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Humans take control of fire-driven diversity changes in Mediterranean Iberia's vegetation during the mid–late Holocene

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Abstract
Fire regime changes are considered a major threat to future biodiversity in the Mediterranean Basin. Such predictions remain uncertain, given that fire regime changes and their ecological impacts occur over timescales that are too long for direct observation. Here we analyse centennial- and millennial-scale shifts in fire regimes and compositional turnover to track the consequences of fire regime shifts on Mediterranean vegetation diversity. We estimated rate-of-change, richness and compositional turnover (beta diversity) in 13 selected high-resolution palaeoecological records from Mediterranean Iberia and compared these with charcoal-inferred fire regime changes. Event sequence analysis showed fire regime shifts to be significantly temporally associated with compositional turnover, particularly during the last three millennia. We find that the timing and direction of fire and diversity change in Mediterranean Iberia are best explained by long-term human–environment interactions dating back perhaps 7500 years. Evidence suggests that Neolithic burning propagated a first wave of increasing vegetation openness and promoted woodland diversity around early farming settlements. Landscape transformation intensified around 5500 to 5000 cal. yr BP and accelerated during the last two millennia, as fire led to permanent transitions in ecosystem state. These fire episodes increased open vegetation diversity, decreased woodland diversity and significantly altered richness on a regional scale. Our study suggests that anthropogenic fires played a primary role in diversity changes in Mediterranean Iberia. Their millennia-long legacy in today's vegetation should be considered for biodiversity conservation and landscape management.

Keywords
charcoal, Iberian Peninsula, paleofire, pollen, Portugal, Spain

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Introduction

The Mediterranean Basin has extraordinarily high levels of plant species diversity (Blondel and Aronson, 1995; Médail and Diadema, 2009). Changes in the frequency, intensity and size of fires are altering landscapes and vegetation around the Mediterranean Basin (Chergui et al., 2018; Fernandes et al., 2016; Karavani et al., 2018; San-Miguel-Ayanz et al., 2013; Viedma et al., 2017). The recent increase in large fires is connected to the interaction of climatic changes with rising fuel loads and fuel

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connectivity, which in turn stem from the combined effects of rural land abandonment, loss of traditional agro-pastoral burning practices and the spread of homogeneous *Pinus* and *Eucalyptus* plantations (Fernandes et al., 2016; Fréjaville and Curt, 2015; Moreira et al., 2011; Pausas and Fernández-Muñoz, 2012). While some Mediterranean plants exhibit traits that enable post-fire recovery (Allen, 2008; Keeley et al., 2011; Paula et al., 2009; Tavşanoğlu and Pausas, 2018), some recent high-severity fire episodes have exceeded vegetation resilience and reduced recovery rates (Díaz-Delgado et al., 2002; Malak and Pausas, 2006; Puerta-Piñero et al., 2012). Fire regime shifts are potentially critical for Mediterranean biodiversity (Keeley et al., 2011; Paula et al., 2009; Pausas et al., 2008). Given the rarity of long historical records of fire (Pausas and Fernández-Muñoz, 2012), it remains unclear whether recent changes in fire characteristics represent natural variability or regime shifts with major biodiversity implications.

Fire regime shifts occur over decades to millennia (Swetnam et al., 1999; Vannière et al., 2008; Whitlock et al., 2010), beyond the temporal scope of monitoring-based ecological studies (e.g. Capitanio and Carcaillet, 2008; Clemente et al., 1996). Longer term perspectives are therefore needed to understand when a fire regime shift is occurring, to identify its causes and to predict its potential ecological impacts. Long-term ecological insights can be gained from the analysis of fossil pollen and sedimentary charcoal. Both proxies are abundant in Holocene sediments and allow for replication through time and space. Pollen data, if sufficiently taxonomically resolved and compared with the vegetation at appropriate scales, can be linked to the floristic richness of the surrounding vegetation (Birks et al., 2016; Felde et al., 2016). Pollen data may also be used to estimate turnover, compositional change, species loss and resilience (Blarquez et al., 2014a; Colombaroli et al., 2009; Davies et al., 2018; Giesecke et al., 2014; Seddon et al., 2015). Charcoal data are a critical proxy for several dimensions of past fire regimes (e.g. frequency and intensity) and, when compared with past vegetation, palaeoclimatic or archaeological data, provide insights into the climatic, fuel–vegetation and human drivers of long-term fire regime change (Marlon et al., 2016; Power et al., 2008; Roberts et al., this volume; Vannière et al., 2016, 2011).

Fire has played a key role in the landscape construction and the biodiversity heritage of the Mediterranean Basin (Bisculm et al., 2012; Colombaroli et al., 2008; Colombaroli and Tinner, 2013; Jouffroy-Bapicot et al., 2016). Charcoal and pollen data, along with climatic inferences from isotopic and lake-level proxies, have contributed to reconstruct a Mediterranean environmental history that is complex, enigmatic and much debated in climatic and anthropogenic terms (Berger et al., 2016; Colombaroli et al., 2008; Kaltenrieder et al., 2010; Magny et al., 2007, 2013; Mensing et al., 2018; Morellón et al., 2018; Roberts et al., 2011; Tinner et al., 2009; Vannière et al., 2008, 2016; Walsh, 2014). Charcoal records have revealed Holocene fire trends characteristic of broad latitudinal and altitudinal belts (Vannière et al., 2011), but these trends are less coherent on a regional scale and their drivers are contested (e.g. Burjachs and Expósito, 2015; Carracedo et al., 2018; Gil-Romera et al., 2010; López-Sáez et al., 2017). Climatic interpretations are weakened by a lack of regional coherence in inferred aridity phases (the entire Holocene is 'arid' according to different authors: see Figure 8 in Schneider et al., 2016) and idiosyncratic ecological responses (Carrión et al., 2010; Morellón et al., 2018) due to complex bioclimatic heterogeneity inherent to Mediterranean landscapes. Anthropogenic interpretations suffer from our inability to define what 'human impact' constitutes and how to recognise human–environment interactions in palaeoenvironmental records representing different spatial scales (Chapman, 2017; Head, 2008). The scarcity of integrated high-resolution palaeoenvironmental and archaeological studies also hampers our ability to identify human-driven changes in the palaeoenvironmental record. The challenge is to expand the capacity of new and existing methods to provide greater insight into Mediterranean ecosystem trajectories and tipping points.

Here we examine Mediterranean fire and vegetation diversity histories by developing alternative approaches based on regime shift detection. Our analysis focuses on the Mediterranean sector of the Iberian Peninsula, given its numerous high-resolution pollen and charcoal series. We aim to determine (1) the timing of major environmental shifts during the last 10,000 years and (2) whether a temporal relationship exists between fire regimes and pollen diversity change in Mediterranean Iberia's Holocene ecosystems. To achieve these aims, we will identify abrupt vegetation changes and common fire histories using objective criteria. We then test the null hypotheses that pollen compositional turnover and fire regime change are unrelated temporally, except by chance. Finally, we discuss the likely drivers of fire regime and diversity change on millennial and centennial timescales.

Methods

Site selection

We selected the Iberian Peninsula for the present study after meta-analysis of Mediterranean pollen and charcoal records, particularly those published in and since the last Mediterranean charcoal synthesis (Vannière et al., 2011). Records were selected for inclusion based on the following criteria: location in the Mediterranean region (boundaries according to Médail and Diadema, 2009; Médail and Quézel, 1997), at least 5000 years of Holocene record, pollen and charcoal data sampled from the same cores with an average sampling resolution of <100 calendar years, an average of <1500 years between dated levels and no major sedimentation hiatuses. Records with strong fluvial signals were also excluded, but we retained lowland sites with minor fluvial influence to avoid skewing the dataset towards high-elevation lake records.

These criteria produced 13 high-resolution records for the Iberian Peninsula (Table 1; Figure 1), representing an altitudinal gradient from sea level to >3000 m a.s.l. (Table 1). The records also lend themselves to comparison in terms of vegetation, climate, land-use history and basin size (source area).

Numerical methods

Sedimentary charcoal data were used as a fire proxy. Microscopic (pollen-slide) charcoal records are traditionally thought to represent regional fire histories and macroscopic (sieved) charcoal to represent local fire histories (Carcaillet et al., 2001). Extensive calibration of recent fires and charcoal in Europe has cast doubt on this division, demonstrating a strong regional component in macroscopic charcoal signals (Adolf et al., 2018), in agreement with charcoal dispersal models (Peters and Higuera, 2007). We included both types of charcoal in our analysis.

Charcoal accumulation rates (CHAR) were calculated for each record using published age models. New age models using Bayesian modelling (Bacon; Blaauw and Christen, 2011) were produced for the BAZ, GAD, NAV and VIL records (Table 1; Supplemental Material Table S1, available online), since revised age-depth models were either unavailable or were overly linear (thus creating artificial inflections in modelled CHAR estimates). While certain aspects of the fire regime can be estimated using contiguous charcoal series, these are presently too scarce in Iberia to permit a synthesis on long temporal and spatial scales (Vannière et al., 2016). Our analysis therefore uses CHAR *z*-scores (Power et al., 2008) and CHAR variance, these being the most accessible parameters with the available data.

Table 1. Pollen and charcoal records analysed in this study, ordered according to elevation.

Site code and name	Elevation (m a.s.l.)	Latitude (DD)	Longitude (DD)	Charcoal analysed	References
LRS–Laguna de Río Seco	3020	37.05	−3.35	Macro	Anderson et al. (2011)
BSM–Basa de la Mora	1914	42.544	0.326	Micro	Pérez-Sanz et al. (2013)
BAZ–Baza	1900	37.23	−2.7	Micro	Carrión et al. (2007)
GAD–Gádor	1530	36.931	−2.905	Micro	Carrión et al. (2003)
CHC–Charco da Candieira	1400	40.35	−7.583	Micro	Van der Knaap and van Leeuwen (1995) and Connor et al. (2012)
ELM–El Maíllo	1100	40.55	−6.217	Micro	Morales-Molino et al. (2013)
TUL–Tubilla del Lago	900	41.817	−3.567	Both	Morales-Molino et al. (2017b)
ESC–Espinosa de Cerrato	885	41.95	−3.933	Micro	Franco-Múgica et al. (2001); Morales-Molino et al. (2017b)
VIL–Villaverde	870	38.799	−2.36	Micro	Carrión et al. (2001)
NAV–Navarrés	255	39.084	−0.688	Both	Carrión and van Geel (1999)
BAN–Banyoles	174	42.133	2.75	Macro	Revelles et al. (2015)
CAS–Castelló	2.4	42.283	3.1	Macro	Ejarque et al. (2016)
RFT–Ribeira do Farelo/Ribeira da Torre	2	37.15	−8.6	Micro	Schneider et al. (2016)

Charcoal *z*-scores differentiate periods with greater or lesser biomass burned (Ali et al., 2012; Vannière et al., 2016). Changes in charcoal variance indicate periods where charcoal peak magnitudes changed in relation to the background, potentially reflecting shifts in fire episodes' frequency or intensity (Gavin et al., 2006; Higuera et al., 2009). Charcoal *z*-scores from all of the sites were combined into a composite curve using a local regression procedure (Daniau et al., 2012; Power et al., 2008). Common trends were compared with potential bioclimatic, palaeoclimatic and anthropogenic drivers (e.g. Fick and Hijmans, 2017; Isern et al., 2014; Roberts et al., 2011).

Rate-of-change analysis is commonly used to estimate compositional change-over-time in pollen sequences (Birks, 2012). It is also used to estimate compositional turnover, but here we use 'turnover' to refer to temporal replacement, estimated via beta diversity indices (Legendre, 2014). To pinpoint periods of rapid vegetation change in the records from Mediterranean Iberia, we used the squared-chord distance (SCD) metric (Overpeck et al., 1985; Seddon et al., 2015; Williams et al., 2001). SCD is favoured for its high signal-to-noise ratio and its robustness to differences in the number of pollen types included (Overpeck et al., 1985). Interpretation of the significance of SCD change-over-time is achieved by empirical thresholds (Davis et al., 2015; Overpeck et al., 1985) and statistical thresholds (Seddon et al., 2015). The former require high-quality modern pollen data from representative vegetation types to validate the thresholds, while the latter depend on confidence intervals estimated from randomisation (bootstrapping) of samples within the pollen sequences. Both approaches were applied here, with the empirical approach validated using 352 modern pollen samples and associated vegetation descriptions from JA López-Sáez's contributions to the European Modern Pollen Database (Davis et al., 2013; López-Sáez et al., 2010).

As rates-of-change may be unreliable when sampling intervals are uneven (Birks, 2012), data are typically interpolated, smoothed or binned to even intervals prior to SCD calculation (Jacobson and Grimm, 1986; Seddon et al., 2015). These manipulations may introduce statistical artefacts that could be mistaken for palaeoecological changes (Birks, 2012). With this in mind, we modified the approach of Seddon et al. (2015): while they used mean pollen percentages from evenly spaced time bins to calculate SCD, we randomly selected one pollen sample from each time bin, then calculated the SCD between it and a randomly selected sample from the next (younger) sample bin. This was repeated 50 times for each pair of bins before calculating the mean SCD score. The method preserves the age structure of the data (comparing older with younger samples) and better accounts for within-time bin variability. SCD was calculated in this way for bin lengths of 200, 250, 300 and 400 years. Only terrestrial pollen types were included.

In estimating diversity, the taxonomic precision of pollen identifications may influence palynological richness (i.e. number of identified taxa: Odgaard, 1999). This effect is minor in ecosystems where pollen diversity is low and taxonomy is consistent between researchers (Reitalu et al., 2015). In contrast, Mediterranean Iberian pollen records are characterised by diverse, taxonomically rich assemblages. To avoid subjectivity and information loss from taxonomic harmonisation, diversity estimates were calculated independently for each pollen record. Major changes in diversity within each record are thus comparable between records, even if the numerical values assigned to the estimates remain influenced by taxonomic precision.

It is more difficult to correct biases conferred by similarities in pollen morphology within certain botanical families (e.g. Poaceae), by differential pollen production, dispersal and taphonomy, or by the structure of the vegetation (Birks et al., 2016; Giesecke et al., 2014; Odgaard, 1999). Pollen production and dispersal biases may be reduced by the application of empirical correction factors or modelled pollen productivity estimates (Felde et al., 2016; Matthias et al., 2015). Such corrections are unavailable for key Mediterranean taxa, have large uncertainties (Giesecke et al., 2014) and have rarely been tested outside Northern Hemisphere temperate and boreal forest zones (but see Duffin and Bunting, 2008; Mariani et al., 2016). Hence, we opted to analyse palynological diversity as an indicator of vegetation change in its own right (Giesecke et al., 2014).

We estimated palynological richness for each pollen record following the randomised procedure of Felde et al. (2016). This method randomly resamples (without replacement) each pollen sample to the minimum sample size (the lowest upland pollen sum in each record). We performed this procedure 100 times for each sample of each pollen record. Results are equivalent to those produced by classical rarefaction (Birks and Line, 1992; Felde et al., 2016). Richness estimates were also calculated to a standard pollen sum (100 grains) to enable multi-record comparisons (Giesecke et al., 2012), keeping in mind that these estimates are influenced by taxonomic precision.

Random resampling was also performed 100 times in the estimation of beta diversity with Ružička's dissimilarity index

$$D_R = \frac{(B+C)}{(A+B+C)}$$

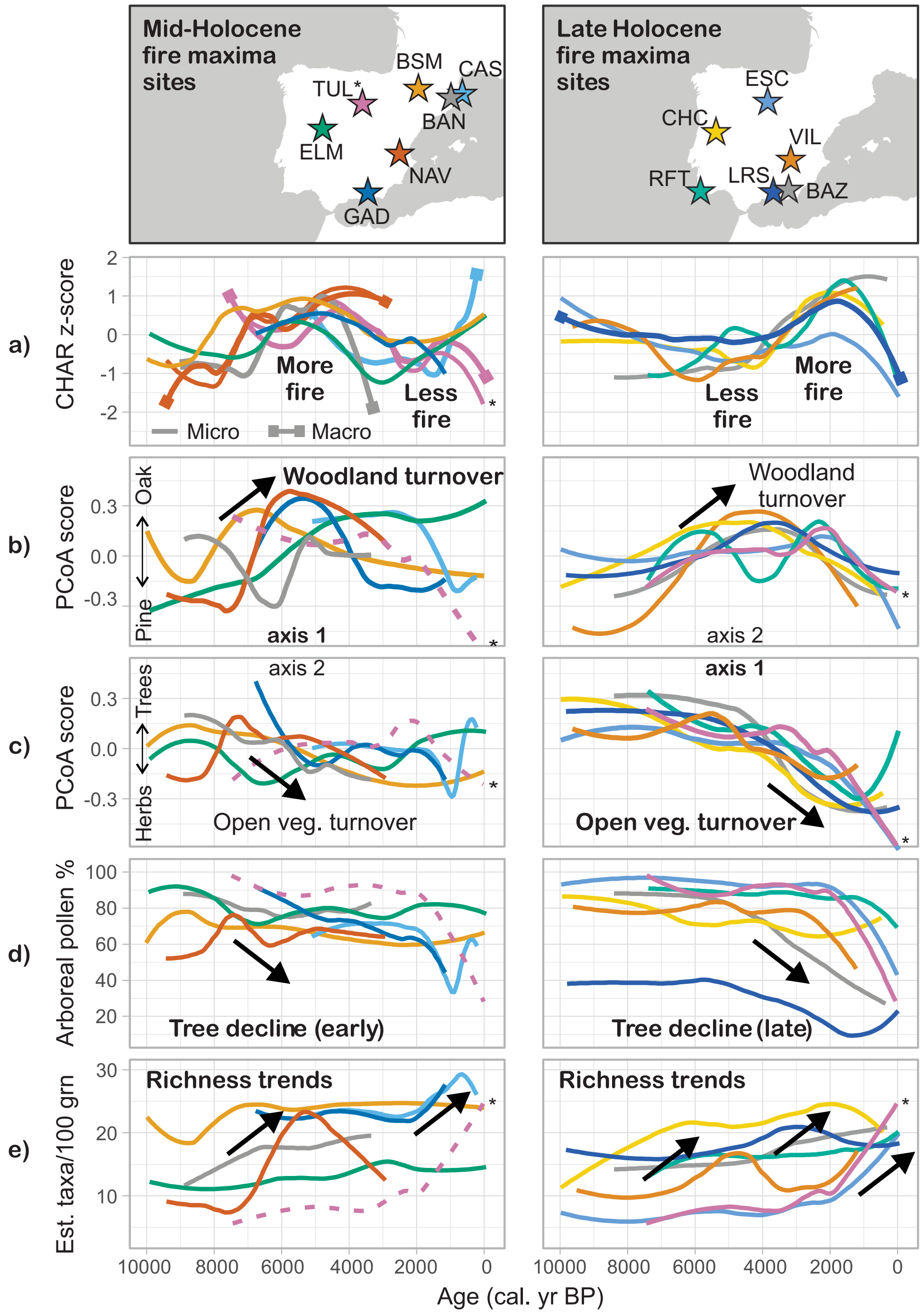

Figure 1. Site locations (maps, top panel) with site codes according to Table 1. Millennial-scale trends in (a) fire activity (CHAR z-scores; micro: pollen-slide charcoal, macro: sieved charcoal), (b, c) turnover axes, (d) arboreal pollen percentages and (e) palynological richness (estimated number of taxa in 100 pollen grains) in the 13 selected Mediterranean Iberian records. Records are grouped into those that exhibit a mid-Holocene fire increase (left panel) and those with a late-Holocene fire increase (right). Turnover trends are aligned and labelled according to the correlations in Supplemental Material Table S2, available online. For clarity, a 0.5 loess smoother is applied. *TUL trends are shown as dotted lines on the left panel and solid lines on the right panel because this record has a mid-Holocene fire peak but its turnover trends fit with records showing a late-Holocene fire increase (Supplemental Material Table S2, available online).

where *A* is the sum of the minimum abundances of each taxon, *B* is one sample's summed abundances minus *A* and *C* is another sample's summed abundances minus *A* (Legendre, 2014). This quantitative form of the Jaccard index may be decomposed into temporal replacement (i.e. turnover) and abundance difference components (Barwell et al., 2015; Legendre, 2014). Decomposition of beta diversity is of interest palaeoecologically because it helps to understand the long-term processes driving turnover and species loss (Birks et al., 2016; Blarquez et al., 2014a; Felde et al., 2016; Jackson and Sax, 2010).

In this study, resampling to the minimum sum in each record means that the abundance difference component of beta diversity is zero (i.e. *B* and *C* are equal). All inter-sample dissimilarities are then estimates of replacement (i.e. turnover). These were square-root transformed, and two major turnover trends were identified using principal coordinates analysis (PCoA; Legendre, 2014). These trends derive from all inter-sample dissimilarities (unlike the SCD approach, which compares only adjacent samples). Here, we use beta diversity decomposition to identify major *turnover events and trends* in individual pollen records, not to compare *turnover values* between records (cf. Birks, 2007).

Turnover trends were compared with arboreal pollen ratios and anthropogenic indicators to identify synchronous changes.

Anthropogenic indicators on the Iberian Peninsula are problematic because many of 'classic' taxa (e.g. *Plantago, Rumex, Urtica* and *Juglans*: Behre, 1981) belong to the original flora (Carrión and Sánchez-Gómez, 1992; Ejarque et al., 2011; Pantaléon-Cano et al., 2003). We used Brassicaceae, *Cannabis/Humulus*-type, *Cerealia*-type, *Castanea, Juglans, Olea, Plantago* spp., *Polygonum aviculare*-type, *Rumex* spp., *Trifolium pratense*-type, *Urtica dioica*-type, *Vitis* and fungal spores of Sordariaceae, *Sporormiella, Podospora, Cercophora* and *Coniochaeta* (Carrión and van Geel, 1999; Ejarque et al., 2011; Revelles et al., 2017). Any of these taxa that occurred in the early-Holocene samples from a record (i.e. prior to Neolithic agriculture) were excluded as anthropogenic indicators from that record.

As our objective was to determine whether a relationship exists between pollen diversity change and fire, we used regime shift detection (Rodionov, 2004) to pinpoint significant change events in plant diversity and fire proxies. Regime shift detection applies a sequential *t*-test to the identification of significant temporal changes in univariate series (e.g. Carter et al., 2018; Morris et al., 2013). This type of analysis delineates 'regime zones' (Morris et al., 2013) or 'change points' (Finsinger et al., 2018), analogous to the results of independent splitting (Connor et al., 2017; Walker and Wilson, 1978).

We implemented regime shift detection (Rodionov, 2004, 2006) with elapsed time as the observation timescale, a significance level of 0.05, a cut-off length of 10 samples and outliers removed with Huber's weight parameter of 5 (Morris et al., 2013). A standard cut-off length was considered appropriate since all our records have high temporal resolution. Cut-off lengths were increased proportionally for higher resolution contiguous charcoal series to match those of the pollen data. Turnover events for the first and second PCoA axes, as well as variance shifts for charcoal data, were detected using the same parameters. Regime shift outliers in the charcoal records were taken to represent anomalous charcoal peaks.

Finally, significant shifts in fire proxies (CHAR *z*-scores and variance) and pollen diversity proxies (richness and turnover) were analysed as event sequences. Event sequence analysis is applied in the social sciences to predict how life events (e.g. marriage, childbirth) impact subsequent life trajectories (Gabadinho et al., 2009). In this study, we define 'events' as significant shifts in diversity and fire. Each event was assigned a value of 1 (vs 0 for non-events). We inferred a potential cause–effect relationship if fire/diversity events occurred simultaneously or within the subsequent 200 years in two or more sediment records. The 200-year interval was based on previous estimates of recovery times in Iberian ecosystems (Burjachs and Expósito, 2015; Carrión et al., 2003; Gil-Romera et al., 2014; Morales-Molino et al., 2017b).

The significance of the real event sequences was assessed by randomly reshuffling the samples from each record 1000 times to generate bootstrapped sequences for comparison with real data using the Poisson distribution and 95% confidence intervals. The same approach was used to determine whether the frequency of fire, turnover and richness shifts was significant during each 500-year interval of the Holocene.

The R packages paleofire (Blarquez et al., 2014b), vegan (Oksanen et al., 2018), adespatial (Dray et al., 2018) and TraMineR (Gabadinho et al., 2009; Ritschard et al., 2013) were used for charcoal series composition, rarefaction, beta diversity partitioning and event sequence analyses, respectively (R Core Team, 2018).

Results

Holocene fire records from the 13 Mediterranean Iberian sites are grouped into (1) records with a mid-Holocene fire maximum (MH group: with highest charcoal values between 8000 and 4000 cal. yr BP) and (2) those with a late-Holocene fire maximum (LH group: with highest charcoal values between 3000 and 1000 cal. yr BP; Figure 1a). Records in the MH group exhibit turnover on both PCoA axes (Figure 1b and c) at the onset of the fire increase, the timing of which varies from site to site (e.g. approx. 8000 cal. yr BP at BSM to approximately 5500 cal. yr BP at BAN: see Table 1 for site codes). Despite showing a mid-Holocene fire increase, TUL's turnover trends group with those of the records in the LH group. LH-group records show turnover on axis 2 between 7000 and 5000 cal. yr BP, several millennia before the late-Holocene fire maximum; both axes then exhibit turnover from 3000 cal. yr BP to the present, coinciding with the late-Holocene fire maximum. For each group of sites, one of the PCoA axes is strongly correlated with arboreal pollen proportions (Figure 1d).

Palynological richness estimates (Figure 1e) reveal minor increases in some records around 7000 to 6000 (BSM, CHC, RFT) and 3000 to 2000 cal. yr BP (LRS, BSM, BAN, CHC, ELM, TUL). Pronounced mid-Holocene richness maxima appear at NAV (approximately 5500 cal. yr BP) and VIL (4500 cal. yr BP). Richness trends for the most recent millennium are highly divergent, with major increases at some sites (TUL and ESC) and steep declines at others (CHC and CAS).

Validation of the SCD empirical threshold (i.e. SCD = 15: Overpeck et al., 1985; Williams et al., 2001) using modern pollen data found that most SCD scores (60%) within each vegetation/regional combination were below the empirical limit. These included pine forests (average SCD 10.8), fir forests (8.5), evergreen oak woods (7.9), maquis (3.0), broom heaths (6.2), ericaceous heaths (8.2), olive groves (6.6), cultivated fields (12.4), high-altitude meadows (12.4), salt marshes (9.9) and vegetation dominated by tamarisk (3.4), *Ephedra* spp. (7.7) and rushes (3.6). A minority of vegetation types had higher average SCD scores, including *dehesas* (29.8), pastures (29.3), marcescent oak forests (38.2), xerophytic maquis (21.9), abandoned fields (32.3), riparian forests (32.7) and beech forest (17.7).

Figure 2 shows average SCD scores alongside anthropogenic indicators, a charcoal composite curve and aggregated fire, richness and turnover events in the 13 palaeorecords. The SCD graph distinguishes 200-year periods of pollen assemblage turbulence from periods of relative stability. Abrupt changes are concentrated around 5500 to 5000 cal. yr BP and since 1800 cal. yr BP. Mean SCD scores for the 13 records exceed the threshold during these periods, and more than 50% of the individual records exceed the threshold at the same time. Sustained increases in charcoal and anthropogenic indicators occur just prior to and during these periods of abrupt vegetation change.

Event sequence analysis showed that turnover events (PCoA axis 1) followed an increase in charcoal variability more often than expected by chance (Table 2; Supplemental Material Figures S1 and S2, available online). This was the only significant result of the 80 different fire–diversity combinations tested. The timing of charcoal, richness and turnover shifts was significant in the mid–late Holocene (Figure 3). Richness increases were significantly more frequent in the period 2000–1500 cal. yr BP and turnover events were significant in the periods 6750–6000, 3250–2750 and 1250–250 cal. yr BP. Charcoal shifts were significant in the periods 5750–4500 and 2250–1750 (increases) and 4500–3750 cal. yr BP (decrease) (Figure 3). The first occurrence of a pre-turnover charcoal peak (regime shift outlier) in each record occurred in two main phases: 7100 to 5500 cal. yr BP and 3300 to 1600 cal. yr BP (Figure 3).

Discussion

Our results show several meaningful shifts in vegetation, fire and landscape dynamics during the mid- and late Holocene, and demonstrate a strong link between fire and pollen diversity in the environmental history of Mediterranean Iberia. These links

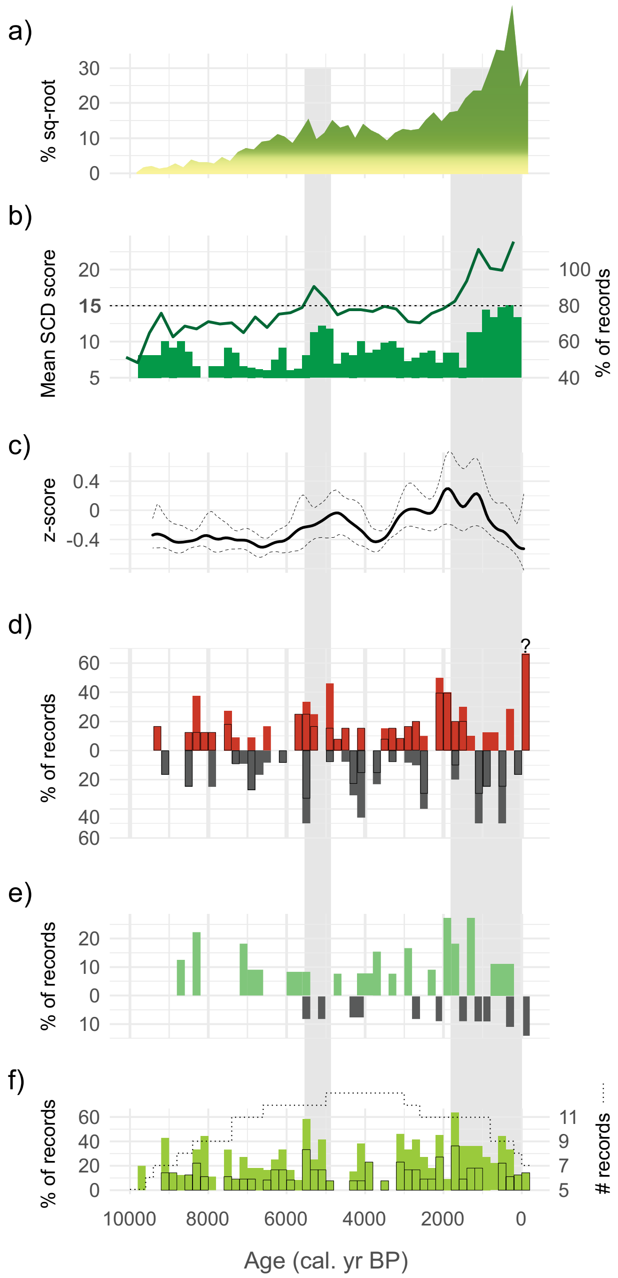

Figure 2. Centennial-scale summary of (a) anthropogenic indicator pollen and fungal spores, (b) significant shifts in palaeovegetation (squared-chord distance (SCD)), (c) synthesised fire history, (d) significant fire shifts, (e) significant palynological richness shifts and (f) significant turnover (beta replacement) events in the 13 Iberian records. Results are binned into 200-year blocks to facilitate comparison with other papers in this volume (e.g. Fyfe et al., 2019). See text for an explanation of the anthropogenic indicator and fire synthesis curves. SCD results are shown in two ways: mean values for the 13 sites (solid line, with empirical threshold shown dotted) and the percentage of sites with an SCD score $>$ 15 (bars). The direction of fire and richness shifts is indicated as +ve (increase) or –ve (decrease). Outlined fire shifts are from microscopic CHAR (pollen-slide method). Mean and variance shifts are combined due to their coherence in terms of timing and direction (see Supplemental Material Figure S2, available online). The dotted line on the lowermost graph shows the number of records that contribute to each period. Percentages that may be biased by having few records are marked with a question mark (?).

were established quantitatively and replicated in multiple palaeorecords. Some of the observed shifts constitute tipping points (sensu Van Nes et al., 2016) in the millennial ecosystem trajectories of the region – quasi-permanent transitions in ecosystem state from wooded to open vegetation and from fire-adapted to fire-prone systems. Before discussing the significance and implications of these results, we outline some methodological considerations.

Methodological considerations

For SCD estimation, randomly resampling within each time bin reduces the bias associated with comparing bin means, while preserving the temporal structure of the data. The empirical threshold of 15 (Overpeck et al., 1985) appears appropriate when compared with modern pollen samples from Iberian vegetation groups. Higher thresholds were found for some groups, for example, *dehesa*. This may relate to the structural rather than floristic vegetation classification or the high diversity or low pollen productivity of Mediterranean shrubland plants (Blondel and Aronson, 1995). Additional modern pollen sampling and detailed vegetation surveys would be required to confirm this. Bootstrapped confidence intervals indicated few significant SCD changes and may be unrealistic for Holocene compositional changes.

Beta diversity can be estimated and decomposed with various diversity indices (Barwell et al., 2015; Legendre, 2014). Ružička's index is a simple quantitative index and other indices produced similar results. To estimate beta diversity, pollen samples were reduced to the minimum sum. While this can cause information loss (Giesecke et al., 2014), repeated random resampling ensures that there is little impact on resulting trends (Supplemental Material Figure S3, available online). Diversity indices applied to pollen data are influenced by equitability (evenness), a product of pollen productivity and dispersal biases (Birks et al., 2016; Odgaard, 1999). Calibration studies (e.g. Matthias et al., 2015) would be required to correct these biases in estimates presented here. It is unlikely that our estimates reflect floristic richness and turnover directly, but we assume that the long-term trends and short-term shifts provide qualitative indications of diversity change in the surrounding landscape (Birks et al., 2016).

Regime shift detection is useful for identifying abrupt events in palaeoecological records (Carter et al., 2018; Finsinger et al., 2018). One drawback is the method's reduced performance at the extreme ends of time series (Andersen et al., 2009); hence, we removed any such shifts. The timing of some fire shifts could be influenced by sediment accumulation rates (Finsinger et al., 2018), but these are unlikely to be significantly associated with pollen turnover events as the latter are independent of sedimentation rates. Another constraint of regime shift detection is its sensitivity to predetermined parameters (e.g. significance levels and treatment of outliers), especially when the variable of interest changes gradually. We opted for $p < 0.05$ to allow detection of significant moderate shifts. A more stringent significance level of $p < 0.001$ resulted in too few event combinations to permit significance testing.

An important consideration for event sequence analysis is defining appropriate time lags in which responses can occur. Ideally, the lag should be less than the sampling interval and not more than what is ecologically relevant. Of the 1431 pollen samples in our dataset, 19% were >100 years apart, 3% were >200 years apart and 1% were >300 years apart. For a fire shift to be ecologically relevant, a response should occur within the recovery time of the vegetation, otherwise inference is weak. Information on recovery times following fire regime change is lacking for most Iberian vegetation types. Palaeoecological studies (Burjachs and Expósito, 2015; Carrión et al., 2003; Gil-Romera et al., 2014; Morales-Molino et al., 2017b) indicate that a period of 100–200 years is a useful approximation. The maximum lag of 200 years is therefore a compromise between sampling intervals and ecological relevance.

Table 2. Event sequence analysis: interactions between variables that occurred more frequently than expected by chance.

Lead variable	Lag variable	*p* value	Sites (timing of reaction, cal. yr BP)
Fire variance increase (microCHAR)	Turnover (PCoA axis 1)	0.011*	BSM (9389, 8389), CHC (3159), VIL (2825), BAZ (2041), ESC (1780), TUL (1262)

CHAR: charcoal accumulation rates; PCoA: principal coordinates analysis.
Significance levels derived from bootstrapping (1000 iterations) according to the Poisson distribution and 95% confidence intervals.
$*p < 0.05$.

Finally, site selection, dating and data quality have an unavoidable influence on the results. We included pollen/charcoal records that met strict data requirements and represent a broad spectrum of vegetation types, climatic zones and elevations. The records cannot hope to capture the full range of variability in Iberian environments and provide only snapshots of fire–diversity interactions in the past. Non-pollen palynomorph indicators of human activity have been identified in eight of the records, but others lack this proxy. Square-root transformation (Figure 2) was applied to dampen these differences. Most Iberian sites are small lakes or mires that have a limited pollen/charcoal source area. The prevalence of pollen-slide charcoal records (microscopic; Table 1) may skew fire history towards regional-scale changes compared with macroscopic charcoal (Carcaillet et al., 2001; cf. Adolf et al., 2018). Charcoal *z*-scores from sites where both fractions were counted show remarkable similarity (NAV, TUB; Figure 1). Most Iberian sites are small lakes or mires that have a limited pollen/charcoal source area. Our capacity to reconstruct key aspects of fire regimes, such as fire return intervals, is limited by the paucity of long charcoal records with contiguous sampling. We hope that future research will fill these gaps in present knowledge with high-resolution multi-proxy datasets.

Drivers of Holocene fire trends in Mediterranean Iberia

Fire has played an undeniably important role in shaping the Holocene vegetation of Mediterranean Iberia (Carrión et al., 2010; López-Sáez et al., 2017). Critical aspects for Holocene vegetation development include fire frequency and the combined impacts of fire and human activity or climatic change (Carrión et al., 2003; Morales-Molino et al., 2017b, 2018). While fire's effects on palaeovegetation are well understood, the drivers of Holocene fire trends are less so.

Two distinct fire trends emerged from our analysis of high-resolution charcoal series: (1) a mid-Holocene fire increase and (2) a late-Holocene fire increase (MH and LH groups; Figures 1a and 3). These trends do not lend themselves to clear interpretation in terms of elevation (Vannière et al., 2016), current fire regime (Moreno and Chuvieco, 2013; Vázquez de la Cueva, 2006) or soil type (Supplemental Material Figure S4, available online). Latitude and longitude emerged as weakly related variables (Supplemental Material Figure S5, available online; Morellón et al., 2018; Vannière et al., 2011). MH group sites tend to be situated further east and north compared with LH sites (Figure 1, top). Today, these sites tend to have a milder bioclimate compared with the LH group, which is weakly associated with greater rainfall seasonality and more extreme winter temperatures (Supplemental Material Figure S5, available online).

At a local scale, aspect influences fire frequency through interactions between topography, prevailing winds and fuel accumulation (Moreno et al., 2011). Several of the MH group sites are situated in N–S-oriented valleys, while LH group sites are often in E–W valleys. Without an understanding of charcoal source area and Holocene wind directions, these local-scale factors remain difficult to reconcile with fire history at appropriate scales. Fire–landscape simulations are needed to shed light on microclimatic and topographic controls (e.g. Snitker, 2018).

At a regional scale, fuel quantity and connectivity interact with climate to promote flammability (Gil-Romera et al., 2014; Pausas and Paula, 2012). Arboreal pollen ratios approximate the level of woody biomass in the site surroundings and may be used to assess Holocene fire–fuel linkages (Burjachs and Expósito, 2015; Marlon et al., 2006). Prior to the mid-Holocene fire increase, neither arboreal pollen ratios (Supplemental Material Figure S5, available online) nor forest type (Supplemental Material Figure S2, available online) anticipate where burning subsequently occurred. Lake-level data (Aranbarri et al., 2014; Fletcher and Zielhofer, 2013) provide little suggestion that aridity, which can increase flammability in moist productive zones (Pausas and Paula, 2012), was a feature of the palaeoclimate around 7500 cal. yr BP, when fire trends from MH and LH groups began to rapidly diverge (Figure 3).

Population density is a key factor influencing recent ignitions in Mediterranean landscapes (Chergui et al., 2018; Ganteaume et al., 2013; Vázquez de la Cueva, 2006). Some sites in the MH group, especially in the lowlands, are located where historical (19th century) population density (Silveira et al., 2013) and agricultural potential (Aubán et al., 2015) were high. The timing of the mid-Holocene fire increase corresponds to the establishment of Neolithic populations across the Iberian Peninsula. This originated at various points along the Mediterranean coast before spreading into northern inland zones and along the Atlantic coast (Aubán et al. 2015; Isern et al., 2014, 2017). Apart from the Pyrenees site (BSM), where early-Holocene fires are linked to climatic instability between 9800 and 8100 cal. yr BP (Pérez-Sanz et al., 2013), an anthropogenic driver is probably consistent with the timing and geographic spread of the mid-Holocene fire increase (Dietze et al., 2018; Vannière et al., 2016).

Abrupt vegetation changes in Mediterranean Iberia

The mid-Holocene spike in SCD scores around 5500 to 5000 cal. yr BP (Figure 2) corresponds to major transition in the environmental history of the Iberian Peninsula and Mediterranean more broadly (Burjachs et al., 2017; Roberts et al., 2011; Vannière et al., 2011). During this environmental transition, lake levels changed abruptly at several Mediterranean sites (Aranbarri et al., 2014; Magny et al., 2011, 2013, cf. Reed et al., 2001), vegetation shifted from mesic to more xeric in numerous Iberian pollen records (e.g. Anderson et al., 2011; Carrión, 2002; Carrión et al., 2010; Fletcher et al., 2007; Gil-Romera et al., 2010; González-Sampériz et al., 2017; Jalut et al., 2000; Morellón et al., 2018) and a fire trend 'reversal' occurred across the Mediterranean, with fire generally increasing south of 40°N and decreasing north of this latitude (Vannière et al., 2011). The north–south divide in fire and lake-level proxies is indicative of a regional-scale climatic driver, potentially involving shifts in the Intertropical Convergence Zone and North Atlantic Oscillation (NAO; Magny et al., 2013; Vannière et al., 2011).

If climate were the main driver of vegetation change in Mediterranean Iberia, it did not affect the vegetation at all sites equally. SCD scores generally remain below threshold at sites where pine was dominant (Supplemental Material Figure S2, available online), perhaps due to pine forests' resilience to environmental

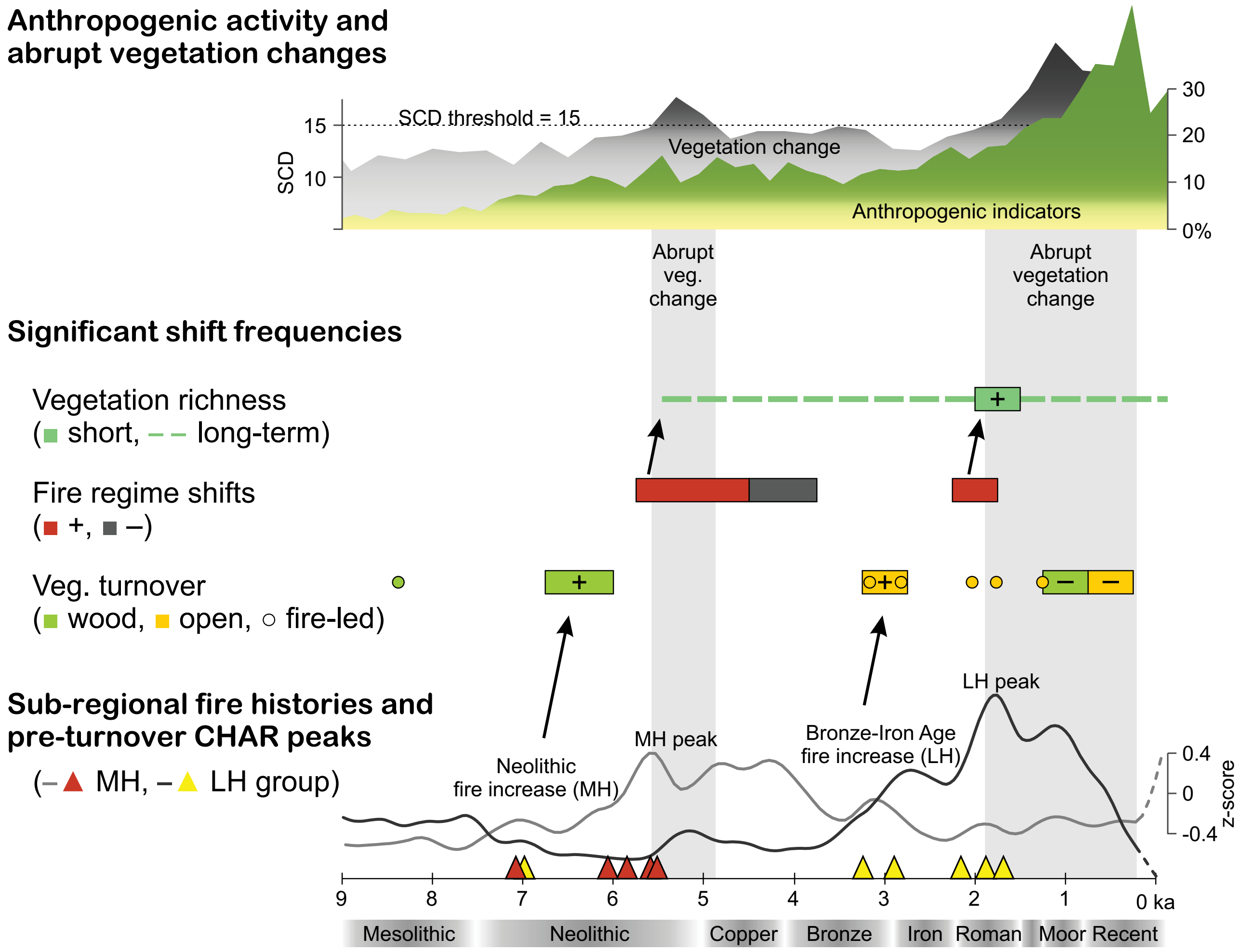

Figure 3. A synthesis of Holocene fire and vegetation diversity change in Mediterranean Iberia. Human activity and abrupt vegetation change proxies (top) compared with significant richness, turnover and fire shift frequencies (middle) and the timing of anomalous charcoal peaks that precede turnover events, the composite fire history and archaeological periods (bottom). Significant shift frequencies are 500-year periods in which the occurrence of shifts was greater than in the bootstrapped dataset ($p < 0.05$). For richness, '+' indicates an increase in palynological richness. For turnover, '+' indicates an increase in woodland (wood) or open vegetation (open) turnover and '–' indicates a decrease (see Figure 1b and c). Dashed lines indicate longer intervals in which the occurrence of richness or turnover shifts was significant. Grey shaded zones indicate abrupt vegetation changes according to above-threshold SCD scores (Figure 2).

change (Morales-Molino et al., 2017a; Rubiales et al., 2010). BSM is an important exception, with its borderline Mediterranean–temperate climate and prevalence of *Pinus uncinata* instead of typical Mediterranean pines (Pérez-Sanz et al., 2013). Here pine expanded rapidly around 5700 cal. yr BP. Sites with a particularly pronounced spike in SCD scores between 5500 and 5000 cal. yr BP are mostly situated in Eastern Iberia (BAN, BSM, NAV and VIL), where the influence of the Western Mediterranean Oscillation on rainfall patterns and seasonality may have modulated the effects of Holocene climatic changes relative to NAO-dominated parts of Iberia (Martin-Vide and Lopez-Bustins, 2006; Morellón et al., 2018). Apart from BSM, these sites experienced a rapid decline in *Pinus nigra* to the benefit of oak and scrub vegetation.

Mid-Holocene expansion of xerophilous scrub and fire-adapted pines (Aranbarri et al., 2014; Carrión et al., 2010; Fletcher et al., 2007) fits well with a change in fire regime, as most Mediterranean shrubland plants have more fire-adaptive traits than *Pinus nigra* and mesophytes (Tavşanoğlu and Pausas, 2018). Charcoal evidence shows a regional-scale increase in burning and fire regime change between 6000 and 4500 cal. yr BP (Figures 2 and 3). Whether this fire increase was triggered by aridity is uncertain. Mediterranean vegetation switches from low- to high-flammability states according to aridity thresholds that vary geographically (Fréjaville and Curt, 2015; Pausas and Paula, 2012). Aridity causes fire probability to increase in productive mesic zones and to decrease in fuel-limited xeric zones (Batllori et al., 2013). Observed fire trends give no indication of geographic divergence between 5500 and 5000 cal. yr BP. If anything, there is a temporary convergence of subregional trends that began diverging much earlier, around 7500 cal. yr BP (Figure 3).

The peak in anthropogenic indicators around 5500 cal. yr BP, while moderate compared with more recent values, suggests increased human activity may be involved in abrupt vegetation change (Figure 2). The anthropogenic indicator signal is dominated by changes at the NE sites (BAN, BSM), but archaeological records attest the spread of human occupation across Iberia around 5500 cal. yr BP (Blanco-González et al., 2018; Fyfe et al., 2019). Recent modelling at NAV indicates that fires during this period were largely anthropogenic (Snitker, 2018). Human use of fire, especially during a phase of rapid demographic change, might explain the significant co-occurrence of fire shifts.

The final phase of abrupt vegetation change corresponds to the most recent 1800 years. Unlike the mid-Holocene transition, this change is not constrained to a defined period and its onset occurs earlier at some sites. Steadily rising and above-threshold SCD scores appear in the west (CHC) at approximately 3200 cal. yr BP and the SE at approximately 2700 cal. yr BP (VIL). These changes are linked with fire shifts (Figures 1–3). Abrupt change began at GAD around 1850 cal. yr BP; at ESC, TUL and CAS at approximately 1300 cal. yr BP; and finally BSM, RFT, LRS and ELM in the last millennium. These abrupt changes have no clear geographic pattern, and the original research papers (Table 1) link them unanimously to human impacts, including deforestation, grazing and fire. The increase in anthropogenic indicators supports this interpretation (Figure 2). The amplitude of these late-Holocene vegetation shifts was, in most cases, greater than the mid-Holocene transition.

Fire-led changes in vegetation richness

Overall richness in Mediterranean pollen records has generally increased through the Holocene. Researchers have related this increase to human impact (Franco-Múgica et al., 2001; Morales-Molino et al., 2017b; Servera-Vives et al., 2018), reductions in local fire frequency/magnitude and the expansion of grazing (Jouffroy-Bapicot et al., 2016), increases in regional fire activity (Colombaroli et al., 2009; Colombaroli and Tinner, 2013), increased landscape openness (e.g. Anderson et al., 2011; Gil-Romera et al., 2014; Morales-Molino, García-Antón, 2014; Muller et al., 2015; Noti et al., 2009; Vescovi et al., 2010), catchment erosion events (Robles-López et al., 2017) and changes in the evenness of plant communities (Beffa et al., 2016).

The variety of interpretations stems in part from the variety of ecosystems considered and potential threshold responses to fire (Colombaroli et al., 2008; Morales-Molino et al., 2017b). Fire changes would be expected to produce different outcomes depending on vegetation type (e.g. coniferous vs sclerophyllous fuels), prevailing climate and the timing, magnitude and nature of human interactions with the vegetation (Carrión et al., 2010; Gil-Romera et al., 2010). Richness sometimes responds positively to fire (Colombaroli and Tinner, 2013), sometimes negatively (Bisculm et al., 2012) and at many sites the relationship is inconsistent (Gil-Romera et al., 2014). It is often unclear whether richness is responding to fire or whether fire is responding to changes in the plant community.

The 13 Mediterranean Iberian pollen sequences exhibit highly divergent Holocene richness trends (Figure 1e), reflecting the complexity of current and past vegetation patterns. Richness is relatively high in oak-, shrub- and herb-dominated palaeovegetation (e.g. CAS) and relatively low in pine-dominated palaeovegetation (e.g. ESC), a pattern that reflects differences in plant diversity between pine forests and other vegetation types (Blondel and Aronson, 1995) and the equitability of the pollen assemblages. Shifts between these palaeocommunities account for most of the richness changes observed. Early–mid Holocene richness increases are associated with forest or woodland vegetation, while mid–late-Holocene richness changes are associated with open vegetation (e.g. scrub, heath, grassland).

Fire and richness are clearly interlinked on a regional scale (Figure 3) and a site level (Supplemental Material Figure S2, available online). The frequency of richness shifts was significant over the entire period from 5500 cal. yr BP to the present. Richness increases were significant between 2000 and 1500 cal. yr BP. Both periods were preceded by a significant rise in positive fire regime shifts (Figure 3), implicating fire as a probable driver of increasing richness (Colombaroli et al., 2007). Richness trends from the different sites tend to converge during the last 2000 years and especially since the Middle Ages (Figure 1e). This may be due to vegetation homogenisation on a regional scale (Colombaroli and Tinner, 2013; González-Sampériz et al., 2017) through the pervasive ecological impacts of the Roman and Medieval periods (Aranbarri et al., 2014; Schneider et al., 2016).

Fire-led vegetation turnover

Turnover provides further insights into fire's impact on diversity, being a key community-level response to external forcing events (Jackson and Sax, 2010). We interpret the turnover trends as representing oak woodland diversity change (Figure 1b) and open vegetation (non-forest) diversity change (Figure 1c). This is based on correlated taxa (Supplemental Material Table S2, available online), richness trends (Figure 1e) and ecological knowledge (e.g. Blondel and Aronson, 1995). In the early Holocene, the only fire-led turnover events occurred at BSM (Pyrenees) around 9390 and 8390 cal. yr BP (Table 2). Fire regime shifts here caused the temporary expansion of pines to the detriment of oak woodlands, linked to rapid climatic changes (Pérez-Sanz et al., 2013). Mid- and late-Holocene fire–turnover relationships are discussed in the following sections.

Mid-Holocene turnover in oak woodlands. On a millennial scale, regardless of whether fire increased in the mid- or late-Holocene, fires precede or coincide with periods of greater turnover (Figures 1 and 2). Woodland turnover trends for the MH group show an early-Holocene drift towards pine forest. This drift rapidly reversed after the onset of increased fire, the turnover trajectory moving towards higher diversity oak-dominated vegetation (Figure 1b), with significant positive turnover in woodlands between 6750 and 6000 cal. yr BP (Figure 3). No event sequences with fire regime shifts leading to turnover events were observed during this period. However, pre-turnover fire peaks might indicate that individual fire episodes rather than fire shifts were driving turnover (Figure 3).

With positive turnover in oak woodlands, turnover in the non-forest component (Figure 1c) also increased and arboreal pollen declined (Figure 1d). Hence, increasing fire at MH sites is accompanied by increasing woodland diversity while woodland cover (biomass) was decreasing. This pattern is more consistent with an anthropogenic fire regime (i.e. land-use controlled) than one governed by climate–fuel linkages (i.e. biomass controlled; Marlon et al., 2006; Pausas and Fernández-Muñoz, 2012). A regional-scale climatic explanation is difficult to justify given the staggered timing of the woodland diversity maximum, its occurrence in diverse bioclimatic zones (Figure 1 and Supplemental Material Figure S5, available online) during a climatic phase of high lake levels and mesophyte expansion (Aranbarri et al., 2014; Fletcher and Zielhofer, 2013).

These fire–turnover patterns are perhaps best explained by manipulation of woodlands to create semi-open agro-silvo-pastoral landscapes. These landscapes harbour the most biodiverse Mediterranean ecosystems and have a cultural heritage stretching back millennia (Blondel and Aronson, 1995; Colombaroli and Tinner, 2013; Stevenson and Harrison, 1992; Zamora et al., 2007). Most of the sites that experienced mid-Holocene fire and turnover increases are located near Neolithic settlements (BAN: Revelles et al., 2015; CAS: Ejarque et al., 2016; GAD: Carrión et al., 2003; NAV: Carrión and van Geel, 1999).

Neolithic settlements in the Western Mediterranean were preferentially located in semi-open vegetation (Battentier et al., 2018; Carrión and van Geel, 1999; Ejarque et al., 2010; Revelles et al., 2015), with settlement cores surrounded by extensive areas used for animal husbandry and exploitation of natural resources (García Puchol et al., 2009). Creation of new semi-open landscapes accompanied Neolithic expansion in lowlands and mountain Iberian areas (Aranbarri et al., 2015; Ejarque et al., 2010; Orengo et al., 2014). Neolithic settlers apparently avoided already populated areas (Aubán et al., 2015; Zilhão, 2001), although in some places preexisting Mesolithic communities may have assimilated Neolithic cultural elements (Bicho, 2009; García Puchol et al., 2009). The divergent fire histories in the MH and LH groups around 7500 cal. yr BP (Figure 3) could represent the gradual decline of Mesolithic fires in areas that were avoided by Neolithic settlers (LH) and/or the assimilation of Neolithic practices (MH). Hunter-gatherers use fire differently to farmers, often targeting landscapes already prone to lightning-strike fires (Coughlan et al., 2018).

A growing number of palaeoecological records indicates Neolithic impacts on Mediterranean vegetation as early as 7500 cal. yr BP, through tree felling (Revelles et al., 2015), arboriculture and cereal agriculture (Tinner et al., 2009) and altering fire regimes (Colombaroli et al., 2008; Kaltenrieder et al., 2010; Snitker, 2018; Vannière et al., 2016).On the Iberian Peninsula, Neolithic populations were distributed from the coastal lowlands and inland plains up to elevations of 2600 m in the Pyrenees, locally exploiting a wide range of wild and domesticated resources (Gassiot Ballbè et al., 2015; González-Sampériz et al., 2017; Montes et al., 2016; Oms et al., 2018; Orengo et al., 2014). These impacts would have varied spatially according to the distribution of resources and the susceptibility of the vegetation to fire–vegetation feedbacks, as well as temporally according to changing socio-economic, climatic and cultural drivers.

The subtlety of Neolithic impacts in pollen diagrams may be illusory, merely reflecting biases in pollen site size and selection (Chapman, 2017) or pollen's reduced capacity to detect cultivated plants compared with other proxies (e.g. Peña-Chocarro et al., 2018; Poher et al., 2017; Schneider et al., 2016). For example, abundant pollen and macrofossils attest to the cultivation and processing of cereals at La Draga, a major Neolithic site on the shores of Lake Banyoles (BAN; Antolín et al., 2015; Bosch et al., 2000; Revelles et al., 2017), yet cereal pollen scarcely appears in the lake sediments of the same period (Revelles et al., 2015).

Some of the site-specific differences in fire and turnover only make sense in the light of archaeological evidence. Exploitation of oak (*Quercus*) timber for construction at La Draga caused local deforestation (López-Bultó and Piqué Huerta, 2018; Revelles et al., 2015), explaining why fire was not implicated in early-Neolithic turnover at BAN. Around Navarrés in SE Iberia, fire models coupled with archaeological surveys suggest early-Neolithic communities used fire to create and maintain semi-open maquis vegetation for grazing (Snitker, 2018), corroborating the spike in fire and grazing indicators at NAV (Carrión and van Geel, 1999). The combined use of pollen, non-pollen palynomorphs and charcoal analyses, together with integrated archaeological and multi-site palaeoenvironmental analyses, can significantly overcome traditional pollen-analytical limitations to detect both mobile and spatially limited prehistoric cropping and grazing practices in the palaeoenvironmental record (Ejarque et al., 2010; Garcés-Pastor et al., 2017).

Late-Holocene turnover in open vegetation. Subregional fire histories (Figure 3) suggest there was little change in biomass burning trends through the Neolithic and into the Chalcolithic. This continuity began to break down around 4500 cal. yr BP, a period of changing settlement distribution on the Iberian Peninsula. Populations are thought to have deserted SW Iberia, while expanding in the SE, NE and Meseta zones (Blanco-González et al., 2018; Fyfe et al., 2019; Lillios et al., 2016). This demographic shift may explain negative turnover in oak woodlands and open vegetation in the SW (RFT), while turnover was positive for both at sites in the SE (BAZ, LRS, VIL) (Figure 1b). The significant occurrence of negative fire shifts in this period (Figure 3) appears to be linked to declining biomass on a regional scale, suggested by rising open vegetation diversity and falling arboreal pollen in most records (Figure 1c and d).

The Bronze and Iron Ages brought a reorganisation of Iberian landscapes and fire regimes. Subregional fire trends (MH and LH groups) began to diverge once again (Figure 3). Forest cover experienced a regional decline (Figure 1c), prompting the first significant episode of open vegetation turnover across the region (Figure 3) apart from the pinewoods of the northern Meseta (ESC, TUL). Positive turnover in open vegetation is closely aligned with the late Bronze Age increase in fire (Figure 3). Indicators of human activity rose steadily (Figure 3), tracking the spread of human influence across the Iberian Peninsula, particularly at mid–high elevations (see Figure 11 in Carrión et al., 2010).

A threshold was reached around 2000 cal. yr BP, when fire peaked, turnover in woodland was negative, turnover in open vegetation was positive and richness increased rapidly at many sites (Figures 1 and 3). Similar changes are recorded in Sicily (Calò et al., 2012; Tinner et al., 2009) and reflect land-use change as territories fell under Rome's globalising influence. More recent history has seen the decline of biomass burning in the LH group, following closely the reduction in fuel indicated by arboreal pollen and open vegetation turnover (Figure 1). Intensification of anthropogenic pressure and landscape homogenisation across Mediterranean Iberia drove significant negative turnover in both oak woodland and open vegetation (Figure 3), a process that appears to be continuing more recently (Figure 3).

We do not wish to argue that climatic changes, soil development and other processes had no impact on Mediterranean Iberia's vegetation diversity patterns (see Allen, 2001; Carrión et al., 2010; Keeley et al., 2012). At the subcontinental scale, the divergent subregional patterns identified here would likely blend into a background dominated by climatic drivers (see Dietze et al., 2018). Iberia's vegetation history is replete with surprises, paradoxes and exceptions (Carrión et al., 2001, 2007, 2010), so we do not expect the same fire–turnover patterns in every record. We merely suggest that turnover in the Mediterranean Iberian records considered here can be parsimoniously explained by the spread of human influence from early-Neolithic centres to more marginal sites over some 7500 years. This spatiotemporal pattern is unrelated to regional-scale climatic reconstructions based on vegetation-independent palaeoclimatic proxies (Aranbarri et al., 2014; Morellón et al., 2018; Roberts et al., 2011). Even so, humans undoubtedly tracked changes in climate and vegetation composition across the landscape, deciding where to farm, where to graze and where to burn to make the best of environmental opportunities (Walsh, 2014).

Our analysis provides a new perspective on Mediterranean environmental history. We see two waves of vegetation modification spreading across the landscape – one wave promoting woodland diversity (e.g. wooded agro-pastoral landscapes) and a second promoting non-forest diversity (e.g. open agro-pastoral landscapes). The first wave was likely accelerated by Neolithic populations and the second propagated by Bronze, Iron Age and Roman populations. These waves arrived earliest in the most fertile coastal lowlands and spread to encompass most of Mediterranean Iberia, propelled by population movements and the progressive exploitation of marginal territories.

Conclusion

This detailed study of Mediterranean Iberian turnover trends and fire history allows conventional proxies to be seen in a new light. The progression of high-diversity semi-open landscapes in Mediterranean Iberia follows a course that can be explained by human activities at many of the studied sites. We suggest that Neolithic impacts have probably been underestimated in the palaeoenvironmental record because of biases in pollen site selection, pollen production and preconceptions about prehistoric human agency (Chapman, 2017; Head, 2008; Walsh, 2014).

Our results implicate humans in the creation and maintenance of diverse vegetation mosaics, supporting recent studies that invoke human-driven vegetation change since the Neolithic in parts of the Iberian Peninsula (Carracedo et al., 2018; Ejarque et al., 2010; Fyfe et al., 2019) and across Europe (Colombaroli and Tinner, 2013; Dietze et al., 2018; Molinari et al., 2013; Vannière et al., 2016). In Iberia, human influence on the vegetation spread upwards and outwards from Neolithic centres during subsequent archaeological periods. Landscape transformation intensified around 5500 to 5000 cal. yr BP and received a final kick during the last two millennia, accelerating the spread of open vegetation and the loss of woodland diversity on a regional scale. Fire regime change was found to play a statistically significant role in initiating turnover events in Mediterranean Iberian pollen records during the mid–late Holocene.

Present-day landscapes in Iberia cannot be understood without considering the deep and cumulative effects of Neolithic, Bronze, Iron Age, Roman and especially more recent activities, both on terrestrial and aquatic systems (Carrión et al., 2010; Delgado et al., 2012). Any attempt to return Mediterranean Iberia's vegetation to an assumed 'natural' state will be swimming against the tide of millennia of dedicated human labour.

Management of Mediterranean biodiversity and fire regimes should consider not only recent fire history (Puerta-Piñero et al., 2012) but also the long-term legacies of prehistoric and historical-era landscape transformations (Colombaroli et al., 2013; Morales-Molino et al., 2017b; Vannière et al., 2016; Whitlock et al., 2018). Biodiversity conservation in ancient cultural landscapes requires active management using traditional practices and local knowledge. Mediterranean landscapes should be treated as living biodiversity heritage, with a human lineage perhaps as long as civilisation itself.

There is enormous scope to improve our understanding of how prehistoric landscape transformations were achieved and how they played out in different environmental zones. Perry et al. (2012) modelled the relative regional contributions of climate, topography, humans and soils to fire-driven forest loss in New Zealand, showing that even small human populations may cause an irreversible shift towards more fire-prone vegetation on a regional scale. This kind of modelling approach could be productively applied in the Mediterranean. In tandem, pollen-based vegetation models (e.g. Mariani et al., 2017), new proxies for human activity (e.g. Poher et al., 2017), contiguously sampled fire histories (e.g. Morales-Molino et al., 2017b; Vannière et al., 2008) and robust palaeoclimatic reconstructions are needed if we are to truly understand the drivers of long-term biodiversity change.

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Supplemental material

Supplemental material for this article is available online.

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