Received: 19 September 2023 | Accepted: 17 February 2024

DOI: 10.1111/1365-2745.14293

Journal of Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Simulating past and future fire impacts on Mediterranean ecosystems

Christoph Schwörer[1] | César Morales-Molino[1,2] | Erika Gobet[1] | Paul D. Henne[3] | Salvatore Pasta[4] | Tiziana Pedrotta[1] | Jacqueline F. N. van Leeuwen[1] | Boris Vannière[1,5] | Willy Tinner[1]

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

[2]Grupo de Ecología y Restauración Forestal, Departamento de Ciencias de la Vida, Facultad de Ciencias, Universidad de Alcalá, Alcalá de Henares, Spain

[3]U.S. Geological Survey, Geosciences and Environmental Change Science Center, Denver, Colorado, USA

[4]Institute of Biosciences and BioResources (IBBR), Italian National Research Council (CNR), Unit of Palermo, Palermo, Italy

[5]Université Bourgogne Franche-Comté, CNRS, MSHE, Chrono-Environnement, Besançon, France

Correspondence
Christoph Schwörer
Email: christoph.schwoerer@unibe.ch

Funding information
Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung, Grant/Award Number: SNF200021_134616; Ministerio de Universidades/Universidad de Alcalá/European Union

Handling Editor: Anping Chen

Abstract

1. Worldwide, large wildfires are becoming increasingly common, leading to economic damages and threatening ecosystems and human health. Under future climate change, more frequent fire disturbance may push ecosystems into non-forested alternative stable states. Fire-prone ecosystems such as those in the Mediterranean Basin are expected to be particularly vulnerable, but the position of tipping points is unclear.
2. We compare long-term palaeoecological data from Sardinia with output from a process-based dynamic vegetation model to investigate the mechanisms controlling the complex interactions between fire, climate, and vegetation in the past and the future.
3. Our results show that past vegetation changes from *Erica*-shrublands to mixed evergreen-broadleaved *Quercus ilex*-dominated forests were driven by a climate-induced fire regime shift. By simulating vegetation dynamics under varying fire regimes, we could reproduce Holocene vegetation trajectories and mechanistically identify tipping points.
4. Without an immediate reduction of greenhouse gas emissions, we simulate future expansion of fire-prone Mediterranean maquis and increasing fire occurrence. Similarly, high anthropogenic ignition frequencies and plantations of non-native, highly flammable trees could induce a shift to fire-adapted *Erica* shrublands. However, our simulations indicate that if global warming can be kept below 2°C, *Quercus ilex* forests will be able to persist and effectively reduce fire occurrences and impacts, making them a valuable restoration target in Mediterranean ecosystems.
5. *Synthesis*. By combining long-term records of ecosystem change with a dynamic vegetation model, we show that past climate-driven fire regime shifts were the main driver of vegetation change, creating alternative stable states that persisted over centuries. Projected future climate change exceeding Holocene variability leads to pronounced vegetation changes and increased fire risks in our

simulations, requiring new fire management strategies to maintain current ecosystem services.

KEYWORDS
alternative stable states, climate change, dynamic vegetation modelling, fire ecology, island ecology, Palaeoecology, Sardinia, tipping points

1 | INTRODUCTION

Fire is a major global disturbance agent that can push ecosystems into alternative stable states. There is considerable concern that increasing wildfire occurrence due to ongoing and future climate change might drive closed forests to reach a tipping point beyond which they transform to open shrublands or grasslands (Adams, 2013; Baudena et al., 2020; Dantas et al., 2013; Guiterman et al., 2018; Tepley et al., 2018; Westerling et al., 2011). Intensified fire regimes therefore not only endanger human lives and property but might permanently alter important ecosystem services. The Mediterranean Basin has been one of the areas most affected by large wildfires in recent years, with a large majority caused by anthropogenic ignition sources (Ganteaume et al., 2013; Vilar et al., 2016). Burned area is projected to increase even further under future climate-change scenarios, because more extremely hot and dry weather conditions will exacerbate rapid fire spread (Dupuy et al., 2020; Lestienne et al., 2022; Turco et al., 2018). Other factors that boost wildfire intensity and size include increasing fuel load and connectivity, both linked to land abandonment (Pausas & Fernández-Muñoz, 2012), and recent plantation of highly flammable pines and eucalypts (Fernandes et al., 2016). The key role of wildfires as a driver of the floristic composition, structure and dynamics of Mediterranean ecosystems has long been emphasized (Di Pasquale et al., 2004; Naveh, 1975; Verdú & Pausas, 2007). However, the combined effect of wildfire and climate change on current plant community dynamics is poorly understood (Buhk et al., 2007; Carrillo-García et al., 2023; Fernández-García et al., 2020; Quézel & Médail, 2003), mainly due to the scarcity of long-term vegetation monitoring studies and large-scale climate-change experiments. Particularly, tipping points that may force vegetation and biome reorganizations after crossing fire-impact thresholds are difficult to detect on short temporal scales. Since at regional or continental levels, fire regime changes usually occur over decades to millennia (Whitlock et al., 2010), they are not (yet) observable in monitoring-based studies. Additionally, determining whether a system has indeed entered a new state can only be made after the occurrence, when the absence of expected successional processes becomes evident, which can also take years to centuries. Long-term perspectives on the impacts of wildfire on vegetation therefore provide unique and novel insights into fire ecology. Specifically, they are crucial to understand if the ongoing and projected future increase in fire events will lead to shifts at the plant community and ecosystem levels, and to identify tipping points that may force ecosystems towards new stable states (Connor et al., 2019).

Linkages among fire, climate and vegetation over long timescales have been increasingly investigated by palaeoecologists using charcoal particles and plant remains deposited in natural archives (Colombaroli et al., 2007; Conedera et al., 2009; Connor et al., 2019). In the Mediterranean Basin, wildfire and vegetation dynamics were controlled primarily by climate before the onset of the Neolithic (ca. 8500–7500 years ago) and by the impact of human activities afterwards (Vannière et al., 2016), although large regional differences exist concerning the timing and intensity of human impact. In Sardinia, the second largest island in the Mediterranean Sea (Figure 1), recent studies show a marked shift from shrub communities dominated by *Erica arborea* and *Erica scoparia* to mixed forests dominated by *Quercus ilex* with *Olea europaea* between 6500 and 5500 years ago, coinciding with a decline in fire (Beffa et al., 2016; Pedrotta et al., 2021). A similar pattern is also documented on neighbouring Corsica (Lestienne, Jouffroy-Bapicot, et al., 2020; Poher et al., 2017; Reille, 1992; Reille et al., 1999; Revelles et al., 2019) and Northern Africa (e.g. Ben Tiba & Reille, 1982; Stambouli-Essassi et al., 2019), but is absent elsewhere in the Mediterranean Basin. It is still unclear whether this marked vegetation change was caused by climatic changes or a shift in fire regimes. It has been hypothesized that with future climate warming, middle Holocene *Erica* shrublands might expand again, resulting in higher fire occurrence (Beffa et al., 2016). However, it is unclear if past ecosystem states and dynamics can be used as an analogue for future vegetation trajectories under climate change. Process-based spatially explicit vegetation models can help by testing specific ecological hypotheses regarding past drivers of ecosystem change, disclosing the mechanisms involved, identifying tipping points, and assessing future vegetation trajectories (Henne et al., 2013, 2015). Here, we use LandClim (Schumacher et al., 2004) to simulate past and future vegetation in Sardinia under different climate and fire disturbance scenarios and test our hypothesis that wildfire is the main driver of long-term vegetation dynamics in the Mediterranean islands. Specifically, we are interested in addressing the following research questions: (1) Was fire regime and/or climate the main driver of Holocene vegetation dynamics on Sardinia? (2) Can dynamic vegetation models mechanistically reproduce shifts in stable states during the Holocene? (3) How will future climate change and wildfire impact Mediterranean ecosystems? (4) Can we constrain

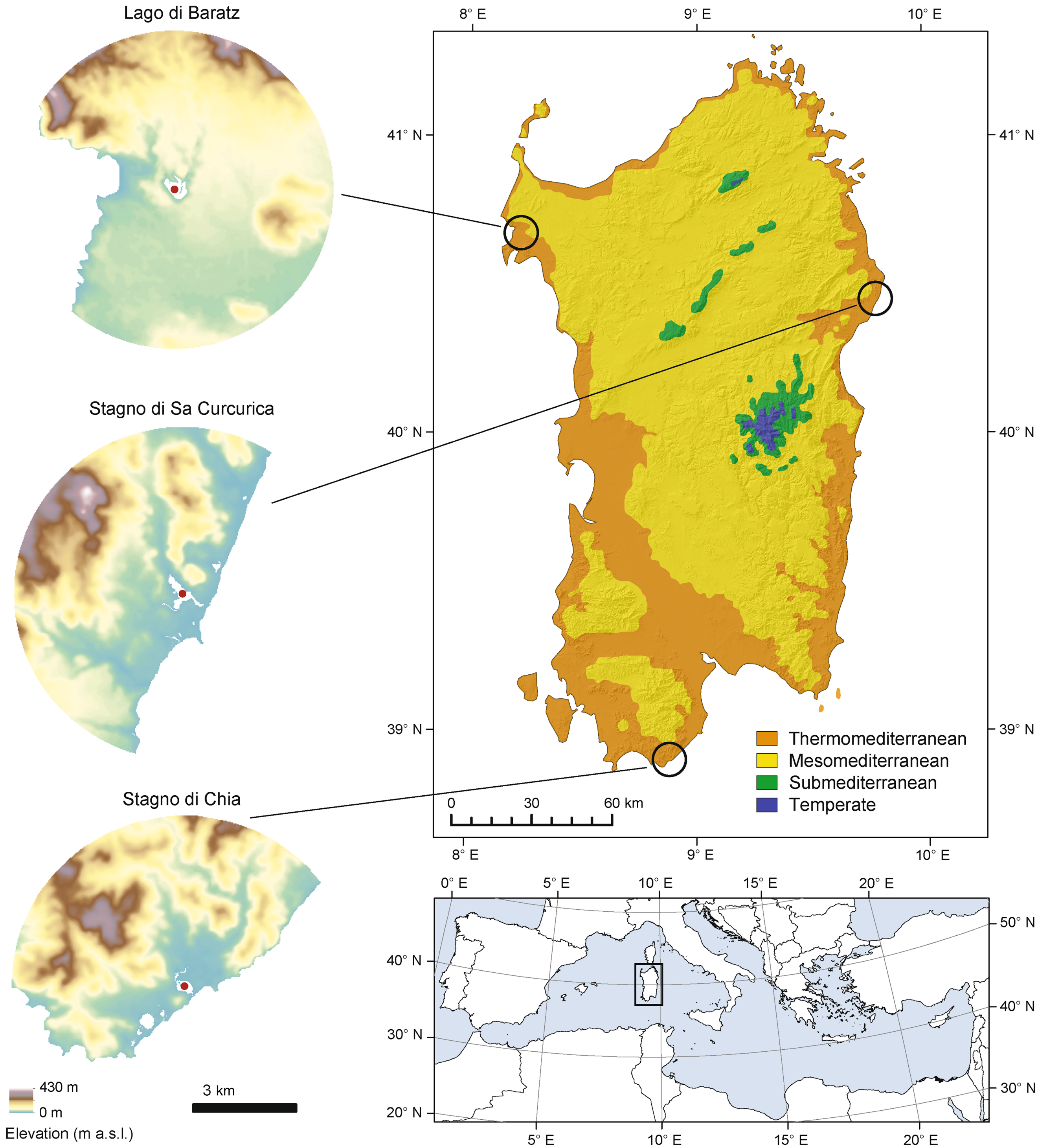


FIGURE 1 Map of Sardinia and the three study areas. Top right: map of Sardinia showing the spatial distribution of the major vegetation zones (Canu et al., 2015; Lang et al., 2023) and the location of the three study areas. Bottom: location of the island of Sardinia in the Mediterranean. Left: close-up of the three study areas used for the vegetation modelling showing elevation. The red dots in the centre of the areas indicate the lake coring locations of the corresponding palaeoecological sites.

the risks and opportunities associated with changing climate, vegetation and disturbance in the Mediterranean realm? By combining long-term palaeoecological data with a process-based vegetation model, we aim to investigate if past plant community shifts in Mediterranean ecosystems can be explained by climate-induced changes in past fire regimes. We also simulate future vegetation dynamics under different climate projections and wildfire scenarios to assess ecosystem stability, identify potential tipping points that lead to ecosystem shifts and inform management strategies to mitigate adverse climate-change impacts.

2 | MATERIALS AND METHODS

We simulated past and future vegetation dynamics and wildfire regime changes in three study areas on the island of Sardinia: Lago di Baratz, Stagno Sa Curcurica and Stagno di Chia (Figure 1; hereafter referred to as Baratz, Sa Curcurica and Chia, respectively). The study areas have a radius of 5km and are centered around palaeoecological archives that provide quantitative information about vegetation changes and biomass burning for the past 8000 years. The three lakes were cored in 2012 and analysed for pollen, plant macrofossils and microscopic charcoal to reconstruct local to regional wildfire and vegetation history (see the Supporting Information for details about palaeoecological analyses and the study sites). Permission for fieldwork was granted by the regional government and the individual communities. Fieldwork was carried out with the assistance and under the supervision of the Corpo Forestale e di Vigilanzia Ambientale della Regione Sardegna (forestry and environmental protection corps of the Region of Sardinia). The size of the study areas was chosen to reflect the relevant pollen source area of our palaeoecological archives (Conedera et al., 2006), in order to facilitate the model–data comparison. All study areas are located close to the sea and mostly fall within the thermomediterranean vegetation belt, where evergreen broadleaved Mediterranean woody species prevail. Nonetheless, the study areas also encompass the mesomediterranean vegetation belt at higher elevations, in which both deciduous and evergreen broadleaved species co-occur (Chiappini, 1988).

Sardinia has a typical Mediterranean climate with hot and dry summers and mild and rainy winters. Both temperature and precipitation follow an altitudinal gradient, with cooler and wetter conditions at higher elevations and warmer and drier conditions at the coast (see Supporting Information). There is also a slight north–south gradient, with higher temperatures in the south, while rather complex precipitation patterns prevail along the west–east gradient (Pedrotta et al., 2021). Sardinia is a fire-prone region with about 2900 fires recorded per year during the period 1998–2016, burning an average of ca. 18,500 ha year^{-1}, which represents ca. 1% of the total area of the island (Salis et al., 2021). Accordingly, the fire return interval (FRI) averaged over entire Sardinia is ca. 100 years. However, certain areas and land cover types, such as shrublands or agricultural areas show a higher ignition frequency and are more affected (Bajocco et al., 2019; Bajocco & Ricotta, 2008). Most fires occur during the summer months with a peak in July. The vast majority of recorded fires are relatively small (<10 ha), with most of the area burned caused by individual fires that burned large areas (>1000 ha; Salis et al., 2014, 2021).

2.1 | LandClim simulations

We simulated vegetation dynamics and fire regime changes at the three study areas with LandClim, a process-based, spatially explicit, dynamic vegetation model (Schumacher et al., 2004). In contrast to palaeoecological records, dynamic simulations have the advantage that the environmental conditions and drivers affecting vegetation communities are known and can be controlled, similar to setting up an ecological experiment. Therefore, comparing the results of dynamic modelling runs under different conditions to palaeoecological data allows to mechanistically investigate the causes of past ecosystem shifts (Henne et al., 2011; Schwörer et al., 2014). Once validated in the past, under strongly changing environmental conditions, dynamic models might be applied to anticipate future conditions under different land use and climate scenarios (Henne et al., 2015; Schwörer et al., 2014). LandClim was originally developed for and applied in central European forest ecosystems, but has also been successfully used in the Mediterranean region (Henne et al., 2013, 2015). The simulated vegetation is fully independent from palaeoecological data and therefore an emergent property of the numerical model simulation. The pollen-inferred vegetation is only used for comparison with the model output. We simulated vegetation development from bare ground with no initial species cover and a spin-up period of 500 years to reach equilibrium. LandClim simulates establishment, growth, dispersal and mortality of species cohorts in individual 25×25 m grid cells, based on species-specific functional traits and thresholds (e.g. growth rate, maximum height, drought tolerance; see Table S3), competitive interactions between species (e.g. light competition), topographic parameters (e.g. elevation, aspect) and monthly climatic parameters (temperature and precipitation). Mortality is caused by biotic (density, competition) and abiotic stress (e.g. drought), disturbances such as wildfire and windthrow, or maximum longevity. Wildfire is simulated over the entire landscape in decadal timesteps. The probability of fire ignition and spread is based on a cumulative beta probability density function related to the drought index of each cell, as well as fuel availability and topography. Wildfire leads to tree mortality depending on species-specific fire sensitivity, tree height, fuel dryness and availability. How well individual species can tolerate fires is based on observed stem survival after fire (Fernandes et al., 2008; González et al., 2007), which was qualitatively summarized in five different fire tolerance classes (Henne et al., 2013). Species with low fire tolerance have higher probabilities of mortality after a fire event. Fire-adapted species that are resprouters (e.g. *Erica arborea*) or have serotinous cones (e.g. *Pinus halepensis*), do not need to establish after a fire event and can thus immediately start accumulating biomass again, which gives them a competitive advantage in the model simulations. Fire frequency and intensity are linked by fuel availability, with lower fire frequencies leading to fuel accumulation and more intense fire events that result in more biomass lost. Conversely, higher fire frequencies result in lower fuel availability and therefore less intense wildfires (Henne et al., 2013; Schumacher et al., 2004). More information about the fire module of LandClim can be found in the Supporting Information.

2.2 | Simulated climate and wildfire scenarios

To simulate past and future vegetation dynamics and wildfire regimes, we developed different climatic scenarios. First, we estimated modern average monthly temperatures and precipitation values by combining data series from nearby climate stations for the period 1951–2010 (SCIA, 2021). For the simulation of past vegetation dynamics, we then combined randomly drawn values from a normal distribution of present climate data with reconstructed July-temperature anomalies for the last 9000 years from Lago Verdarolo (Henne et al., 2013; Samartin et al., 2017), or in the case of precipitation with downscaled transient precipitation anomalies from the TraCE21k global climate model dataset (Karger et al., 2023; Liu et al., 2009). For the future climate scenarios, we used the same approach as outlined above, but restricted the present-day climate data to the reference period 1980–2010 and combined them with downscaled model output of an ensemble of five climate models and three emission scenarios ('ssp126': low emission scenario; 'ssp370': intermediate emission scenario; and, 'ssp585': high emission scenario; Karger et al., 2017). The emission scenarios were chosen to represent the full range of future climate-change conditions, from worst to best case (O'Neill et al., 2016). For the period 2100–2500 climate projections have been kept constant at the level of 2100 with current climatic variation (Figure 4), to enable vegetation to reach a new equilibrium. Finally, LandClim uses the monthly climate input data to calculate values for every grid cell in the landscape, based on altitudinal lapse rates that we determined by linear regression using data from climate stations at different elevations in the regions surrounding each study site (see Supporting Information).

To simulate the effect of different fire regimes on past and future vegetation, we developed three different fire scenarios with low, moderate and high fire occurrence. The fire scenarios vary in the minimum fire probability and the shape of the curve of the probability function that relates fuel dryness to fire spread. In other words, they range from infrequent small fires in the low fire scenario, to frequent large fires in the high fire scenario, consistent with previous applications to simulate different fire regimes in the Mediterranean (Henne et al., 2013, 2015; Figure S5). To test the hypothesis that climate was the main driver of vegetation trajectories on Sardinia, we simulated vegetation dynamics for the last 8000 years at all three study areas (Figure 2) under a low fire frequency, and compared model output with the reconstructed vegetation. To test our hypothesis that fire regime changes were driving vegetation changes, we assigned in a second step the three fire scenarios to time periods with high, moderate or low biomass burning at each study area based on individual charcoal influx data series from the three sites (Figure 3; Figure S6). Microscopic charcoal influx recorded in lake sediment archives has been widely used as a proxy for regional fire occurrence (Conedera et al., 2009; Connor et al., 2019; Lestienne, Jouffroy-Bapicot, et al., 2020; Whitlock et al., 2010), based on regional calibration studies (e.g. Leys et al., 2015; MacDonald et al., 1991; Tinner et al., 1998), and theoretical considerations regarding particle emission, transport and deposition (e.g. Clark, 1988; Gilgen et al., 2018). A recent continental-scale calibration study of microscopic charcoal influx with satellite-inferred fire parameters confirmed a significant correlation between charcoal particles deposited in lakes and fire number and intensity (Adolf et al., 2018). By prescribing different fire regimes based on palaeoecological data, we aim to test our hypothesis that fire is the main driver of observed vegetation change during the Holocene. For the future vegetation dynamics, we combined all climate and fire scenarios to explore a wide array of future vegetation trajectories. Since human activity is not explicitly included in LandClim, we use the low and high fire frequency scenario to represent different anthropogenic fire regimes, with intensified land use causing higher anthropogenic ignitions in the high fire scenario. To avoid unrealistically large fires, we restricted maximum individual fire size to 10% of the study area. However, cumulative fire size over a decade can be larger than this value, with multiple fire events occurring in the study area and even on the same gridcells, if fuel availability is still high enough. Even though these fire scenarios are prescribed, the fire module of LandClim still allows for feedback loops between climate and fire. Warmer temperatures and/or less precipitation, for example, increase fuel dryness and enhance fire spread, leading to a larger area burned.

3 | RESULTS

3.1 | Simulation of past vegetation dynamics

The simulation results under the low fire frequency scenario show that *Quercus ilex* is projected to grow in all study areas (Figure 2j–l), particularly where soils are deep or at higher elevations (Figure 2p–r; Figure S3a–f). Around Baratz (Figure 2j), LandClim simulates abundant *Q. ilex* forests with an increasing biomass trend throughout the Holocene, linked to the cooling following the Holocene Thermal Maximum (HTM), between 9000 and 5500 calibrated years before present (cal. BP; Figure 2a). Drier periods result in a decrease in biomass, but simulated forests quickly recover within ca. 50–100 years. Simulated burned area and associated fire return intervals at all sites only show minor changes during the past 8000 years, with slightly higher burned area and lower FRI during the (warmer) HTM (Figure 2m–o). FRI are lower at Sa Curcurica (50–100 years) and Chia (30–60 years) than at Baratz (70–250 years), where *Q. ilex* attains higher biomass. Overall, the simulations with low fire frequency only match the reconstructed vegetation at our study areas from ca. 5500 cal. BP onwards. The dominance of *Erica* at the start of the three records (Figure 2d–f) cannot be recreated with this scenario, rejecting the hypothesis that climate was the main driver of vegetation change.

In a second step, to test the hypothesis that varying wildfire regimes caused the observed vegetation changes, we simulated Holocene vegetation dynamics with different fire regime scenarios, according to reconstructed periods of high, moderate and low biomass burning of each record. Since LandClim is not able to reproduce reconstructed fire regimes based on climatic input data alone, we prescribe different fire frequencies over the entire simulation period to study the effect on the vegetation. Under high fire frequencies, as reconstructed for the start of all three records, LandClim simulates vegetation (co-)dominated by *Erica* around the three lakes (Figure 3j–l), which is particularly evident in the spatial data

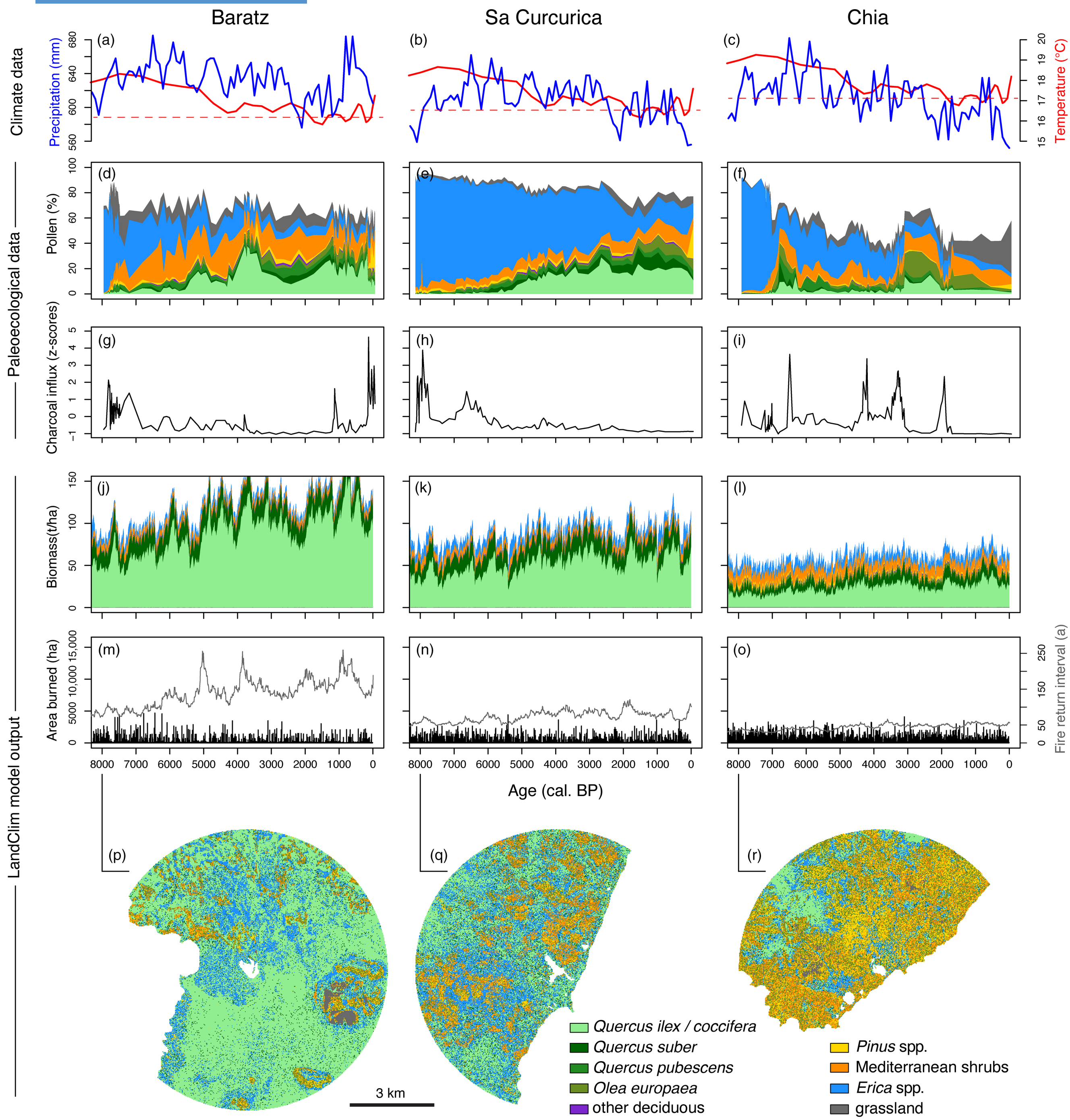


FIGURE 2 Simulated past vegetation and biomass burning in the three study areas under a low fire regime scenario compared to palaeoecological data (Beffa et al., 2016; Pedrotta et al., 2021). The top row shows climate input data used for the simulations (a–c). Annual temperatures are based on July temperature reconstructions from Lago Verdarolo (Samartin et al., 2017), adjusted to the study areas based on present-day temperature differences. Precipitation data are based on downscaled Trace-21k global climate model data (Karger et al., 2023; Liu et al., 2009). Palaeoecological data show stacked pollen percentages of selected species over time (d–f) as well as *z*-scores of charcoal influx as a proxy for biomass burning (g–i; Beffa et al., 2016; Pedrotta et al., 2021). LandClim model output shows the biomass (t/ha) of different species in the three study areas (j–l), as well as area burned (ha) and related fire return interval (m–o). Maps of the three study areas show simulated dominant species per gridcell at 8000 cal. BP (p–r). 'Other deciduous' includes *Fraxinus ornus* and *Ostrya carpinifolia*; 'Mediterranean shrubs' include *Arbutus unedo*, *Cistus salviifolius*, *Phillyrea latifolia*, *Phillyrea angustifolia*, *Pistacia lentiscus*, *Rhamnus alaternus* and *Rhamnus oleoides*; '*Pinus* spp.' includes *Pinus pinea*, *Pinus pinaster* and *Pinus halepensis*.

(Figure 3p–r). Area burned is high and FRI are very low (5–10 years) at all sites (Figure 3m–o). With the change to moderate fire frequencies between 7000 and 5000 cal. BP, *Quercus ilex* expands and becomes the dominant species in the simulated study areas, except around the warmest site Chia, where it only dominates at higher elevations. Considering that most of the pollen deposited in lakes of this size

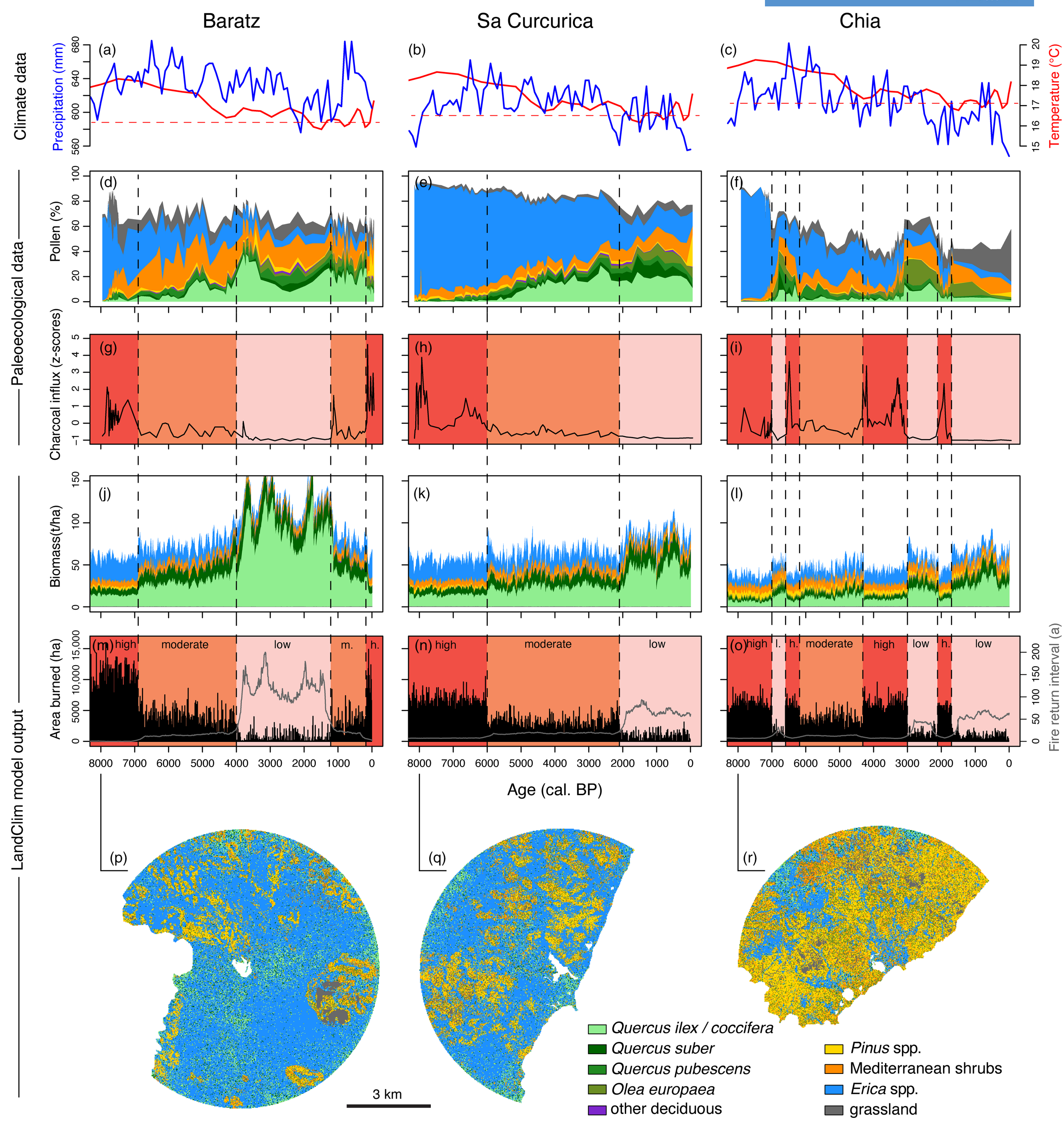
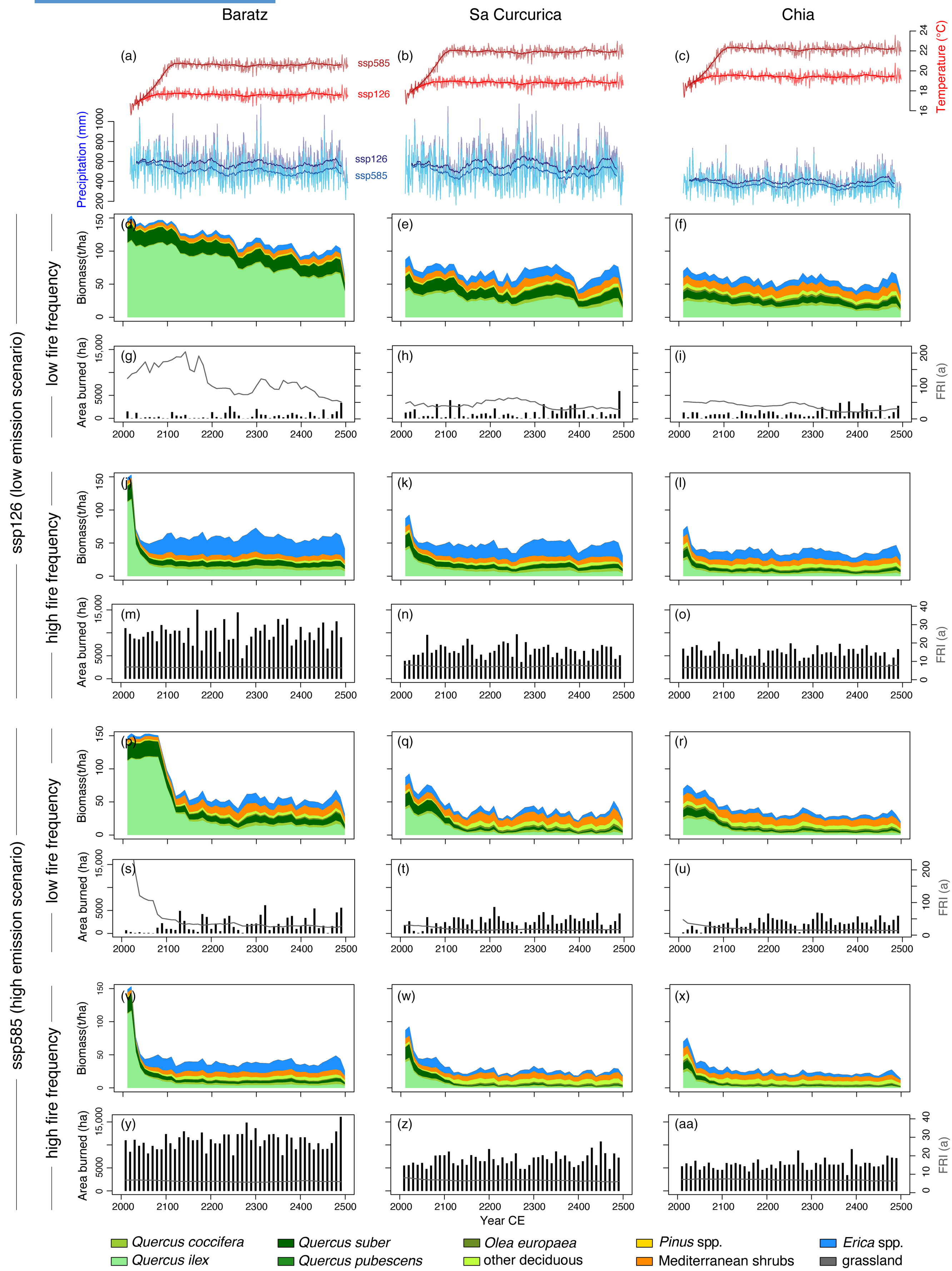


FIGURE 3 Simulated past vegetation and biomass burning in the three study areas under a combination of three different fire scenarios (low, moderate and high fire regime) compared to palaeoecological data (d–f; Beffa et al., 2016; Pedrotta et al., 2021). We use the charcoal influx records at each lake (g–i) to infer fire regimes characterized by high, moderate or low fire activity and applied these scenarios to the simulation. LandClim model output shows the biomass of different species at the three study areas (j–l) as well as area burned (ha) and related fire return interval (m–o). Maps of the three study areas show simulated dominant species per gridcell at 8000 cal. BP (p–r). Climate (a–c), palaeoecological data and species legends are the same as in Figure 2.

comes from their immediate surroundings, simulated and pollen-inferred vegetation match well for this period. Area burned is lower with FRI between 15 and 25 years. Under low fire frequencies, *Q. ilex* further increases in biomass and even forms closed forests at Baratz (>50 t/ha; Figure 3j). At Chia, our southernmost site, LandClim consistently simulates the lowest amount of biomass (Figure 3l). The rather open Mediterranean vegetation simulated for the entire period generally agrees well with the pollen record (Figure 3f). Even the two short expansion phases of *Q. ilex* and *Olea europaea* at 7000–6200 and 3000–2500 cal. BP are evident in our simulations and linked to short periods of lower fire occurrence. Only during the last 1800 years of the simulation there is a pronounced mismatch



Baratz
Sa Curcurica
Chia
(a)
(b)
(c)
ssp585
ssp126
ssp126
ssp585
Temperature (°C)
Precipitation (mm)
ssp126 (low emission scenario)
ssp585 (high emission scenario)
low fire frequency
high fire frequency
Biomass(t/ha)
Area burned (ha)
FRI (a)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
(m)
(n)
(o)
(p)
(q)
(r)
(s)
(t)
(u)
(v)
(w)
(x)
(y)
(z)
(aa)
Year CE
Quercus coccifera
Quercus ilex
Quercus suber
Quercus pubescens
Olea europaea
other deciduous
Pinus spp.
Mediterranean shrubs
Erica spp.
grassland

FIGURE 4 Simulated future vegetation and wildfire dynamics under two different climate and two different fire scenarios. Top row shows ensemble climate data used to run the simulations, with lines indicating individually downscaled annual temperatures (red) and precipitation (blue) as well as a 30-year running mean under the 'ssp126' and 'ssp585' pathway, respectively (a–c; Karger et al., 2020). The plot show species biomass (t/ha), area burned (ha) and fire return intervals (FRI) under low (d–i, p–u) and high (j–o, v–aa) fire regime for the two emission pathways. See the supporting information for simulation output under the intermediate 'ssp370' scenario.

between the model and the pollen data. With simulated low fire frequencies, *Q. ilex* expands in the model, whereas the pollen record indicates Mediterranean shrubland and open grassland. A marked increase in indicator taxa of human disturbance during this time (Figure S2) suggests that the vegetation opening was caused by anthropogenic activities.

3.2 | Simulation of future vegetation dynamics under different climate and fire scenarios

Under low fire frequencies and the lowest emission scenario ('ssp126'), which results in an increase of mean annual temperatures by 1.5–1.6°C, *Quercus ilex* is projected to prevail in the three study areas, together with Mediterranean shrubland (Figures 4d–f and 5a–c). This result suggests that natural vegetation is resilient to temperature and precipitation changes that do not exceed Holocene climate variability. In contrast, an increase in fire frequency leads to dramatic changes in species composition, with a decline of *Q. ilex* and the expansion of fire-adapted *Erica arborea* and *Erica scoparia* (Figures 4j–l and 5d–f). The resulting vegetation is similar to that dominating 8000–5500 years ago, under warm conditions. With intensified exploitation of fossil fuel resources (as assumed in the high emission scenario 'ssp585'), mean annual temperatures are projected to increase by 4.3–4.7°C, resulting in mean annual temperatures around 22–23°C (Figure 4a–c) well exceeding Holocene reconstructions (Samartin et al., 2017), including the HTM. This is combined with ca. 15% lower annual precipitation and, more importantly, longer summer drought. Even under low fire frequencies, a climatic change of this magnitude leads to pronounced vegetation changes in the simulation. *Quercus ilex* forests decline in all three study areas and are replaced by Mediterranean maquis or open grasslands (Figure 4p–r). However, in areas with high soil water holding capacity or at higher elevations, *Q. ilex* is still able to persist at low abundances (Figure 5g–i). Simulated *Quercus ilex* forests already decline under the intermediate emission scenario ('ssp370'; Figure S7) in all study areas. Our simulation results also show that the high emission scenario 'ssp585' will lead to more simulated wildfires and a higher fire return interval compared to the 'ssp126' scenario (Figure 4s–u). Under a combination of high fire frequencies and unmitigated climate change, *Q. ilex* almost completely disappears from the study areas (Figure 4v–x). *Erica arborea* and *E. scoparia* are again able to expand, but only where soils are deep enough, such as around Baratz or at higher elevations (Figure 5j–l). Besides open grasslands on shallow soils, the study areas are mainly characterized by Mediterranean maquis and *Pinus*.

4 | DISCUSSION

Our modelling results suggest that *Erica* species (*E. arborea* and *E. scoparia*) only achieve dominance in scenarios with very high fire frequency (Figure 3), confirming statistical evidence of the positive relationship between *Erica* and wildfires (Pedrotta et al., 2021). Other palaeoecological studies from the Mediterranean Basin also show a positive relationship between *Erica* and biomass burning (Connor et al., 2012; Lestienne, Jouffroy-Bapicot, et al., 2020; Morales-Molino et al., 2013, 2022). In the Bale Mountains of Ethiopia, where *Erica arborea* currently characterizes the subtropical Afromontane vegetation belt, palaeoecological investigations also documented long-term linkages between biomass burning and *Erica* abundances (Gil-Romera et al., 2019). Similar to Sardinia, higher fire frequency between 11,000 and 6000 cal. BP led to the dominance of *Erica* in the landscape, causing a significant positive feedback with fire occurrence. Ultimately, this led to a self-stabilizing system of high resilience (Gil-Romera et al., 2019). *Erica arborea* is very well adapted to wildfire and can quickly resprout from its lignotuber, a basal burl that stores carbohydrates and contains many dormant buds (La Mantia et al., 2007; Mesléard & Lepart, 1989). Young, shrublike *Erica* is also highly flammable (Johansson & Granström, 2014), which can lead to a so-called 'fire-trap', with rapid fuel accumulation within a few decades causing high fire frequencies (Gil-Romera et al., 2019). This observation matches well with our simulation results for the middle Holocene on Sardinia, indicating that high fire frequency was primarily responsible for the dominance of *Erica* (Figure 3). In simulations with low fire frequencies, *Erica* is outcompeted by the more shade-tolerant *Quercus ilex* (Figure 2).

Why *Erica* communities were widespread on Corsica and Sardinia but did not dominate in other areas of the Mediterranean Basin is unclear. Several Mediterranean islands show distinct vegetation trajectories, particularly if they are geographically isolated from the mainland (Burjachs et al., 2017). Sicily, for example, shows high abundances of *Pistacia* during this period, which has been linked to dry conditions in the early Holocene and exceptionally high biomass burning (Calò et al., 2012; Tinner et al., 2009). Intriguingly, vegetation reconstructions from Sardinia and Corsica indicate that evergreen oak or pine forests were abundant before 9000 cal. BP (Kalis & Schoch, 2019; Lestienne, Jouffroy-Bapicot, et al., 2020; Reille, 1992), with *Erica* expanding only afterwards. The presence of *Quercus ilex* during the early Holocene on Sardinia rules out a

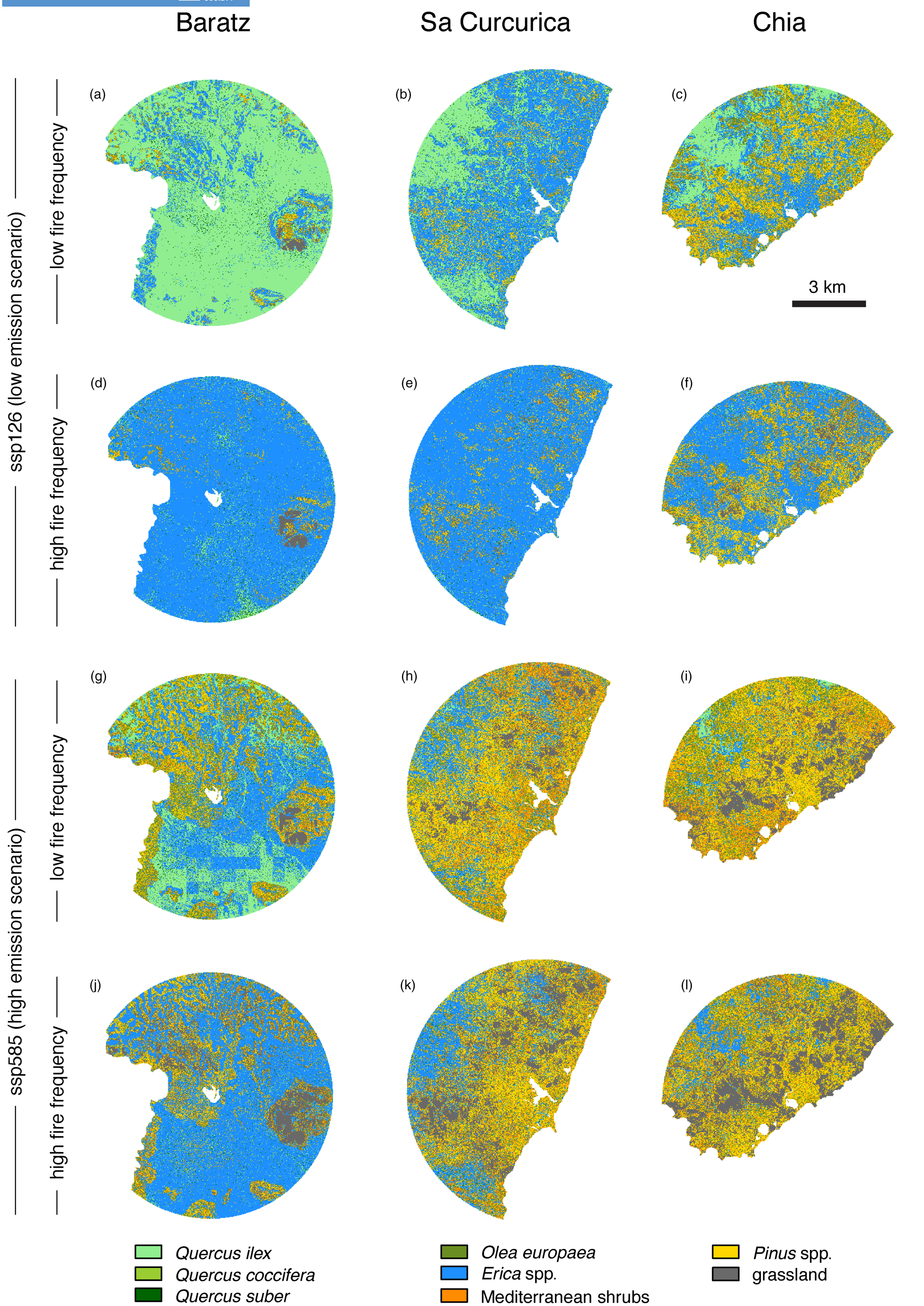


FIGURE 5 Spatial maps showing dominant species per gridcell at the year 2300 for different climate ('ssp126': a–f; 'ssp585': g–l; Karger et al., 2020) and fire scenarios in the three study areas. See the Supporting Information for simulation output under the intermediate 'ssp370' scenario.

'home-field-advantage' situation favouring *Erica* species. Maximum values of *Erica* between 9000 and 7000 cal. BP are also recorded in Tunisia (Ben Tiba & Reille, 1982; Stambouli-Essassi et al., 2019) and off its coast (Desprat et al., 2013), indicating that the dominance of *Erica* is not just an insular exception. We hypothesize that the high abundance of *Erica* during the early to middle Holocene in Sardinia might have been caused by an optimal combination of high fire frequency and reduced moisture availability. Under cooler mesomediterranean conditions with lower fire frequency and/or higher moisture availability such as on the Italian mainland, *Quercus ilex* was able to expand or persist, in combination with deciduous oaks and the rather mesophilous *Abies alba* and/or *Fagus sylvatica* (Allen et al., 2002; Colombaroli et al., 2007; Drescher-Schneider et al., 2007; Henne et al., 2015; Magri & Sadori, 1994). Different environmental conditions effectively prevented the expansion of *Erica* during the Holocene, resulting in an alternative stable state. Conversely, under warmer thermomediterranean conditions with very high fire frequency and lower moisture availability, such as on the coastal areas of southern Sicily or Malta, *Erica* could not become dominant, because more drought-tolerant Mediterranean shrubs and trees such as *Pistacia lentiscus* and/or *Olea europaea* had a competitive advantage (Calò et al., 2012; Curry et al., 2016; Djamali et al., 2013; Henne et al., 2015; Noti et al., 2009; Tinner et al., 2009). Indeed, the expansion of *Erica* during the late Holocene in pollen records from the Southern Mediterranean and Northern Africa has been attributed to a slight increase in moisture availability (Benslama et al., 2010; Calò et al., 2013; Stambouli-Essassi et al., 2019), if compared to the very dry early Holocene conditions.

Our simulation results suggest that millennial scale climatic changes alone, such as the post-HTM cooling starting around 5500 cal. BP coupled with increasing moisture availability (Henne et al., 2013; Magny et al., 2007; Samartin et al., 2017; Tinner et al., 2009, 2013), cannot account for the pronounced shifts in vegetation communities and fire regime observed in the palaeoecological records (Figure 2). However, these climatic changes very likely affected fire regimes by altering fuel dryness, which controls fire spread, and perhaps also ignition frequency (e.g. by lightning). Additionally, a shift to cooler and wetter climatic conditions may have promoted the establishment of less flammable species, further reducing fire frequencies (Lestienne, Hély, et al., 2020). Since our model is not able to integrate the full complexity of fire-climate-vegetation interactions, we prescribed changes in fire regimes based on reconstructed biomass burning, to study the effect on simulated vegetation. Such fire regime changes immediately resulted in a shift in vegetation types in the simulations (Figure 3), pushing the system into a new stable state. The step-like changes in reconstructed wildfire occurrence at our sites and the good agreement with simulation results indicates that FRI crossed a threshold of c. 25–50 years, allowing the expansion of *Quercus ilex* forests. The asynchronous expansion, however, suggests that local factors such as topography and soil conditions (Schwörer et al., 2017), as well as perhaps human impact (Jouffroy-Bapicot et al., 2021; Lestienne, Jouffroy-Bapicot, et al., 2020) also played an important role. Once established, closed evergreen oak forest likely also affected the fire regime. The cooler and moister microclimate of the understory reduces the flammability of living and dead biomass (Azevedo et al., 2013; Henne et al., 2015; Tinner et al., 2009), resulting in a self-stabilizing system with low fire occurrence. This is particularly apparent in the two northern sites of Baratz and Sa Curcurica. In Chia, *Q. ilex* was never able to dominate the landscape for long periods of time, except for 7000–6200 and 3000–2500 cal. BP, when reconstructed biomass burning was also low. Rapid switching between the two alternative stable states of *Erica*-dominated vegetation with high fire frequency and *Q. ilex* woodlands with low fire frequency indicate that this site is closer to a climatic moisture-mediated threshold (Scheffer et al., 2009). Indeed, the spatially explicit data (Figure 2) points out that in contrast to the two northern sites, *Quercus ilex* was restricted to higher elevations and was not able to establish closed forests around the lake, even under low fire frequencies.

Mixed *Quercus ilex* woodlands were abundant in the Mediterranean Basin, covering large areas from Turkey to Iberia including Northern Africa, before human impact transformed the landscape (Quézel & Médail, 2003). Since these forests are projected to be resilient to future climate change and may mitigate an expected increase in biomass burning due to their lower flammability, they have been suggested as a valuable management goal (Henne et al., 2015). Our simulation results under a low and intermediate emission scenario ('ssp126', Figures 4 and 5; see Figures S7 and S8 for 'ssp370') agree with Henne et al. (2015) and confirm the potential for closed evergreen oak forests in coastal areas of Sardinia, particularly in those with deeper soils or at higher elevations. However, without an immediate reduction of greenhouse gas emissions, our simulations project that climate change will lead to pronounced changes in plant communities, with closed forests being replaced by highly flammable maquis or grassland. Similar communities have also been projected to occur under climate warming on the island of Sicily further south (Henne et al., 2015). Such a shift in plant communities might result in a change in fire regimes, which has the potential to further alter the vegetation by favouring fire-adapted species. Indeed, the simulations with a high emission scenario show more area burned and a higher fire frequency than under the low emission scenario, agreeing well with other studies that predict an increase in fire events in the Mediterranean Basin under climate change (Dupuy et al., 2020; Lestienne et al., 2022; Turco et al., 2018). Given that the climate projections for the highest emission scenario are ca. 3°C warmer and likely drier than the HTM, increased fuel dryness and fire season length will further increase the probability of fire spread. However, under the very warm 'ssp585' scenario, *Erica* does not become dominant in the simulations, even under high fire frequencies (Figures 4 and 5). This is consistent with our hypothesis that *Erica* is only able to dominate under an optimal combination of enhanced fire occurrence and moisture availability. With mean annual temperatures of 22–23°C, lower precipitation, extended summer drought, and recurrent wildfires, xeric shrublands or open woodlands with *Pistacia lentiscus* and *Pinus halepensis*, as well as grasslands will dominate the vegetation, except for areas with deeper soils or at higher elevations, where *Erica* can still prevail. Such plant communities have no analogue on Sardinia throughout the Holocene, but were abundant on Sicily and Malta under very dry and warm conditions during the early and middle Holocene (Calò et al., 2012; Djamali et al., 2013; Henne et al., 2015; Tinner et al., 2009). Hence, in agreement with previous dynamic vegetation simulations (Henne et al., 2015; Hickler et al., 2012), we can project a poleward shift of vegetation zones in response to climate change in the Mediterranean Basin, if climate warming exceeds the Holocene variability (of ca. +2°C compared to recent decades; Samartin et al., 2017). Besides latitudinal shifts, plant species will also move upslope to cooler and wetter areas to stay within their optimal climatic niche. Such upward shifts of species ranges are already documented in European mountain ranges (Steinbauer et al., 2018) and match vegetation models from the Alps (Henne et al., 2011; Schwörer et al., 2014). However, since the limiting factor for many species in the Mediterranean is moisture availability, tree species might be able to also persist in areas with deeper soils or a shallow water table.

In contrast to other studies from the Mediterranean Basin (Colombaroli et al., 2007; Tinner et al., 2009), increasing human impact during the past 4000 years did not consistently result in an increase in biomass burning on Sardinia. Such a pattern is only observed at Baratz, where an increase in fire occurrence caused by anthropogenic activities during the Middle Ages and again in recent times led to the decline of *Quercus ilex* (Pedrotta et al., 2021), as also reproduced by our simulations. At Sa Curcurica and Chia fire occurrence progressively declined, even if human impact increased. Whereas at Sa Curcurica, *Quercus ilex* was still abundant and might have inhibited the probability of fire occurrence, the vegetation at Chia was dominated by Mediterranean shrubs, *Olea europaea* and open grasslands during the last 1500 years. Our simulations clearly point out that this landscape is a result of human land use. However, it is likely that these intensive human activities effectively suppressed wildfires by reducing fuel loads and connectivity. Indeed, several studies from the Mediterranean Basin indicate that grazing by sheep or goats reduces particularly flammable fine fuels (Colantoni et al., 2020; Damianidis et al., 2021; Mancilla-Leytón et al., 2013). Much in contrast to conditions during the past 4000 years, current and future anthropogenic ignitions and land use have the potential to cause unprecedented fire impacts. Specifically, simulated fire-driven vegetation shifts (Figures 4 and 5) might be particularly exacerbated by plantations of non-native trees such as pines and eucalypts that are highly flammable. Native *Erica arborea* and *Erica scoparia* in the undergrowth or in neighbouring natural vegetation could immediately benefit by resprouting and building up biomass, thereby supporting a higher frequency fire regime, if left unchecked. Indeed, trees and shrubs with fire-adapted seeds or resprouting capacity show enhanced postfire abundance in burned pine plantations on Sardinia (Ladd et al., 2005).

By including charcoal-based reconstructions of wildfire regime shifts in our simulations of past vegetation dynamics, we were able for the first time to mechanistically simulate ecosystem switches to alternative stable states that have been recorded in natural archives. This suggests that the model is well suited to identify future climate-driven tipping points that threaten current ecosystem stability. It also indicates that the underlying causes of rapid vegetation change in response to fire regime shifts and associated feedbacks that can maintain different ecosystem states are ecologically well understood. In summary, we could show that wildfire was an important driver of vegetation change during the past 8000 years and will continue to be so in the future. The fire regime itself, however, is the product of climatic factors, the extant vegetation and anthropogenic or natural ignition sources. The interplay of these factors is likely to determine future vegetation composition on the island and the wider Mediterranean region. Anticipatory forest and landscape management can directly influence some of these factors to mitigate adverse effects of future climate change. By promoting *Quercus ilex* and other less flammable trees including *Olea europaea* instead of plantations of highly flammable non-native trees such as *Eucalyptus* spp., fire risks would be reduced and important ecosystem services such as watershed stability or carbon storage improved. Even though such evergreen oak forests may be less profitable over short time scales compared to plantations if only timber production is considered and fire occurrence is neglected (Hanewinkel et al., 2013), they would be more economical over longer time scales by reducing fire risks, maintaining ecosystem services (e.g. inhibiting soil erosion), and preventing associated economic losses. To prevent a return of conditions similar to 8000 years ago, when *Erica* was dominating the local natural vegetation, a reduction of anthropogenic ignition sources is needed. Considering that 95% of all fires in the Mediterranean region are caused by humans with the majority even started deliberately (Ganteaume et al., 2013), a significant reduction would be feasible, but needs the support of the local population and strict enforcement. In addition, mitigating the possibility of fire spread may be aided by reducing the amount of fine fuel by promoting traditional pastoral activities such as grazing by sheep or goats. Once evergreen oak forests have reestablished, different microclimatic conditions within the dense, dark and moist forests would result in a lower fire occurrence. However, our simulations indicate that this can only be achieved if anthropogenic greenhouse gas emissions are significantly reduced to keep global climate warming below the 2°C threshold. If not, the system will switch to a new alternative stable state with the expansion of flammable Mediterranean shrubland along the coast. Such ecosystems would require different fire management strategies that may also include prescribed fires outside the fire season (Fernandes et al., 2013). Current wildfire management in Mediterranean areas is still mostly focused on fire suppression instead of including fire mitigation strategies (Moreira et al., 2020). Mixed evergreen oak forests that represent today's potential natural vegetation will be restricted to higher elevations, leading to a deterioration of ecosystem services and an increase in fire events in the lowlands, where most larger population centres are located.

Our ecological inferences are broadly applicable beyond the study region of Sardinia for the wider Mediterranean Basin and other subtropical ecosystems around the world. This is also highlighted by the close analogies of past vegetation dynamics between our sites and the Afromontane belt of Ethiopia. Both our palaeoecological reconstructions and dynamic simulations show the potential for rapid changes in plant communities driven by fire regime shifts and climate change, once a disturbance threshold is passed. Most importantly, if future climatic changes will exceed the Holocene variability, increasing fire frequencies may cross tipping points and push fire-tolerant ecosystems to transient, highly unstable reorganization stages, possibly showing unprecedented structural and floristic features, before a new alternative stable state is reached.

AUTHOR CONTRIBUTIONS

Christoph Schwörer, César Morales-Molino, Erika Gobet and Willy Tinner designed the research; César Morales-Molino, Tiziana Pedrotta and Jacqueline F. N. van Leeuwen contributed palaeoecological data, which were analysed by Christoph Schwörer and César Morales-Molino; Salvatore Pasta contributed site descriptions; Christoph Schwörer performed simulations with help from Paul D. Henne; Christoph Schwörer created all figures and wrote the first draft of the manuscript. All co-authors commented and substantially contributed to the final manuscript.

ACKNOWLEDGEMENTS

We dedicate this article to the memory of our dear friend and colleague Daniele Colombaroli, who unexpectedly passed away during the completion of this manuscript. We thank Willi Tanner and Carole Adolf for help during fieldwork and all the participants of the XLIII International Moor Excursion to Sardinia in 2019 for the fruitful discussions in the field. We would also like to thank four anonymous reviewers for constructive comments on a previous version of this manuscript. Funding for this study was provided by the Swiss National Science Foundation (SNF200021_134616). César Morales-Molino was supported by a 'María Zambrano' fellowship (Ministerio de Universidades/Universidad de Alcalá/European Union). Open access funding provided by Universität Bern.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14293.

DATA AVAILABILITY STATEMENT

All input files to run the dynamic vegetation model and R code to analyse output are available on Github: https://github.com/Schwoeri/LandClim and archived on Zenodo https://doi.org/10.5281/zenodo.10732256 (Schwörer, 2024). All palaeoecological data is archived in the Alpine Palynological Database (ALPADABA), a constituent database of the Neotoma Palaeoecology Database (www.neotomadb.org). Lago di Baratz: https://doi.org/10.21233/EB00-W497 (pollen), https://doi.org/10.21233/VAHC-V730 (charcoal); Stagno di Sa Curcurica: https://doi.org/10.21233/89TB-QN51 (pollen), https://doi.org/10.21233/2TV2-NP52 (charcoal); Stagno di Chia: https://doi.org/10.21233/MSJ5-3P61 (pollen), https://doi.org/10.21233/967D-Q473 (charcoal).

ORCID

Christoph Schwörer https://orcid.org/0000-0002-8884-8852
César Morales-Molino https://orcid.org/0000-0002-9464-862X
Erika Gobet https://orcid.org/0000-0002-3487-8108
Paul D. Henne https://orcid.org/0000-0003-1211-5545
Salvatore Pasta https://orcid.org/0000-0003-3265-9072
Tiziana Pedrotta https://orcid.org/0000-0001-8490-7731
Boris Vannière https://orcid.org/0000-0002-6779-6053
Willy Tinner https://orcid.org/0000-0001-7352-0144

REFERENCES

Adams, M. A. (2013). Mega-fires, tipping points and ecosystem services: Managing forests and woodlands in an uncertain future. *Forest Ecology and Management*, *294*, 250–261. https://doi.org/10.1016/j.foreco.2012.11.039

Adolf, C., Wunderle, S., Colombaroli, D., Weber, H., Gobet, E., Heiri, O., van Leeuwen, J. F. N., Bigler, C., Connor, S. E., Gałka, M., La Mantia, T., Makhortykh, S., Svitavská-Svobodová, H., Vannière, B., & Tinner, W. (2018). The sedimentary and remote-sensing reflection of biomass burning in Europe. *Global Ecology and Biogeography*, *27*(2), 199–212. https://doi.org/10.1111/geb.12682

Allen, J. R. M., Watts, W. A., McGee, E., & Huntley, B. (2002). Holocene environmental variability—The record from Lago Grande di Monticchio, Italy. *Quaternary International*, *88*(1), 69–80. https://doi.org/10.1016/S1040-6182(01)00074-X

Azevedo, J. C., Possacos, A., Aguiar, C. F., Amado, A., Miguel, L., Dias, R., Loureiro, C., & Fernandes, P. M. (2013). The role of holm oak edges in the control of disturbance and conservation of plant diversity in fire-prone landscapes. *Forest Ecology and Management*, *297*, 37–48. https://doi.org/10.1016/j.foreco.2013.02.007

Bajocco, S., Ferrara, C., Guglietta, D., & Ricotta, C. (2019). Fifteen years of changes in fire ignition frequency in Sardinia (Italy): A rich-get-richer process. *Ecological Indicators*, *104*, 543–548. https://doi.org/10.1016/j.ecolind.2019.05.030

Bajocco, S., & Ricotta, C. (2008). Evidence of selective burning in Sardinia (Italy): Which land-cover classes do wildfires prefer? *Landscape Ecology*, *23*(2), 241–248. https://doi.org/10.1007/s10980-007-9176-5

Baudena, M., Santana, V. M., Baeza, M. J., Bautista, S., Eppinga, M. B., Hemerik, L., Garcia Mayor, A., Rodriguez, F., Valdecantos, A., Vallejo, V. R., Vasques, A., & Rietkerk, M. (2020). Increased aridity drives post-fire recovery of Mediterranean forests towards open shrublands. *New Phytologist*, *225*(4), 1500–1515. https://doi.org/10.1111/nph.16252

Beffa, G., Pedrotta, T., Colombaroli, D., Henne, P. D., van Leeuwen, J. F. N., Süsstrunk, P., Kaltenrieder, P., Adolf, C., Vogel, H., Pasta, S., Anselmetti, F. S., Gobet, E., & Tinner, W. (2016). Vegetation and fire history of coastal north-eastern Sardinia (Italy) under changing Holocene climates and land use. *Vegetation History and Archaeobotany*, *25*(3), 271–289. https://doi.org/10.1007/s00334-015-0548-5

Ben Tiba, B., & Reille, M. (1982). Recherches pollenanalytiques dans les montagnes de Kroumirie (Tunisie septentrionale): Premiers résultats. *Ecologia Mediterranea*, *8*(4), 75–86. https://doi.org/10.3406/ecmed.1982.1004

Benslama, M., Andrieu-Ponel, V., Guiter, F., Reille, M., de Beaulieu, J.-L., Migliore, J., & Djamali, M. (2010). Nouvelles contributions à l'histoire tardiglaciaire et holocène de la végétation en Algérie: Analyses polliniques de deux profils sédimentaires du complexe humide d'El-Kala. *Comptes Rendus Biologies*, *333*(10), 744–754. https://doi.org/10.1016/j.crvi.2010.08.002

Buhk, C., Meyn, A., & Jentsch, A. (2007). The challenge of plant regeneration after fire in the Mediterranean Basin: Scientific gaps in our knowledge on plant strategies and evolution of traits. *Plant Ecology*, *192*(1), 1–19. https://doi.org/10.1007/s11258-006-9224-2

Burjachs, F., Pérez-Obiol, R., Picornell-Gelabert, L., Revelles, J., Servera-Vives, G., Expósito, I., & Yll, E.-I. (2017). Overview of environmental changes and human colonization in the Balearic Islands (Western Mediterranean) and their impacts on vegetation composition during the Holocene. *Journal of Archaeological Science: Reports*, *12*, 845–859. https://doi.org/10.1016/j.jasrep.2016.09.018

Calò, C., Henne, P. D., Curry, B., Magny, M., Vescovi, E., La Mantia, T., Pasta, S., Vannière, B., & Tinner, W. (2012). Spatio-temporal patterns of Holocene environmental change in southern Sicily. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *323–325*, 110–122. https://doi.org/10.1016/j.palaeo.2012.01.038

Calò, C., Henne, P. D., Eugster, P., van Leeuwen, J., Gilli, A., Hamann, Y., La Mantia, T., Pasta, S., Vescovi, E., & Tinner, W. (2013). 1200 years of decadal-scale variability of Mediterranean vegetation and climate at Pantelleria Island, Italy. *The Holocene*, *23*(10), 1477–1486. https://doi.org/10.1177/0959683613493935

Canu, S., Rosati, L., Fiori, M., Motroni, A., Filigheddu, R., & Farris, E. (2015). Bioclimate map of Sardinia (Italy). *Journal of Maps*, *11*(5), 711–718. https://doi.org/10.1080/17445647.2014.988187

Carrillo-García, C., Girola-Iglesias, L., Guijarro, M., Hernando, C., Madrigal, J., & Mateo, R. G. (2023). Ecological niche models applied to post-megafire vegetation restoration in the context of climate change. *Science of the Total Environment*, *855*, 158858. https://doi.org/10.1016/j.scitotenv.2022.158858

Chiappini, M. (1988). *Guida alla flora pratica della Sardegna: Vegetazione. Specie interessanti. Glossari e Dizionario vernacolare sardo*. Carlo Delfino.

Clark, J. S. (1988). Effect of climate change on fire regimes in northwestern Minnesota. *Nature*, *334*(6179), 233–235. https://doi.org/10.1038/334233a0

Colantoni, A., Egidi, G., Quaranta, G., D'Alessandro, R., Vinci, S., Turco, R., & Salvati, L. (2020). Sustainable land management, wildfire risk and the role of grazing in Mediterranean urban-rural interfaces: A regional approach from Greece. *Land*, *9*(1), 21. https://doi.org/10.3390/land9010021

Colombaroli, D., Marchetto, A., & Tinner, W. (2007). Long-term interactions between Mediterranean climate, vegetation and fire regime at Lago di Massaciuccoli (Tuscany, Italy). *Journal of Ecology*, *95*(4), 755–770. https://doi.org/10.1111/j.1365-2745.2007.01240.x

Conedera, M., Tinner, W., Crameri, S., Torriani, D., & Herold, A. (2006). Taxon-related pollen source areas for lake basins in the southern Alps: An empirical approach. *Vegetation History and Archaeobotany*, *15*(4), 263–272. https://doi.org/10.1007/s00334-006-0056-8

Conedera, M., Tinner, W., Neff, C., Meurer, M., Dickens, A. F., & Krebs, P. (2009). Reconstructing past fire regimes: Methods, applications, and relevance to fire management and conservation. *Quaternary Science Reviews*, *28*(5–6), 555–576. https://doi.org/10.1016/j.quascirev.2008.11.005

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. https://doi.org/10.1016/j.quascirev.2012.08.007

Connor, S. E., Vannière, B., Colombaroli, D., Anderson, R. S., Carrión, J. S., Ejarque, A., Gil Romera, G., González-Sampériz, P., Hoefer, D., Morales-Molino, C., Revelles, J., Schneider, H., van der Knaap, W. O., van Leeuwen, J. F., & Woodbridge, J. (2019). Humans take control of fire-driven diversity changes in Mediterranean Iberia's vegetation during the mid–late Holocene. *The Holocene*, *29*(5), 886–901. https://doi.org/10.1177/0959683619826652

Curry, B., Henne, P. D., Mesquita-Joanes, F., Marrone, F., Pieri, V., La Mantia, T., Calò, C., & Tinner, W. (2016). Holocene paleoclimate inferred from salinity histories of adjacent lakes in southwestern Sicily (Italy). *Quaternary Science Reviews*, *150*, 67–83. https://doi.org/10.1016/j.quascirev.2016.08.013

Damianidis, C., Santiago-Freijanes, J. J., den Herder, M., Burgess, P., Mosquera-Losada, M. R., Graves, A., Papadopoulos, A., Pisanelli, A., Camilli, F., Rois-Díaz, M., Kay, S., Palma, J. H. N., & Pantera, A. (2021). Agroforestry as a sustainable land use option to reduce wildfires risk in European Mediterranean areas. *Agroforestry Systems*, *95*(5), 919–929. https://doi.org/10.1007/s10457-020-00482-w

Dantas, V. L., Batalha, M. A., & Pausas, J. G. (2013). Fire drives functional thresholds on the savanna–forest transition. *Ecology*, *94*(11), 2454–2463. https://doi.org/10.1890/12-1629.1

Desprat, S., Combourieu-Nebout, N., Essallami, L., Sicre, M. A., Dormoy, I., Peyron, O., Siani, G., Bout Roumazeilles, V., & Turon, J. L. (2013). Deglacial and Holocene vegetation and climatic changes in the southern Central Mediterranean from a direct land–sea correlation. *Climate of the Past*, *9*(2), 767–787. https://doi.org/10.5194/cp-9-767-2013

Di Pasquale, G., Di Martino, P., & Mazzoleni, S. (2004). Forest history in the Mediterranean region. In S. Mazzoleni, G. Di Pasquale, M. Mulligan, P. Di Martino, & F. Rego (Eds.), *Recent dynamics of the Mediterranean vegetation and landscape* (pp. 13–20). Wiley.

Djamali, M., Gambin, B., Marriner, N., Andrieu-Ponel, V., Gambin, T., Gandouin, E., Lanfranco, S., Médail, F., Pavon, D., Ponel, P., & Morhange, C. (2013). Vegetation dynamics during the early to mid-Holocene transition in NW Malta, human impact versus climatic forcing. *Vegetation History and Archaeobotany*, *22*(5), 367–380. https://doi.org/10.1007/s00334-012-0380-0

Drescher-Schneider, R., de Beaulieu, J.-L., Magny, M., Walter-Simonnet, A.-V., Bossuet, G., Millet, L., Brugiapaglia, E., & Drescher, A. (2007). Vegetation history, climate and human impact over the last 15,000 years at Lago dell'Accesa (Tuscany, Central Italy). *Vegetation History and Archaeobotany*, *16*(4), 279–299. https://doi.org/10.1007/s00334-006-0089-z

Dupuy, J., Fargeon, H., Martin-StPaul, N., Pimont, F., Ruffault, J., Guijarro, M., Hernando, C., Madrigal, J., & Fernandes, P. (2020). Climate change impact on future wildfire danger and activity in southern Europe: A review. *Annals of Forest Science*, *77*(2), 35. https://doi.org/10.1007/s13595-020-00933-5

Fernandes, P. M., Barros, A. M. G., Pinto, A., & Santos, J. A. (2016). Characteristics and controls of extremely large wildfires in the western Mediterranean Basin. *Journal of Geophysical Research: Biogeosciences*, *121*(8), 2141–2157. https://doi.org/10.1002/2016JG003389

Fernandes, P. M., Davies, G. M., Ascoli, D., Fernández, C., Moreira, F., Rigolot, E., Stoof, C. R., Vega, J. A., & Molina, D. (2013). Prescribed burning in southern Europe: Developing fire management in a dynamic landscape. *Frontiers in Ecology and the Environment*, *11*(s1), e4–e14. https://doi.org/10.1890/120298

Fernandes, P. M., Vega, J. A., Jiménez, E., & Rigolot, E. (2008). Fire resistance of European pines. *Forest Ecology and Management*, *256*(3), 246–255. https://doi.org/10.1016/j.foreco.2008.04.032

Fernández-García, V., Marcos, E., Fulé, P. Z., Reyes, O., Santana, V. M., & Calvo, L. (2020). Fire regimes shape diversity and traits of vegetation under different climatic conditions. *Science of the Total Environment*, *716*, 137137. https://doi.org/10.1016/j.scitotenv.2020.137137

Ganteaume, A., Camia, A., Jappiot, M., San-Miguel-Ayanz, J., Long-Fournel, M., & Lampin, C. (2013). A review of the main driving factors of forest fire ignition over Europe. *Environmental Management*, *51*(3), 651–662. https://doi.org/10.1007/s00267-012-9961-z

Gilgen, A., Adolf, C., Brugger, S. O., Ickes, L., Schwikowski, M., van Leeuwen, J. F. N., Tinner, W., & Lohmann, U. (2018). Implementing microscopic charcoal particles into a global aerosol–climate model. *Atmospheric Chemistry and Physics*, *18*(16), 11813–11829. https://doi.org/10.5194/acp-18-11813-2018

Gil-Romera, G., Adolf, C., Benito, B. M., Bittner, L., Johansson, M. U., Grady, D. A., Lamb, H. F., Lemma, B., Fekadu, M., Glaser, B., Mekonnen, B., Sevilla-Callejo, M., Zech, M., Zech, W., & Miehe, G. (2019). Long-term fire resilience of the Ericaceous Belt, Bale Mountains, Ethiopia. *Biology Letters*, *15*(7), 20190357. https://doi.org/10.1098/rsbl.2019.0357

González, J. R., Trasobares, A., Palahí, M., & Pukkala, T. (2007). Predicting stand damage and tree survival in burned forests in Catalonia (North-East Spain). *Annals of Forest Science*, *64*(7), 733–742. https://doi.org/10.1051/forest:2007053

Guiterman, C. H., Margolis, E. Q., Allen, C. D., Falk, D. A., & Swetnam, T. W. (2018). Long-term persistence and fire resilience of oak shrubfields in dry conifer forests of northern New Mexico. *Ecosystems*, *21*(5), 943–959. https://doi.org/10.1007/s10021-017-0192-2

Hanewinkel, M., Cullmann, D. A., Schelhaas, M.-J., Nabuurs, G.-J., & Zimmermann, N. E. (2013). Climate change may cause severe loss in the economic value of European forest land. *Nature Climate Change*, *3*(3), 203–207. https://doi.org/10.1038/nclimate1687

Henne, P. D., Elkin, C., Colombaroli, D., Samartin, S., Bugmann, H., Heiri, O., & Tinner, W. (2013). Impacts of changing climate and land use on vegetation dynamics in a Mediterranean ecosystem: Insights from paleoecology and dynamic modeling. *Landscape Ecology*, *28*(5), 819–833. https://doi.org/10.1007/s10980-012-9782-8

Henne, P. D., Elkin, C., Franke, J., Colombaroli, D., Calò, C., La Mantia, T., Pasta, S., Conedera, M., Dermody, O., & Tinner, W. (2015). Reviving extinct Mediterranean forest communities may improve ecosystem potential in a warmer future. *Frontiers in Ecology and the Environment*, *13*(7), 356–362. https://doi.org/10.1890/150027

Henne, P. D., Elkin, C. M., Reineking, B., Bugmann, H., & Tinner, W. (2011). Did soil development limit spruce (*Picea abies*) expansion in the Central Alps during the Holocene? Testing a palaeobotanical hypothesis with a dynamic landscape model. *Journal of Biogeography*, *38*(5), 933–949. https://doi.org/10.1111/j.1365-2699.2010.02460.x

Hickler, T., Vohland, K., Feehan, J., Miller, P. A., Smith, B., Costa, L., Giesecke, T., Fronzek, S., Carter, T. R., Cramer, W., Kühn, I., & Sykes, M. T. (2012). Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. *Global Ecology and Biogeography*, *21*(1), 50–63. https://doi.org/10.1111/j.1466-8238.2010.00613.x

Johansson, M. U., & Granström, A. (2014). Fuel, fire and cattle in African highlands: Traditional management maintains a mosaic heathland landscape. *Journal of Applied Ecology*, *51*(5), 1396–1405. https://doi.org/10.1111/1365-2664.12291

Jouffroy-Bapicot, I., Pedrotta, T., Debret, M., Field, S., Sulpizio, R., Zanchetta, G., Sabatier, P., Roberts, N., Tinner, W., Walsh, K., & Vannière, B. (2021). Olive groves around the lake. A ten-thousand-year history of a Cretan landscape (Greece) reveals the dominant role of humans in making this Mediterranean ecosystem. *Quaternary Science Reviews*, *267*, 107072. https://doi.org/10.1016/j.quascirev.2021.107072

Kalis, A., & Schoch, W. H. (2019). Anthracological studies on the early Holocene sediments of the Grotta di Corbeddu (Nuoro, Sardinia). *Archäologische Berichte*, *30*, 193–210. https://doi.org/10.11588/propyleum.492

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*(1), 170122. https://doi.org/10.1038/sdata.2017.122

Karger, D. N., Nobis, M. P., Normand, S., Graham, C. H., & Zimmermann, N. E. (2023). CHELSA-TraCE21k—High-resolution (1 km) downscaled transient temperature and precipitation data since the last glacial maximum. *Climate of the Past*, *19*, 439–456. https://doi.org/10.5194/cp-19-439-2023

Karger, D. N., Schmatz, D. R., Dettling, G., & Zimmermann, N. E. (2020). High-resolution monthly precipitation and temperature time series from 2006 to 2100. *Scientific Data*, *7*(1), 248. https://doi.org/10.1038/s41597-020-00587-y

La Mantia, T., Giaimi, G., Veca, D. S. L. M., & Pasta, S. (2007). The role of traditional Erica arborea L. management practices in maintaining northeastern Sicily's cultural landscape. *Forest Ecology and Management*, *249*(1), 63–70. https://doi.org/10.1016/j.foreco.2007.05.029

Ladd, P. G., Crosti, R., & Pignatti, S. (2005). Vegetative and seedling regeneration after fire in planted Sardinian pinewood compared with that in other areas of Mediterranean-type climate. *Journal of Biogeography*, *32*(1), 85–98. https://doi.org/10.1111/j.1365-2699.2004.01168.x

Lang, G., Ammann, B., Schwörer, C., & Tinner, W. (2023). Today's vegetation and woody flora. In G. Lang, B. Ammann, K.-E. Behre, & W. Tinner (Eds.), *Quaternary vegetation dynamics of Europe* (pp. 145–149). Haupt.

Lestienne, M., Hély, C., Curt, T., Jouffroy-Bapicot, I., & Vannière, B. (2020). Combining the monthly drought code and paleoecological data to assess Holocene climate impact on Mediterranean fire regime. *Firehouse*, *3*(2), 1–22. https://doi.org/10.3390/fire3020008

Lestienne, M., Jouffroy-Bapicot, I., Leyssenne, D., Sabatier, P., Debret, M., Albertini, P.-J., Colombaroli, D., Didier, J., Hély, C., & Vannière, B. (2020). Fires and human activities as key factors in the high diversity of Corsican vegetation. *The Holocene*, *30*(2), 244–257. https://doi.org/10.1177/0959683619883025

Lestienne, M., Vannière, B., Curt, T., Jouffroy-Bapicot, I., & Hély, C. (2022). Climate-driven Mediterranean fire hazard assessments for 2020–2100 on the light of past millennial variability. *Climatic Change*, *170*(1), 1–18. https://doi.org/10.1007/s10584-021-03258-y

Leys, B., Brewer, S. C., McConaghy, S., Mueller, J., & McLauchlan, K. K. (2015). Fire history reconstruction in grassland ecosystems: Amount of charcoal reflects local area burned. *Environmental Research Letters*, *10*(11), 114009. https://doi.org/10.1088/1748-9326/10/11/114009

Liu, Z., Otto-Bliesner, B. L., He, F., Brady, E. C., Tomas, R., Clark, P. U., Carlson, A. E., Lynch-Stieglitz, J., Curry, W., Brook, E., Erickson, D., Jacob, R., Kutzbach, J., & Cheng, J. (2009). Transient simulation of last deglaciation with a new mechanism for Bølling-Allerød warming. *Science*, *325*(5938), 310–314. https://doi.org/10.1126/science.1171041

MacDonald, G. M., Larsen, C. P. S., Szeicz, J. M., & Moser, K. A. (1991). The reconstruction of boreal forest fire history from lake sediments: A comparison of charcoal, pollen, sedimentological, and geochemical indices. *Quaternary Science Reviews*, *10*(1), 53–71. https://doi.org/10.1016/0277-3791(91)90030-X

Magny, M., de Beaulieu, J.-L., Drescher-Schneider, R., Vannière, B., Walter-Simonnet, A.-V., Miras, Y., Millet, L., Bossuet, G., Peyron, O., Brugiapaglia, E., & Leroux, A. (2007). Holocene climate changes in the central Mediterranean as recorded by lake-level fluctuations at Lake Accesa (Tuscany, Italy). *Quaternary Science Reviews*, *26*(13), 1736–1758. https://doi.org/10.1016/j.quascirev.2007.04.014

Magri, D., & Sadori, L. (1994). Late-quaternary history of vegetation at Lago Di Vico (Central Italy). *Giornale Botanico Italiano*, *128*(1), 434. https://doi.org/10.1080/11263509409437244

Mancilla-Leytón, J. M., Pino Mejías, R., & Martín Vicente, A. (2013). Do goats preserve the forest? Evaluating the effects of grazing goats on combustible Mediterranean scrub. *Applied Vegetation Science*, *16*(1), 63–73. https://doi.org/10.1111/j.1654-109X.2012.01214.x

Mesléard, F., & Lepart, J. (1989). Continuous basal sprouting from a lignotuber: *Arbutus unedo* L. and *Erica arborea* L., as woody Mediterranean examples. *Oecologia*, *80*(1), 127–131. https://doi.org/10.1007/BF00789941

Morales-Molino, C., García-Antón, M., Postigo-Mijarra, J. M., & Morla, C. (2013). Holocene vegetation, fire and climate interactions on the westernmost fringe of the Mediterranean Basin. *Quaternary Science Reviews*, *59*, 5–17. https://doi.org/10.1016/j.quascirev.2012.10.027

Morales-Molino, C., Leunda, M., Morellón, M., Gardoki, J., Ezquerra, F. J., Muñoz Sobrino, C., Rubiales, J. M., & Tinner, W. (2022). Millennial land use explains modern high-elevation vegetation in the submediterranean mountains of southern Europe. *Journal of Biogeography*, *49*(10), 1779–1792. https://doi.org/10.1111/jbi.14472

Moreira, F., Ascoli, D., Safford, H., Adams, M. A., Moreno, J. M., Pereira, J. M. C., Catry, F. X., Armesto, J., Bond, W., González, M. E., Curt, T., Koutsias, N., McCaw, L., Price, O., Pausas, J. G., Rigolot, E., Stephens, S., Tavsanoglu, C., Vallejo, V. R., … Fernandes, P. M. (2020). Wildfire management in Mediterranean-type regions: Paradigm change needed. *Environmental Research Letters*, *15*(1), 011001. https://doi.org/10.1088/1748-9326/ab541e

Naveh, Z. (1975). The evolutionary significance of fire in the mediterranean region. *Vegetatio*, *29*(3), 199–208. https://doi.org/10.1007/BF02390011

Noti, R., van Leeuwen, J. F. N., Colombaroli, D., Vescovi, E., Pasta, S., La Mantia, T., & Tinner, W. (2009). Mid- and late-Holocene vegetation and fire history at Biviere di Gela, a coastal lake in southern Sicily, Italy. *Vegetation History and Archaeobotany*, *18*(5), 371–387. https://doi.org/10.1007/s00334-009-0211-0

O'Neill, B. C., Tebaldi, C., van Vuuren, D. P., Eyring, V., Friedlingstein, P., Hurtt, G., Knutti, R., Kriegler, E., Lamarque, J.-F., Lowe, J., Meehl, G. A., Moss, R., Riahi, K., & Sanderson, B. M. (2016). The scenario model intercomparison project (ScenarioMIP) for CMIP6. *Geoscientific Model Development*, *9*(9), 3461–3482. https://doi.org/10.5194/gmd-9-3461-2016

Pausas, J. G., & Fernández-Muñoz, S. (2012). Fire regime changes in the Western Mediterranean Basin: From fuel-limited to drought-driven fire regime. *Climatic Change*, *110*(1), 215–226. https://doi.org/10.1007/s10584-011-0060-6

Pedrotta, T., Gobet, E., Schwörer, C., Beffa, G., Butz, C., Henne, P. D., Morales-Molino, C., Pasta, S., van Leeuwen, J. F. N., Vogel, H., Zwimpfer, E., Anselmetti, F. S., Grosjean, M., & Tinner, W. (2021). 8,000 years of climate, vegetation, fire and land-use dynamics in the thermo-mediterranean vegetation belt of northern Sardinia (Italy). *Vegetation History and Archaeobotany*, *30*(6), 789–813. https://doi.org/10.1007/s00334-021-00832-3

Poher, Y., Ponel, P., Médail, F., Andrieu-Ponel, V., & Guiter, F. (2017). Holocene environmental history of a small Mediterranean Island in response to sea-level changes, climate and human impact. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *465*, 247–263. https://doi.org/10.1016/j.palaeo.2016.10.037

Quézel, P., & Médail, F. (2003). *Ecologie et Biogéographie des Forêts du Bassin Méditerranéen*. Elsevier.

Reille, M. (1992). New pollen-analytical researches in Corsica: The problem of *Quercus ilex* L. and *Erica arborea* L., the origin of *Pinus halepensis* Miller forests. *New Phytologist*, *122*(2), 359–378. https://doi.org/10.1111/j.1469-8137.1992.tb04241.x

Reille, M., Gamisans, J., Andrieu-Ponel, V., & de Beaulieu, J.-L. (1999). The Holocene at Lac de Creno, Corsica, France: A key site for the whole Island. *The New Phytologist*, *141*(2), 291–307. https://doi.org/10.1046/j.1469-8137.1999.00343.x

Revelles, J., Ghilardi, M., Rossi, V., Currás, A., López-Bultó, O., Brkojewitsch, G., & Vacchi, M. (2019). Coastal landscape evolution of Corsica Island (W. Mediterranean): Palaeoenvironments, vegetation history and human impacts since the early Neolithic period. *Quaternary Science Reviews*, *225*, 105993. https://doi.org/10.1016/j.quascirev.2019.105993

Salis, M., Ager, A. A., Alcasena, F. J., Arca, B., Finney, M. A., Pellizzaro, G., & Spano, D. (2014). Analyzing seasonal patterns of wildfire exposure factors in Sardinia, Italy. *Environmental Monitoring and Assessment*, *187*(1), 4175. https://doi.org/10.1007/s10661-014-4175-x

Salis, M., Arca, B., Del Giudice, L., Palaiologou, P., Alcasena-Urdiroz, F., Ager, A., Fiori, M., Pellizzaro, G., Scarpa, C., Schirru, M., Ventura, A., Casula, M., & Duce, P. (2021). Application of simulation modeling for wildfire exposure and transmission assessment in Sardinia, Italy. *International Journal of Disaster Risk Reduction*, *58*, 102189. https://doi.org/10.1016/j.ijdrr.2021.102189

Samartin, S., Heiri, O., Joos, F., Renssen, H., Franke, J., Brönnimann, S., & Tinner, W. (2017). Warm Mediterranean mid-Holocene summers inferred from fossil midge assemblages. *Nature Geoscience*, *10*(3), 207–212. https://doi.org/10.1038/ngeo2891

Scheffer, M., Bascompte, J., Brock, W. A., Brovkin, V., Carpenter, S. R., Dakos, V., Held, H., van Nes, E. H., Rietkerk, M., & Sugihara, G. (2009). Early-warning signals for critical transitions. *Nature*, *461*(7260), 53–59. https://doi.org/10.1038/nature08227

Schumacher, S., Bugmann, H., & Mladenoff, D. J. (2004). Improving the formulation of tree growth and succession in a spatially explicit landscape model: Modelling disturbance and succession in forest landscapes using LANDIS. *Ecological Modelling*, *180*(1), 175–194. https://doi.org/10.1016/j.ecolmodel.2003.12.055

Schwörer, C. (2024). Schwoeri/LandClim: Zenodo archive (v.1.0.0). *Zenodo*, https://doi.org/10.5281/zenodo.10732256

Schwörer, C., Gavin, D. G., Walker, I. R., & Hu, F. S. (2017). Holocene tree line changes in the Canadian Cordillera are controlled by climate and topography. *Journal of Biogeography*, *44*(5), 1148–1159. https://doi.org/10.1111/jbi.12904

Schwörer, C., Henne, P. D., & Tinner, W. (2014). A model-data comparison of Holocene timberline changes in the Swiss Alps reveals past and future drivers of mountain forest dynamics. *Global Change Biology*, *20*(5), 1512–1526. https://doi.org/10.1111/gcb.12456

SCIA. (2021). *Sistema nazionale per l'elaborazione e diffusione di dati climatici*. Instituto Superiore per la Protezione e la Ricerca Ambientale. http://www.scia.isprambiente.it/wwwrootscia/Home_new.html

Stambouli-Essassi, S., Roche, E., & Bouzid, S. (2019). Evolution of vegetation and climatic changes in North-Western Tunisia during the last 40 millennia. *Geo-Eco-Trop*, *31*, 171–214.

Steinbauer, M. J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., Rixen, C., Winkler, M., Bardy-Durchhalter, M., Barni, E., Bjorkman, A. D., Breiner, F. T., Burg, S., Czortek, P., Dawes, M. A., Delimat, A., Dullinger, S., Erschbamer, B., Felde, V. A., … Wipf, S. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, *556*(7700), 231–234. https://doi.org/10.1038/s41586-018-0005-6

Tepley, A. J., Thomann, E., Veblen, T. T., Perry, G. L. W., Holz, A., Paritsis, J., Kitzberger, T., & Anderson-Teixeira, K. J. (2018). Influences of fire–vegetation feedbacks and post-fire recovery rates on forest landscape vulnerability to altered fire regimes. *Journal of Ecology*, *106*(5), 1925–1940. https://doi.org/10.1111/1365-2745.12950

Tinner, W., Colombaroli, D., Heiri, O., Henne, P. D., Steinacher, M., Untenecker, J., Vescovi, E., Allen, J. R. M., Carraro, G., Conedera, M., Joos, F., Lotter, A. F., Luterbacher, J., Samartin, S., & Valsecchi, V. (2013). The past ecology of Abies alba provides new perspectives on future responses of silver fir forests to global warming. *Ecological Monographs*, *83*(4), 419–439. https://doi.org/10.1890/12-2231.1

Tinner, W., Conedera, M., Ammann, B., Gaggeler, H., Gedye, S., & Jones, R. (1998). Pollen and charcoal in lake sediments compared with historically documented forest fires in southern Switzerland since AD 1920. *Holocene*, *8*(1), 31–42. https://doi.org/10.1191/095968398667205430

Tinner, W., van Leeuwen, J. F. N., Colombaroli, D., Vescovi, E., van der Knaap, W. O., Henne, P. D., Pasta, S., D'Angelo, S., & La Mantia, T. (2009). Holocene environmental and climatic changes at Gorgo

Basso, a coastal lake in southern Sicily, Italy. *Quaternary Science Reviews*, *28*(15), 1498–1510. https://doi.org/10.1016/j.quascirev.2009.02.001

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*(1), 3821. https://doi.org/10.1038/s41467-018-06358-z

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

Verdú, M., & Pausas, J. G. (2007). Fire drives phylogenetic clustering in Mediterranean Basin woody plant communities. *Journal of Ecology*, *95*(6), 1316–1323. https://doi.org/10.1111/j.1365-2745.2007.01300.x

Vilar, L., Camia, A., San-Miguel-Ayanz, J., & Martín, M. P. (2016). Modeling temporal changes in human-caused wildfires in Mediterranean Europe based on land use-land cover interfaces. *Forest Ecology and Management*, *378*, 68–78. https://doi.org/10.1016/j.foreco.2016.07.020

Westerling, A. L., Turner, M. G., Smithwick, E. A. H., Romme, W. H., & Ryan, M. G. (2011). Continued warming could transform greater Yellowstone fire regimes by mid-21st century. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(32), 13165–13170. https://doi.org/10.1073/pnas.1110199108

Whitlock, C., Higuera, P. E., McWethy, D. B., & Briles, C. E. (2010). Paleoecological perspectives on fire ecology: Revisiting the fire-regime concept. *The Open Ecology Journal*, *3*(1), 6–23. https://doi.org/10.2174/1874213001003020006

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Radiocarbon dates and calibrated ages from the Stagno di Chia sediment record (indet. = indeterminate). Radiocarbon dates were calibrated using the IntCal20 calibration curve (Reimer et al., 2020).

Table S2: Geographic and climatic parameters of the three study landscapes in Sardinia.

Table S3: Species and associated parameters that have been used for the LandClim simulations.

Table S4: Number of annual fires and area burned in the three different study sites under different fire scenarios.

Figure S1: Age-depth models of the three study sites calculated using the program clam with the IntCal20 calibration curve (Reimer et al., 2020).

Figure S2: Pollen percentage diagram of selected taxa from Stagno di Chia, including spores, microscopic charcoal concentrations and influx, and lithology.

Figure S3: Maps of topographical and edaphic input parameters used in the LandClim simulations.

Figure S4: Maps of present-day (1951–2010) annual precipitation sums (mm) and mean annual temperature (°C) of the three study landscapes calculated based on lapse rates used in the LandClim simulation runs.

Figure S5: LandClim simulation output for different combinations of fire size and frequency as a result of changes in the ignition probability and the curve of the fire spread probability.

Figure S6: Change point analysis of the charcoal influx records from (a) Baratz, (b) Sa Curcurica and (c) Chia, showing statistically significant changes in mean values (solid red lines).

Figure S7: Simulated future vegetation and wildfire dynamics under the ssp370 climate scenario and two different fire scenarios.

Figure S8: Maps of future vegetation showing dominant species per gridcell in the year 2300 under three emission scenarios and low/high fire frequency.

How to cite this article: Schwörer, C., Morales-Molino, C., Gobet, E., Henne, P. D., Pasta, S., Pedrotta, T., van Leeuwen, J. F. N., Vannière, B., & Tinner, W. (2024). Simulating past and future fire impacts on Mediterranean ecosystems. *Journal of Ecology*, *00*, 1–17. https://doi.org/10.1111/1365-2745.14293