Journal of Vegetation Science*, *21*, 832–842. https://doi.org/10.1111/j.1654-1103.2010.01204.x

López-Merino, L., Sánchez, N. S., Kaal, J., López-Sáez, J. A., & Martínez Cortizas, A. (2012). Post-disturbance vegetation dynamics during the Late Pleistocene and the Holocene: An example from NW Iberia. *Global and Planetary Change*, *92–93*, 58–70. https://doi.org/10.1016/j.gloplacha.2012.04.003

Maia, P., Pausas, J. G., Vasques, A., & Keizer, J. J. (2012). Fire severity as a key factor in post-fire regeneration of *Pinus pinaster* (Ait.) in Central Portugal. *Annals of Forest Science*, *69*, 489–498. https://doi.org/10.1007/s13595-012-0203-6

Mateus, J. E. (1989). Pollen morphology of Portuguese Ericales. *Revista De Biologia (Lisboa)*, *14*, 135–208.

Mateus, J. (1992). *Holocene and present-day ecosystems of the Carvalhal Region, Southwest Portugal*. PhD thesis. Rijksuniversiteit Utrecht.

Mateus, J. E., & Queiroz, P. F. (1993). Os estudos de vegetação quaternária em Portugal: contextos, balanço de resultados, perspectivas. In *O Quaternário em Portugal, Balanço e Perspectivas* (pp. 105–131). APEQ, Edições Colibri.

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G., & Yepez, E. A. (2008). Tansley Review: Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, *178*, 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x

Midgley, J. J., Lawes, M. J., & Chamaillé-Jammes, S. (2010). Savanna woody plant dynamics: The role of fire and herbivory, separately and synergistically. *Australian Journal of Botany*, *58*, 1–11. https://doi.org/10.1071/BT09034

Moore, P. D., Webb, J. A., & Collinson, M. E. (1991). *Pollen analysis*. Blackwell Science Publishers.

Morales-Molino, C., Postigo-Mijarra, J. M., Morla, C., & García-Antón, M. (2012). Long-term persistence of Mediterranean pine forests in the Duero Basin (central Spain) during the Holocene: The case of *Pinus pinaster* Aiton. *The Holocene*, *22*, 561–570.

Morales-Molino, C., Tinner, W., García-Antón, M., & Colombaroli, D. (2017). The historical demise of *Pinus nigra* forests in the Northern Iberian Plateau (south-western Europe). *Journal of Ecology*, *105*, 634–646.

Moreno-Fernández, D., Montes, F., Sánchez-González, M., Gordo, F. J., & Cañellas, I. (2018). Regeneration dynamics of mixed stands of *Pinus pinaster* Ait. and *Pinus pinea* L. in Central Spain. *European Journal of Forest Research*, *137*, 17–27. https://doi.org/10.1007/s10342-017-1086-8

Mouillot, F., Rambal, S., & Joffre, R. (2002). Simulating climate change impacts on fire frequency and vegetation dynamics in a Mediterranean-type ecosystem. *Global Change Biology*, *8*, 423–437. https://doi.org/10.1046/j.1365-2486.2002.00494.x

Navarro-Cerrillo, R. M., Rodriguez-Vallejo, C., Silveiro, E., Hortal, A., Palacios-Rodríguez, G., Duque-Lazo, J., & Camarero, J. J. (2018). Cumulative drought stress leads to a loss of growth resilience and explains higher mortality in planted than in naturally regenerated *Pinus pinaster* stands. *Forests*, *9*, 358. https://doi.org/10.3390/f9060358

Nuñez, M. R., Bravo, F., & Calvo, L. (2003). Predicting the probability of seed germination in *Pinus sylvestris* L. and four competitor shrub species after fire. *Annals of Forest Science*, *60*, 75–81.

Odgaard, B. V. (1992). The fire history of Danish heathland areas as reflected by pollen and charred particles in lake sediments. *The Holocene*, *2*, 218–226. https://doi.org/10.1177/095968369200200303

Odgaard, B. V., & Rasmussen, P. (2000). Origin and temporal development of macro-scale vegetation patterns in the cultural landscape of Denmark. *Journal of Ecology*, *88*, 733–748. https://doi.org/10.1046/j.1365-2745.2000.00490.x

Papachristou, T. G., Dziba, L. E., & Provenza, F. D. (2005). Foraging ecology of goats and sheep on wooded rangelands. *Small Ruminant Research*, *59*, 141–156. https://doi.org/10.1016/j.smallrumres.2005.05.003

Parra, A., & Moreno, J. M. (2018). Drought differentially affects the post-fire dynamics of seeders and resprouters in a Mediterranean shrubland. *Science of the Total Environment*, *626*, 1219–1229. https://doi.org/10.1016/j.scitotenv.2018.01.174

Pausas, J. G. (2004). Changes in fire and climate in the Eastern Iberian Peninsula (Mediterranean Basin). *Climatic Change*, *63*, 337–350. https://doi.org/10.1023/B:CLIM.0000018508.94901.9c

Pausas, J. G., Llovet, J., Rodrigo, A., & Vallejo, R. (2008). Are wildfires a disaster in the Mediterranean basin? – A review. *International Journal of Wildland Fire*, *17*, 713–723. https://doi.org/10.1071/WF07151

Pausas, J., & Paula, S. (2012). Fuel shapes the fire–climate relationship: Evidence from Mediterranean ecosystems. *Global Ecology and Biogeography*, *21*, 1074–1082. https://doi.org/10.1111/j.1466-8238.2012.00769.x

Pausas, J. G., & Ribeiro, E. (2013). The global fire–productivity relationship. *Global Ecology and Biogeography*, *22*, 728–736. https://doi.org/10.1111/geb.12043

Perea, R., López-Sánchez, A., & Roig, S. (2016). The use of shrub cover to preserve Mediterranean oak dehesas: A comparison between sheep, cattle and wild ungulate management. *Applied Vegetation Science*, *19*, 244–253. https://doi.org/10.1111/avsc.12208

Power, M. J., Marlon, J., Ortiz, N., Bartlein, P. J., Harrison, S. P., Mayle, F. E., Ballouche, A., Bradshaw, R. H. W., Carcaillet, C., Cordova, C., Mooney, S., Moreno, P. I., Prentice, I. C., Thonicke, K., Tinner, W., Whitlock, C., Zhang, Y., Zhao, Y., Ali, A. A., … Zhang, J. H. (2008). Changes in fire regimes since the Last Glacial Maximum: An assessment based on a global synthesis and analysis of charcoal data. *Climate Dynamics*, *30*, 887–907. https://doi.org/10.1007/s00382-007-0334-x

Prieto-Recio, C., Martín-García, J., Bravo, F., & Diez, J. J. (2015). Unravelling the associations between climate, soil properties and forest management in *Pinus pinaster* decline in the Iberian Peninsula. *Forest Ecology and Management*, *356*, 74–83. https://doi.org/10.1016/j.foreco.2015.07.033

Queiroz, P. F. (1999). *Ecologia Histórica da Paisagem do Noroeste Alentejano*. PhD thesis. Universidade de Lisboa.

Queiroz, P. F., & Mateus, J. E. (2004). Paleoecologia litoral entre Lisboa e Sines - do Tardiglaciário aos tempos de hoje. In A. A. Tavares, M. J. F. Tavares, & J. L. Cardoso (Eds.), *Evolução Geohistórica do Litoral Português e Fenómenos Correlativos – Geologia, História, Arqueologia e Climatologia – Actas* (pp. 257–304). Universidade Aberta.

R Core Team (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Richardson, D. M., Rundel, P. W., Jackson, S. T., Teskey, R. O., Aronson, J., Bytnerowicz, A., Wingfield, M. J., & Procheş, Ş. (2007). Human

impacts in pine forests: Past, present, and future. *Annual Review of Ecology, Evolution, and Systematics*, *38*, 275–297. https://doi.org/10.1146/annurev.ecolsys.38.091206.095650

Rodrigues, T., Grimalt, J. O., Abrantes, F. G., Flores, J. A., & Lebreiro, S. M. (2009). Holocene interdependences of changes in sea surface temperature, productivity, and fluvial inputs in the Iberian continental shelf (Tagus mud patch). *Geochemistry Geophysics Geosystems*, *10*, Q07U06. https://doi.org/10.1029/2008GC002367

Rogosic, J., Pfister, J. A., Provenza, F. D., & Grbesa, D. (2006). Sheep and goat preference for and nutritional value of Mediterranean maquis shrubs. *Small Ruminant Research*, *64*, 169–179. https://doi.org/10.1016/j.smallrumres.2005.04.017

Salvador, L., Alía, R., Agúndez, D., & Gil, L. (2000). Genetic variation and migration pathways of maritime pine (*Pinus pinaster* Ait) in the Iberian Peninsula. *Theoretical and Applied Genetics*, *100*, 89–95. https://doi.org/10.1007/s001220050013

Santos, L., & Sánchez Goñi, M. F. (2003). Lateglacial and Holocene environmental changes in Portuguese coastal lagoons 3: Vegetation history of the Santo André coastal area. *The Holocene*, *13*, 459–464.

Savage, M., & Swetnam, T. W. (1990). Early 19th century fire decline following sheep pasturing in a Navajo ponderosa pine forest. *Ecology*, *71*, 2374–2378. https://doi.org/10.2307/1938649

Schneider, H., Höfer, D., Trog, C., & Mäusbacher, R. (2016). Holocene landscape development along the Portuguese Algarve coast – A high resolution palynological approach. *Quaternary International*, *407*, 47–63. https://doi.org/10.1016/j.quaint.2016.02.039

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M. J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T. A., & Reyer, C. P. O. (2017). Forest disturbances under climate change. *Nature Climate Change*, *7*, 395–402. https://doi.org/10.1038/nclimate3303

Slingsby, J. A., Merow, C., Aiello-Lammens, M., Allsopp, N., Hall, S., Mollman, H. K., Turner, R., Wilson, A. M., & Silander, J. A. (2017). Intensifying postfire weather and biological invasion drive species loss in a Mediterranean-type biodiversity hotspot. *Proceedings of the National Academy of Sciences of the United States of America*, *114*, 4697–4702. https://doi.org/10.1073/pnas.1619014114

Soares, J. (1995). Para uma reconstrução do processo de neolitização em Portugal. *Ophiussa*, *1*, 39–50.

Soares, J. (1996). Padrões de povoamento e subsistência no Mesolítico da costa sudoeste portuguesa. *Zephyrus*, *49*, 109–124.

Stegner, M. A., Ratajczak, Z., Carpenter, S. R., & Williams, J. W. (2019). Inferring critical transitions in paleoecological time series with irregular sampling and variable time-averaging. *Quaternary Science Reviews*, *207*, 49–63. https://doi.org/10.1016/j.quascirev.2019.01.009

Swetnam, T. W., Allen, C. D., & Betancourt, J. (1999). Applied historical ecology: Using the past to manage for the future. *Ecological Applications*, *9*, 1189–1206.10.1890/1051-0761(1999)009[1189:AHEUTP]2.0.CO;2

Taboada, A., Tárrega, R., Marcos, E., Valbuena, L., Suárez-Seoane, S., & Calvo, L. (2017). Fire recurrence and emergency post-fire management influence seedling recruitment and growth by altering plant interactions in fire-prone ecosystems. *Forest Ecology and Management*, *402*, 63–75. https://doi.org/10.1016/j.foreco.2017.07.029

Tapias, R., Climent, J., Pardos, J. A., & Gil, L. (2004). Life histories of Mediterranean pines. *Plant Ecology*, *171*, 53–68. https://doi.org/10.1023/B:VEGE.0000029383.72609.f0

Taranu, Z. E., Carpenter, S. R., Frossard, V., Jenny, J.-F., Thomas, Z., Vermaire, J. C., & Perga, M.-E. (2018). Can we detect ecosystem critical transitions and signals of changing resilience from paleoecological records? *Ecosphere*, *9*, e02438. https://doi.org/10.1002/ecs2.2438

Tavşanoğlu, Ç., & Pausas, J. G. (2018). A functional trait database for Mediterranean Basin plants. *Scientific Data*, *5*, 180135. https://doi.org/10.1038/sdata.2018.135

Thatcher, D. L., Wanamaker, A. D., Denniston, R. F., Asmerom, Y., Polyak, V. J., Fullick, D., Ummenhofer, C. C., Gillikin, D. P., & Haws, J. A. (2020). Hydroclimate variability from western Iberia (Portugal) during the Holocene: Insights from a composite stalagmite isotope record. *The Holocene*, *30*, 966–981. https://doi.org/10.1177/0959683620908648

Torres, I., Pérez, B., Quesada, J., Viedma, O., & Moreno, J. M. (2016). Forest shifts induced by fire and management legacies in a *Pinus pinaster* woodland. *Forest Ecology and Management*, *361*, 309–317. https://doi.org/10.1016/j.foreco.2015.11.027

Trumbore, S., Brando, P., & Hartmann, H. (2015). Forest health and global change. *Science*, *349*, 814–818. https://doi.org/10.1126/science.aac6759

Turco, M., Rosa-Cánovas, J. J., Bedia, J., Jerez, S., Montávez, J. P., Llasat, M. C., & Provenzale, A. (2018). Exacerbated fires in Mediterranean Europe due to anthropogenic warming projected with non-stationary climate–fire models. *Nature Communications*, *9*, 3821. https://doi.org/10.1038/s41467-018-06358-z

van der Knaap, W. O., & van Leeuwen, J. F. N. (1995). Holocene vegetation succession and degradation as responses to climatic change and human activity in the Serra da Estrela, Portugal. *Review of Palaeobotany and Palynology*, *89*, 153–211.

van Geel, B., & Aptroot, A. (2006). Fossil ascomycetes in Quaternary deposits. *Nova Hedwigia*, *82*, 313–329. https://doi.org/10.1127/0029-5035/2006/0082-0313

Vannière, B., Blarquez, O., Rius, D., Doyen, E., Brücher, T., Colombaroli, D., Connor, S., Feurdean, A., Hickler, T., Kaltenrieder, P., Lemmen, C., Leys, B., Massa, C., & Olofsson, J. (2016). 7000-year human legacy of elevation-dependent European fire regimes. *Quaternary Science Reviews*, *132*, 206–212. https://doi.org/10.1016/j.quascirev.2015.11.012

Vega, J., Jimenez, E., Vega, D., Ortiz, L., & Pérez, J. R. (2011). *Pinus pinaster* Ait. tree mortality following wildfire in Spain. *Forest Ecology and Management*, *261*, 2232–2242. https://doi.org/10.1016/j.foreco.2010.10.019

Vieira, J., Rossi, S., Campelo, F., Freitas, H., & Nabais, C. (2013). Seasonal and daily cycles of stem radial variation of *Pinus pinaster* in a drought-prone environment. *Agricultural and Forest Meteorology*, *180*, 173–181. https://doi.org/10.1016/j.agrformet.2013.06.009

Vis, G.-J. (2009). *Fluvial and marine sedimentation at a passive continental margin: The late Quaternary Tagus depositional system*. PhD thesis. VU University Amsterdam.

Whitlock, C., & Larsen, C. (2001). Charcoal as a fire proxy. In J. P. Smol, H. J. B. Birks, & W. M. Last (Eds.), *Tracking Environmental Change Using Lake Sediments*, *Volume 3: Terrestrial, Algal, and Siliceous Indicators* (pp. 75–97). Kluwer Academic Publishers.

Whitman, E., Parisien, M.-A., Thompson, D. K., & Flanigan, M. D. (2019). Short-interval wildfire and drought overwhelm boreal forest resilience. *Scientific Reports*, *9*, 18796. https://doi.org/10.1038/s41598-019-55036-7

Willis, K. J., Bailey, R. M., Bhagwat, S. A., & Birks, H. J. B. (2010). Biodiversity baselines, thresholds and resilience: Testing predictions and assumptions using palaeoecological data. *Trends in Ecology and Evolution*, *25*, 583–591. https://doi.org/10.1016/j.tree.2010.07.006

Willis, K. J., Jeffers, E. S., & Tovar, C. (2018). What makes terrestrial ecosystems resilient? *Science*, *359*, 988–989.

Zas, R., Sampedro, L., Solla, A., Vivas, M., Lombardero, M. J., Alia, R., & Rozas, V. (2020). Dendroecology in common gardens: Population differentiation and plasticity in resistance, recovery and resilience to extreme drought events in *Pinus pinaster*. *Agricultural and Forest Meteorology*, *291*, 108060. https://doi.org/10.1016/j.agrformet.2020.108060

Zeppel, M. J. B., Harrison, S. P., Adams, H. D., Kelley, D. I., Li, G., Tissue, D. T., Dawson, T. E., Fensham, R., Medlyn, B. E., Palmer, A., West, A. G., & McDowell, N. G. (2016). Drought and resprouting plants. *New Phytologist*, *206*, 583–589. https://doi.org/10.1111/nph.13205

BIOSKETCH

The multidisciplinary research team has diverse interests in Mediterranean environmental change and its relevance for biodiversity conservation in a changing world. These research interests include long-term ecology, vegetation dynamics, sea-level change, coastal processes, human–environment interactions and fire history.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Connor SE, Araújo J, Boski T, et al. Drought, fire and grazing precursors to large-scale pine forest decline. *Divers Distrib*. 2021;27:1138–1151. https://doi.org/10.1111/ddi.13261