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Invited research article

Land-use history as a major driver for long-term forest dynamics in the Sierra de Guadarrama National Park (central Spain) during the last millennia: implications for forest conservation and management

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ABSTRACT

In the Mediterranean Basin, long-lasting human activities have largely resulted in forest degradation or destruction. Consequently, conservation efforts aimed at preserving and restoring Mediterranean forests often lack well-defined targets when using current forest composition and structure as a reference. In the Iberian mountains, the still widespread *Pinus sylvestris* and *Quercus pyrenaica* woodlands have been heavily impacted by land-use. To assess future developments and as a baseline for planning, forest managers are interested in understanding the origins of present ecosystems to disclose effects on forest composition that may influence future vegetation trajectories. Quantification of land-use change is particularly interesting to understand vegetation responses. Here we use three well-dated multi-proxy palaeoecological sequences from the Guadarrama Mountains (central Spain) to quantitatively reconstruct changes occurred in *P. sylvestris* forests and the *P. sylvestris-Q. pyrenaica* ecotone at multi-decadal to millennial timescales, and assess the driving factors. Our results show millennial stability of *P. sylvestris* forests under varying fire and climate conditions, with few transient declines caused by the combined effects of fire and grazing. The high value of pine timber in the past would account for long-lasting pine forest preservation and partly for the degradation of native riparian vegetation (mostly composed of *Betula* and *Corylus*). Pine forests further spread after planned forest management started at 1890 CE. In contrast, intensive coppicing and grazing caused *Q. pyrenaica* decline some centuries ago (ca. 1500–1650 CE), with unprecedented grazing during the last decades seriously compromising today's oak regeneration. Thus, land-use history played a major role in determining vegetation changes. Finally, we must highlight that the involvement of forest managers in this work has guaranteed a practical use of palaeoecological data in conservation and management practice.

1. Introduction

Land-use has long been causing important changes in the distribution, structure and composition of forest ecosystems in the Mediterranean realm, often involving their overexploitation, degradation and even destruction (Carrión et al., 2003; Urbieta et al., 2008; Valbuena-Carabaña et al., 2010). Despite this long history of intense land-use, the Mediterranean mountains of south-western Europe still host relatively extensive forested areas that provide not only valuable natural resources such as timber, firewood and pastures, but also ecosystem services like protection against natural hazards, carbon sequestration and biodiversity (Díaz-Pinés et al., 2011; Pardos et al., 2016). All these values justify the need for protecting Mediterranean forested areas. However, the disturbed conditions of most Mediterranean forest ecosystems make it difficult to define precise conservation and restoration goals. Thus, disclosing the effects of past human activities on current forest composition and structure is a major question for Spanish forest managers to assess future vegetation dynamics. In this context, a palaeoecological perspective on ecological processes can provide relevant insights into ecosystem baseline conditions (i.e. prior to relevant ecosystem disruption by human agency), the impact of land-use history on vegetation composition and structure, and the range of disturbance variability, thus guiding ecosystem

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conservation and management (Willis and Birks, 2006; Froyd and Willis, 2008; Morales-Molino et al., 2015). In fact, in northern and central Europe multi-proxy studies of sedimentary and peat sequences have usually informed management and conservation of protected areas (e.g. Lindbladh et al., 2008; Valsecchi et al., 2010; Clear et al., 2013), but to our knowledge these studies are still lacking in the Mediterranean Basin.

In the Mediterranean Spanish mountains *Pinus sylvestris* and *Quercus pyrenaica* stands are widespread ecosystems of high ecological value, listed as priority habitats for preservation within the Spanish National Parks (NPs) network. However, the lack of undisturbed *P. sylvestris*- and *Q. pyrenaica*-dominated stands hindered the declaration of National Parks focusing on their protection until recently, because the Spanish NPs aims at protecting ecosystems mostly free of human activities. One of the major goals of the recently declared Sierra de Guadarrama NP in the Iberian Central Range is preserving the extensive and quite continuous *P. sylvestris* forests and *Q. pyrenaica* woodlands of these mountains. However, documentary sources show that *P. sylvestris* and *Q. pyrenaica* stands within this NP have been intensively exploited for centuries to produce timber (pine), firewood/charcoal (oak) and pasturelands (mostly oak), with very different land-use histories depending on the dominant tree species (Manuel-Valdés, 1997). Although multi-centennial coppicing of *Q. pyrenaica* forests for firewood and charcoal production explains the present abundance of highly degraded coppiced stands (Salomón et al., 2016), many questions about human-induced disturbances affecting oak woodlands and their responses to disturbance variability remain open. Likewise, some authors allege that forest management has promoted the spread of *P. sylvestris* stands at low altitudes, below 1500–1700 m a.s.l., at the expense of *Q. pyrenaica* woodlands because of the high economic value of pine timber (Rivas-Martínez et al., 1999, 2002). Oppositely, other authors consider, on the basis of historical archives, that 'low-altitude' pine stands are natural (Martínez-García and Montero, 2000). This likely human-induced change in forest dominant species is still not fully resolved and, more importantly, little is known about the historical impacts of human activities on these pine stands. Finally, natural riparian vegetation within the *P. sylvestris* forests has been severely disturbed by forest management and overgrazing, with its species composition remaining mostly unknown. In summary, the Sierra de Guadarrama forest ecosystems are far from a pristine condition and, therefore, a good area to test the impact of land-use history on Mediterranean forests, understanding the associated variability in disturbance regimes and detailing their baseline composition using palaeoecology. Despite several palaeoecological records are available in the Sierra de Guadarrama NP, their chronology, resolution and/or location hinder their usefulness to discuss forest ecological processes in detail (summarized in López-Sáez et al., 2014). Therefore, new palaeoecological analyses of well-dated high-resolution sedimentary and peat sequences will provide a detailed quantitative long-term perspective (i.e. multi-decadal to millennial) on these gaps in the knowledge about Mediterranean forest ecology.

These questions about ecosystem management and conservation that involve a long-term (multi-centennial) perspective arose from our collaborative work with the Valsaín forests managers (Sierra de Guadarrama NP protected area). This site-based approach promotes an effective and practical use of palaeoecological data in ecosystem conservation and management (Davies et al., 2014) but it has been barely used so far. In this case, managers' specific questions covered most of the areas in which palaeoecology can guide forest conservation and management (Froyd and Willis, 2008; Lindbladh et al., 2013), i.e. vegetation composition, vegetation responses to disturbances and range of variability of such disturbances. We produced three new multi-proxy (pollen, spores, stomata, microscopic charcoal, plant macrofossils) well-dated palaeoecological records from two small forest hollows in the *P. sylvestris* forest and a small mire at the current *P. sylvestris*-*Q. pyrenaica* ecotone to address the following questions. Firstly, we quantitatively assessed the responses of *P. sylvestris* and *P.sylvestris*-*Q.pyrenaica* forest ecosystems to their different land-use histories as well as climatic variability at a nearly-decadal timescale. We emphasized the last centuries (since ca. 1300–1400 CE), when detailed records of human activities (mostly qualitative documentary archives) and climatic fluctuations are available, and paid particular attention to the range of variability of disturbance regimes (fire, grazing) and their effects on vegetation. And secondly, we drew on our palaeoecological data to inform about the composition of the lost riparian vegetation and the lower altitudinal limit of *P. sylvestris* forests.

2. Regional setting

The Sierra de Guadarrama NP and its Peripheral Protected Zone stretch over around 100,000 ha of the Guadarrama Mountains (central Spain, Fig. 1a), protecting forests and high-mountain ecosystems. Here we focus on the "Valsaín forests" area (north-western slopes of the Guadarrama Mountains, Fig. 1b), where the main forest ecosystems of the National Park are well-represented and historical archives allow tracking land-use changes through time (since the early Modern Period, ca. 1500 CE). The bedrock is siliceous, mostly granite and gneiss, and soils are consequently acidic. The climate is mountain continental Mediterranean. At 1200 m a.s.l. (lower section of the forest), mean annual temperature is 10 °C and the average annual precipitation is 700 mm, with mean temperatures of the coldest ($T_{January}$) and the warmest months (T_{July}) of 3 °C and 19 °C, respectively. At 1900 m a.s.l. (local timberline) mean annual temperature, $T_{January}$ and T_{July} drop to 6 °C, −1 °C and 16 °C, respectively, with annual precipitation rising to 1300 mm. Summer drought is not particularly severe, lasting around two months at low altitudes and only one month in the summit area.

Five vegetation belts can be distinguished according to altitude. Sclerophyllous oak woodlands (*Quercus ilex* subsp. *ballota*) dominate at the lowest altitudes, until 1000–1200 m a.s.l., under a more pronounced summer drought. They are replaced at higher altitudes, up to 1500–1700 m a.s.l., with less drought-tolerant deciduous oak woodlands (*Q. pyrenaica*). The highest forest belt corresponds to pine forests (*P. sylvestris*) that mostly grow between 1400–1700 and 1900–2100 m a.s.l. but descend until 1200 m a.s.l. along north-facing humid valleys. Finally, *Juniperus communis* subsp. *alpina* and *Cytisus oromediterraneus* shrublands and dry cryophilic *Festuca curvifolia* grasslands dominate above the timberline. The main human activities in the Valsaín forests area (and the Sierra de Guadarrama NP) are extensive cattle ranching, pine logging and recreation activities.

3. Material and methods

We cored three sites in the Valsaín forests (Fig. 1c) with a Russian peat sampler: two small forest hollows located in the lower part of the *P. sylvestris* forest, Arroyo de las Cárcavas (40°50′31″N, 004°01′53″W, 1300 m a.s.l., 30 m diameter) and Arroyo de Navalacarreta (40°51′08″ N, 004°01′52″W, 1250 m a.s.l., 25 m diameter), and a small mire lying on an open ridge at the *P. sylvestris*-*Q. pyrenaica* ecotone, Arroyo de Valdeconejos (40°51′44″N, 004°03′35″W, 1380 m a.s.l., 40 m diameter). According to their small size, all the sites have reduced relevant source areas for pollen and charcoal, mostly coming from several hundred metres radii (Sugita, 1994) and thus reflecting nearly stand-scale vegetation changes (Bradshaw, 2013). However, Valdeconejos may receive a certain proportion of pollen and charcoal from a few kilometres distance because sites lying on ridges at higher altitude are more exposed to upward winds (Andrade et al., 1994). At Navalacarreta and Cárcavas we obtained 135-cm and 149-cm long cores, respectively. The Valdeconejos sequence was 203-cm long, but pollen was well-preserved only for the top 147 cm. All cores were stored at 4 °C and into the dark until sub-sampling. The chronology of the peat sequences is mostly based on AMS radiocarbon dating of terrestrial plant macrofossils and peat (Table 1). To account for changes in peat accumulation, we built age-depth models by fitting smoothing splines (Navalacarreta

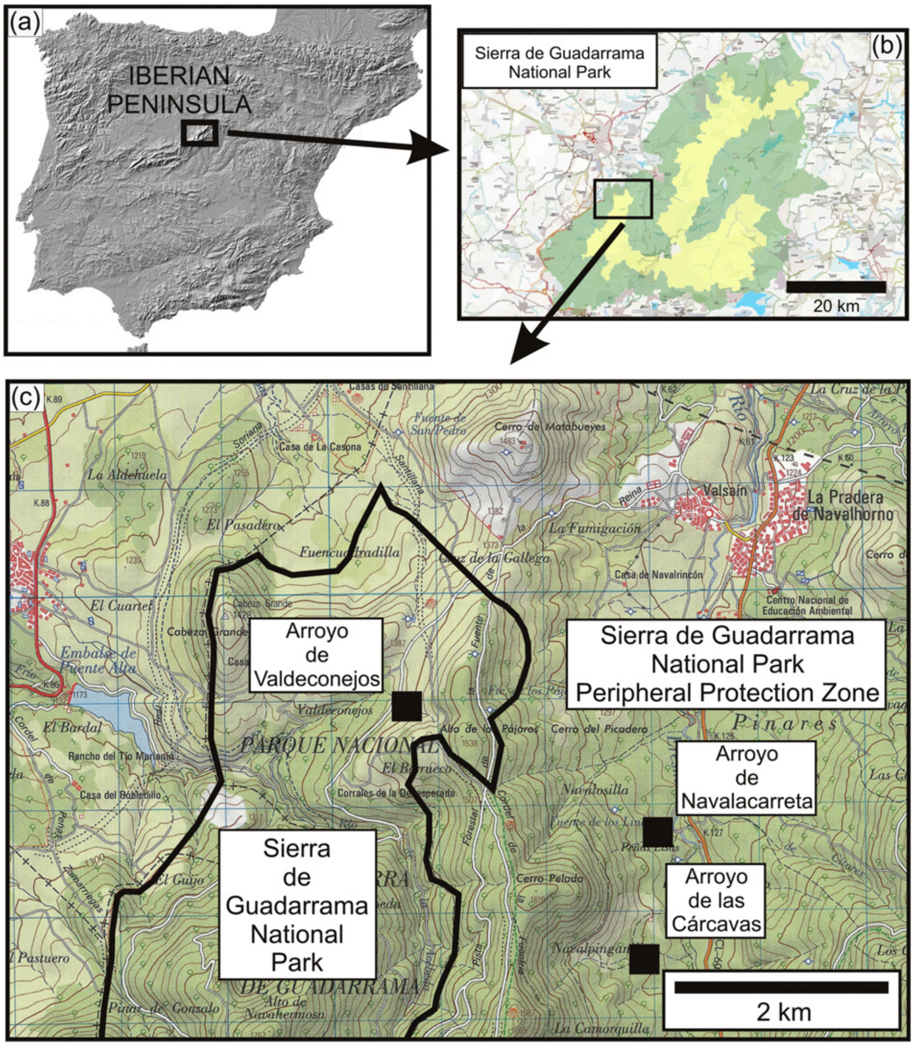

Fig. 1. (a) Map with the location of the Sierra de Guadarrama National Park in the Iberian Peninsula. (b) Location of the study area between the limits of the National Park (yellow) and its Peripheral Protection Zone (green). (c) Detailed map of the study area, the lower part of the Valsaín forests, with the location of the three studied sites (black squares).

Table 1
Radiocarbon dates for the three sites presented in this paper: Cárcavas (CAR), Navalacarreta (NVC) and Valdeconejos (VDC). All calibrated ages were obtained using CALIB 7.1 (Reimer et al., 2013). The only exception was the sample UBA-26699, which was calibrated with CALIBomb because it was younger than 1950 CE, i.e. 0 cal year BP (Hua et al., 2013; Reimer et al., 2013).

Site	Laboratory code	Depth (cm)	Material	^{14}C age (^{14}C year BP)	Calibrated age (cal year BP (BCE/CE), 95.4% confidence interval)	Calibrated age (cal year BP (BCE/CE), median)
CAR	UBA-26703	62–63	*Pinus sylvestris* cone scales, coniferous periderm, bark	280 ± 25	159–433 (1517–1891 CE)	375 (1575 CE)
	UBA-29826	100–104	*Pinus* needles, coniferous periderm	1850 ± 30	1715–1865 (85–235 CE)	1784 (166 CE)
	UBA-26704	110	*Pinus* twig	1860 ± 35	1714–1875 (75–236 CE)	1796 (154 CE)
	UBA-25290	136	*Pinus sylvestris* t. (t. = type) wood	1850 ± 35	Rejected	Rejected
	UBA-25291	145–146	Bulk	2320 ± 30	2184–2376 (426–234 BCE)	2342 (392 BCE)
NVC	UBA-26705	80	*Pinus sylvestris* t. wood	480 ± 25	502–537 (1413–1448 CE)	519 (1431 CE)
	UBA-25292	121–122	*Pinus sylvestris* t. wood	610 ± 30	547–654 (1296–1403 CE)	602 (1348 CE)
	UBA-26706	126–127	*Pinus sylvestris* t. wood and charcoal	680 ± 30	561–680 (1270–1389 CE)	652 (1298 CE)
	UBA-29825	130–134	Charcoal	5150 ± 35	Rejected	Rejected
	UBA-25293	133–134	Bulk	2350 ± 30	Rejected	Rejected
VDC	UBA-26699	32–33	Peat	102.5 ± 0.3 pMC	−6.9/−5.4 (1955–1957 CE)	−6 (1956 CE)
	UBA-26700	62–63	Peat	40 ± 25	−5/254 (1696–1955 CE)	55 (1895 CE)
	UBA-26701	100–101	Peat	130 ± 30	9–275 (1675–1941 CE)	129 (1821 CE)
	UBA-25288	116–117	Peat	380 ± 35	316–508 (1442–1634 CE)	442 (1508 CE)
	UBA-26702	130–131	Silty peat	150 ± 30	Rejected	Rejected
	UBA-29831	140–146	Charcoal	3220 ± 30	Rejected	Rejected
	UBA-25289	146–147	Bulk	1960 ± 35	Rejected	Rejected

and Valdeconejos) or linear interpolation (Cárcavas) to the accepted calibrated radiocarbon dates using CLAM 2.2 (Blaauw, 2010).

In the laboratory, we treated 122 peat sub-samples (1 cm^3), separated 2 or 4 cm, following the standard methods for palynological analysis (Faegri and Iversen, 1989): 40 from Cárcavas, 38 from Navalacarreta and 44 from Valdeconejos. We added a known concentration of *Lycopodium* spores to estimate pollen and spore concentration (Stockmarr, 1971). Then, we identified and counted pollen and spores using identification keys (Punt et al., 1976–2009; Beug, 2004) and photographic atlases (Reille, 1992) until a minimum terrestrial pollen sum, excluding pollen from aquatic and wetland plants and spores, of 300 grains per sample. Pollen counts were lower than 300 (minimum of 250) in three samples of the Valdeconejos sequence featuring worse pollen preservation. We have named the deciduous *Quercus* pollen type as *Quercus pyrenaica*-t. (t. = pollen type) because of the regional abundance of *Q. pyrenaica* today. We delimited local pollen assemblage zones (LPAZs) using optimal partitioning by sums-of-squares (Birks and Gordon, 1985) with statistically significant zones obtained by comparison with a broken stick model (Bennett, 1996) using PSIMPOLL (Bennett, 2009). We also identified conifer stomata and dung-related fungal spores following Trautmann (1953) and van Geel and Aptroot (2006), respectively. Conifer stomata are a good proxy for the local presence of conifer trees (Ammann et al., 2014) while coprophilous fungal spores are quantitatively related to local grazing activities (Raper and Bush, 2009; Gill et al., 2013; Baker et al., 2016). Finally, we quantified microscopic charcoal (10–250 μm) on pollen slides, a proxy for regional fire activity (Tinner et al., 1998), following Tinner and Hu (2003) and Finsinger and Tinner (2005). We estimated charcoal concentration (# cm^{-3}) using the same approach as for pollen and then converted it to charcoal accumulation rate (CHAR; # cm^{-2} $year^{-1}$) dividing by the peat/sediment deposition rate (year cm^{-1}). Past charcoal production in the oak stands around Valdeconejos should not have caused a significant deposition of non wildfire-related charcoal particles on the site. First, because the traditional process of charcoal production in the region involves wood pyrolisis under controlled entry of air into charcoal kilns, which avoids wood burning away to ashes as in conventional fire (FAO, 1983) and consequently the release of charcoal particles rising up to the air. And second, we have not found any differentiated charcoal layer in the peat profile suggestive of the past direct settlement of charcoal kilns on the coring site.

We first conducted multivariate statistical analyses on the full Valsaín forests pollen dataset, inclusive of Cárcavas, Navalacarreta and Valdeconejos sequences, to get a quantitative overview of the relationships between the pollen records from the three study sites. We then focused on the Navalacarreta and Valdeconejos sequences for further multivariate analyses because they are representative of the two main forest ecosystems (pine forest and pine-oak ecotone), have precise chronologies and fine time resolution (nearly decadal) and embrace a similar time span (last 600–700 years). The Cárcavas record was excluded due to its coarser resolution. All terrestrial pollen types were included in the analysis. The underlying ecological gradients in the pollen percentage datasets (Birks and Gordon, 1985; ter Braak and Prentice, 1988) were extracted using CANOCO 4.5. First, we performed detrended correspondence analysis (DCA; Birks and Gordon, 1985) by segments without down-weighting of rare species to assess whether unimodal or linear models of species responses fitted our pollen percentage data. The length-of-gradient of the first DCA axes is short in the three datasets (Valsaín: 1.456 SD; Navalacarreta: 0.451 SD; Valdeconejos: 1.024 SD), so we selected principal component analysis (PCA) for further ordination analyses (Birks and Gordon, 1985; ter Braak and Prentice, 1988). Two passive environmental variables were added to the Navalacarreta and Valdeconejos PCA plots, microscopic CHAR and *Sporormiella* influx, to compare pollen-inferred vegetation with the main ecological disturbances in the study area (i.e. fire activity and local grazing, respectively). We used influx values for environmental variables (i.e. CHAR and *Sporormiella* influx) and pollen percentage data to avoid spurious correlations probably emerging from internal changes in the percentage data or the occurrence of trends in the sedimentation rate when comparing influx vs. influx or percentages vs. percentages (Schwörer et al., 2015). Further, the use of influx values is recommended for both proxies, i.e. charcoal and *Sporormiella* (Whitlock and Larsen, 2001; Baker et al., 2013). Finally, we calculated palynological richness (PRI), a proxy for past plant diversity at local to landscape scale, using rarefaction analysis (Birks and Line, 1992) with a constant pollen sum of $n = 250$, the minimum pollen sum of Navalacarreta and Valdeconejos sites. To assess to what extent few dominant pollen types might be biasing PRI, we estimated pollen evenness as the probability of interspecific encounter (PIE; Hurlbert, 1971; Colombaroli et al., 2013). Finally, we calculated evenness-detrended palynological richness (DE-PRI) to account for the potential effects of evenness on PRI (Colombaroli and Tinner, 2013). Pollen diversity indices were obtained using R (R Development Core Team, 2016).

4. Results

The three sequences show a similar lithostratigraphy with a sandy silt bottom section, an intermediate silty peat section and a peaty top section (Fig. 2). Several issues must be noted concerning the chronology. First, we rejected CAR 136 (Table 1) because this sample could correspond to a younger pine root that may have grown into the older sediment. Four more radiocarbon dates from the basal sections of the VDC and NVC sequences were rejected because old material from the surrounding slopes (bulk, charcoal) was probably washed into the sedimentary basins through erosive events, as suggested by the dominance of sandy silts (Fig. 2). Finally, the sample VDC 130–131 was rejected because it is probably too young due to the presence of recent roots in the bulk sediment. The age-depth models for the three sequences are shown in Fig. 2; the chronologies of the bottom sections must be taken cautiously as they are based on extrapolation or bulk dating. The resulting time resolution of the pollen sequences is 61 ± 44 (Cárcavas), 19 ± 12 (Navalacarreta) and 15 ± 7 (Valdeconejos) years between samples.

The Cárcavas palynological sequence (Fig. 3) shows the dominance of *Pinus* (70–90%) for the last ca. 2500 years, with an almost continuous record of pine stomata (5–15%) since ca. 150 BCE. Minor changes in *Pinus* pollen abundance define three LPAZs characterized by a trend towards increased pine dominance. The sequence starts (CAR-1; ca. 400 BCE) with the lowest *Pinus* abundance of the record (70%), a certain presence of *Q. pyrenaica*-t. (5%) and the maxima of herbs (25%; Poaceae, Cichorioideae and *Artemisia*) and CHAR (18,500 # cm^{-2} $year^{-1}$). Later, during CAR-2 (ca. 400 BCE–1300 CE) *Pinus* increases (80–90%), whereas Poaceae decreases (5–10%). CHAR values oscillate (5000–10,000 # cm^{-2} $year^{-1}$) forming a secondary peak between 400 BCE and 150 CE, decreasing afterwards to low values (1000–2000 # cm^{-2} $year^{-1}$) with the exception of another secondary peak around 850 CE (8000 # cm^{-2} $year^{-1}$). *Sedum*-t. (2–4%), *Pteridium* (3–5%) and coprophilous fungi (*Sporormiella* = 1–2%) show conspicuous increases following this latter CHAR peak. Finally, the most recent LPAZ (CAR-3; 1300–2014 CE) presents *Pinus* values around 90% while CHAR remains first low to peak again at 1650–1900 CE (5000–10,000 # cm^{-2} $year^{-1}$).

The Navalacarreta pollen sequence (Fig. 4) is dominated by *Pinus* pollen throughout the record (70–90%), with a continuous curve of pine stomata since 1400 CE. *Pinus* dominates (75–80%) zone NVC-1 (ca. 1300–1330 CE), with a minor presence of *Betula*, *Corylus* and *Q. pyrenaica*-t., while Poaceae (5–10%) and *Sedum*-t. (2–5%) are the main herbs. CHAR values are high (15000–40,000 # cm^{-2} $year^{-1}$) and the *Sporormiella* curve is continuous. Later, *Pinus* slightly increases (80–90%) during NVC-2 (1330–1550 CE), with several oscillations counterbalanced by Poaceae (5–10%). CHAR remains high until 1400 CE (20000–40,000 # cm^{-2} $year^{-1}$), then decreasing (4000–10,000 # cm^{-2} $year^{-1}$). The records of coprophilous fungi, *Pteridium* and *Sedum*-t. are almost continuous during this zone. The

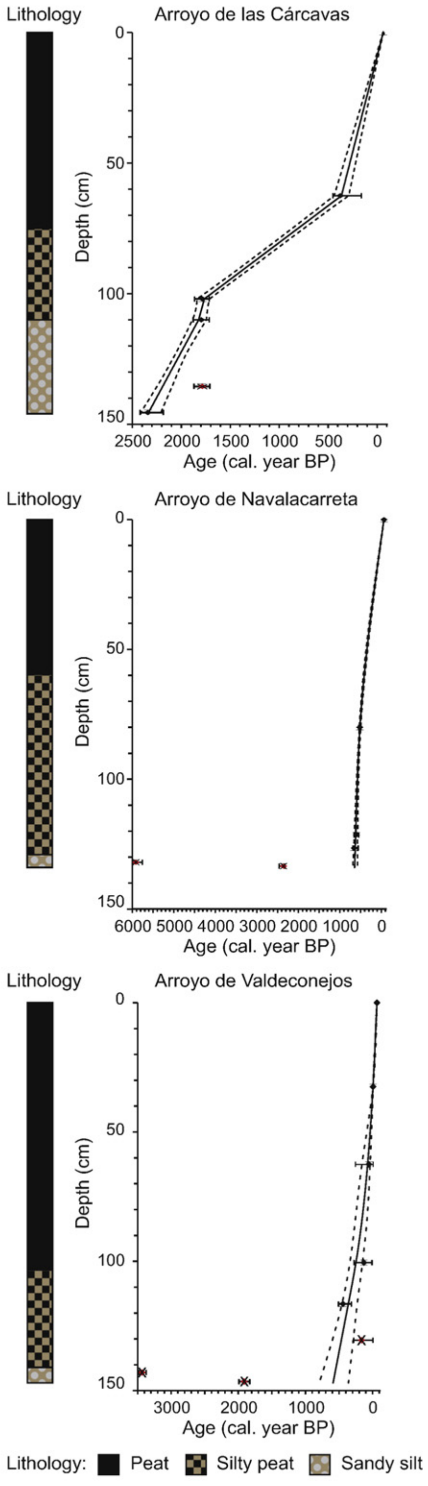

Fig. 2. Lithology and age-depth models of the studied sequences, note the different scale in the X (age) axes of the three plots. The dashed lines limit the 95% confidence intervals of the estimated ages.

most recent LPAZ, NVC-3 (1550–2014 CE), features a further increase in *Pinus* (90%) and a general decrease in herb pollen, with low CHAR values (500–3000 # cm^{-2} year^{-1}). However, Poaceae, Cardueae and *Lotus*-t. slightly increase together with *Sporormiella* and *Sordaria* at ca. 1800 CE.

The Valdeconejos pollen record (Fig. 5) shows six statistically significant LPAZs, separating a first phase with a marked presence of *Q. pyrenaica*-t. (VDC-1; ca. 1350–1600 CE), a second period characterized by a *Q. pyrenaica*-t. decrease associated with a spread of Poaceae (VDC-2; 1600–1940 CE), and a final series of marked oscillations within a general increasing *Pinus* trend in the most recent peat section (VDC-3 to VDC-6; 1940–2014 CE). The records of Cerealia-t. and *Secale* are almost continuous but with low percentages (Fig. 5) and tree pollen is usually <60–80%. Zone VDC-1 (ca. 1350–1600 CE) shows moderate values of tree pollen (mostly 50–60%), mostly *Pinus* (25–35%) and *Q. pyrenaica*-t. (15–20%). Poaceae (20–35%), Cichorioideae and *Artemisia* are the main herbs, CHAR values are moderate-to-high (2000–5000 # cm^{-2} year^{-1}), and dung fungal spores are rare (e,g. *Sporormiella* = 0–2%). The next zone, VDC-2 (1600–1940 CE) shows a decrease in tree pollen (25–40%), especially of *Q. pyrenaica*-t. (1–5%), whereas Poaceae (40–60%), Cichorioideae (≈10%) and *Plantago lanceolata*-t. (< 2%) rise along with coprophilous fungal spores (*Sporormiella* = 1–5%; *Sordaria* = 1–3%; *Podospora* = 1–2%). CHAR values are mostly low during VDC-2 (1000–2000 # cm^{-2} year^{-1}) although a maximum occurs at the end of this LPAZ (ca. 1920 CE; 3000–5000 # cm^{-2} year^{-1}). A trend towards increasing *Pinus* values (from 18 to 76%) starts at ca. 1910 CE, whereas *Q. pyrenaica*-t. percentages remain very low (1–4%). An initial pine peak (50–60%) occurs during VDC-3 (1940–1960 CE) mainly at the expense of Poaceae (25–35%). CHAR reaches the maximum of the record (8000 # cm^{-2} year^{-1}) and *Sporormiella* (5%) and *Sordaria*-t. increase (1–2%). Then, VDC-4 (1960–1980 CE) shows a decrease in pine pollen (10–30%) and the recovery of Poaceae (45–60%) and Cichorioideae (≈10%), together with decreases in *Sporormiella* (1–3%) and CHAR (2000–4000 # cm^{-2} year^{-1}). Finally, zones VDC-5 and VDC-6 (1980–2014 CE) record the final rise of *Pinus* (reaching a maximum of 80%) along with high values of *Sporormiella* (5–10%) and low-to-moderate of CHAR (300–4000 # cm^{-2} year^{-1}). The topmost sample of the core (i.e. moss polster) shows high tree pollen values (90%), with *Pinus* dominating (80%) and low values for *Q. pyrenaica*-t. (3%), *Q. ilex*-t. (3%), Poaceae (8%) and *Sporormiella* (0.5%).

The first PCA axis explains the 95.3% of the variance in the Valsaín forests pollen dataset (Fig. 6a), separating pine forests (Cárcavas and Navalacarreta) from more open environments such as oak woodlands and pasturelands (Valdeconejos). On the other hand, the second PCA axis only explains the 3.8% of the variance and it seems to show an anthropogenic disturbance gradient. Cárcavas and Navalacarreta samples are extremely close together and there is a strong overlap between both sequences. On the contrary, Valdeconejos samples are less similar among them and are generally well-separated from those of the other two sequences, with the exception of the most recent samples (pollen zone VDC-6) that are intermingled with the Cárcavas and Navalacarreta samples.

The first PCA axis explains 87.4% of the variance in the Navalacarreta pollen dataset (Fig. 6b), showing a gradient from closed and almost pure pine forests (*Pinus*) to open woods with a more diverse understory (*Betula*, *Q. pyrenaica*-t., *Erica arborea*-t., *Genista*-t., Poaceae). In contrast, the second PCA axis only explains 4.8% of the variance of the pollen data and is related to the abundance of deciduous trees (*Q. pyrenaica*-t., *Betula*, *Corylus*) or herbs (Poaceae, *Rumex*, *Artemisia*) in the understory of the pine forest. The environmental variables CHAR and *Sporormiella* influx are highly-correlated, almost overlapping. They are positively correlated with fire- and disturbance-tolerant plants (e.g. *E. arborea*-t., *Q. pyrenaica*-t., *Betula*, *Corylus*, Poaceae, *Artemisia*) and negatively correlated with *Pinus*. Pollen samples are arranged along the first PCA axis in clusters corresponding with the LPAZs, from more open and diverse (positive values) to almost pure pine stands (negative values). Pollen evenness is low (mostly 0.1–0.3) and stable throughout the sequence (Fig. 7f). PRI and DE-PRI follow the same trends, with low values (<20) throughout the record (Fig. 7g) and minor oscillations at ca. 1300–1520 CE.

In the Valdeconejos pollen record, the first PCA axis explains 69.4% of the variance (Fig. 6c), showing a gradient of ecosystem openness, from meadows (negative values) to woodlands/forests (positive values). Meanwhile, the second axis explains 26.4% of the variance in the pollen

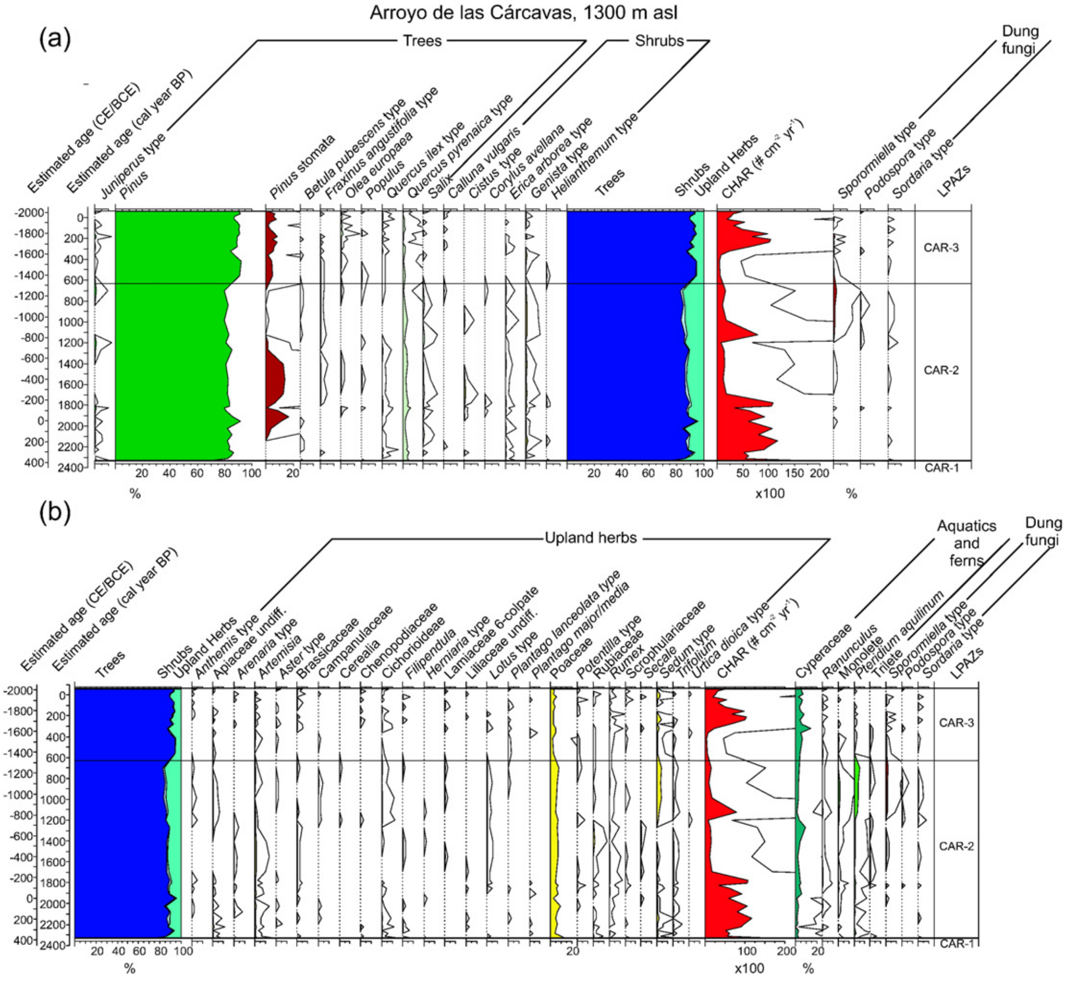

Fig. 3. Diagrams showing pollen percentages (selected types), obligate coprophilous fungi percentages and charcoal accumulation rates (CHAR) of the Cárcavas sequence: (a) trees, shrubs, CHAR and dung fungi and (b) upland herbs, CHAR, aquatic and wetland plants, ferns and dung fungi. Empty curves represent 10 × exaggerations.

dataset, presenting a gradient of land-use/management, from *Q. pyrenaica* woodlands to meadows (Poaceae, Cichorioideae), trampled pasturelands (*Sagina*, *Plantago lanceolata*-t., *Plantago coronopus*-t.) and pine stands. *Sporormiella* influx positively correlates with plants adapted to heavy grazing (*Sagina*, *P. lanceolata*-t., *P. coronopus*-t.) and *Pinus*, whereas *Q. pyrenaica*-t. and shrubs show negative correlations with *Sporormiella*. Disturbance-adapted (*Cistus*, *Sedum*-t., *Artemisia*) and fire-resistant (*Q. pyrenaica*-t., *Genista*-t., *E. arborea*-t., *Calluna*) plants show positive correlations with CHAR, while *Pinus* and meadow species are negatively correlated. Samples are clustered according to the different LPAZs (Fig. 6c), with three main groups according to the vegetation changes inferred from the pollen data: disturbed *Q. pyrenaica* woodlands (VDC-1), more or less grazed grasslands (VDC-2, VDC-4) and grazed pine stands (VDC-3, VDC-5, VDC-6). Pollen evenness is moderately high and follows a decreasing trend (from 0.8 to 0.6) until it suddenly drops to 0.4 during the final *Pinus* increase starting at 1980 CE (Fig. 7f). In this case, pollen evenness seems to affect palynological richness during the stages with higher tree pollen percentages, i.e. ca. 1350–1700 CE and 1940 CE–present, and consequently PRI and DE-PRI show different trends (Fig. 7g). For instance, PRI is quite stable (≈30) at ca. 1350–1700 CE, whereas DE-PRI starts around 25 and rises to 30 from as *Quercus* pollen abundance decreases. PRI and DE-PRI decrease to <25 (ca. 1780 CE). Finally, PRI continues its decrease until reaching <15 while DE-PRI oscillates around 25. The differences are mostly due to increasing *Pinus* dominance (Fig. 7g).

5. Discussion

5.1. Long-term vegetation dynamics in the Guadarrama Mountains in response to human activities, fire and climate variability

Our macrofossil and stomata records (Figs. 3, 4; Table 1) provide firm evidence on the local presence of *P. sylvestris* at altitudes as low as 1250–1300 m a.s.l. in the Guadarrama Mountains since at least 2000 years ago. Previous pollen records had already shown the regional importance of pine forests at mid- and mostly high-altitude sites (López-Sáez et al., 2014), but lacked macrofossil/stomata evidence allowing a more precise spatial reconstruction of their presence. Furthermore, our pollen data show that at least during the last two millennia pine forests have dominated at mid-elevation on these mountains, at least along north-facing narrow valleys (Figs. 3, 4). Our data point to certain naturalness of *P. sylvestris*-dominated stands in the lower Supramediterranean belt of the Guadarrama Mountains before land-use intensification, taking into account the low evidence of human impact. However, longer detailed multi-proxy palaeoecological records comprising vegetation-independent palaeoclimatic indicators and extending back in time until prior to the onset of human activities are necessary to fully assess present and future potential natural vegetation in this area.

Pine forest stability throughout the last ca. 2500 years in the Guadarrama Mountains (Figs. 3, 4, 6a) contrasts with the late Holocene

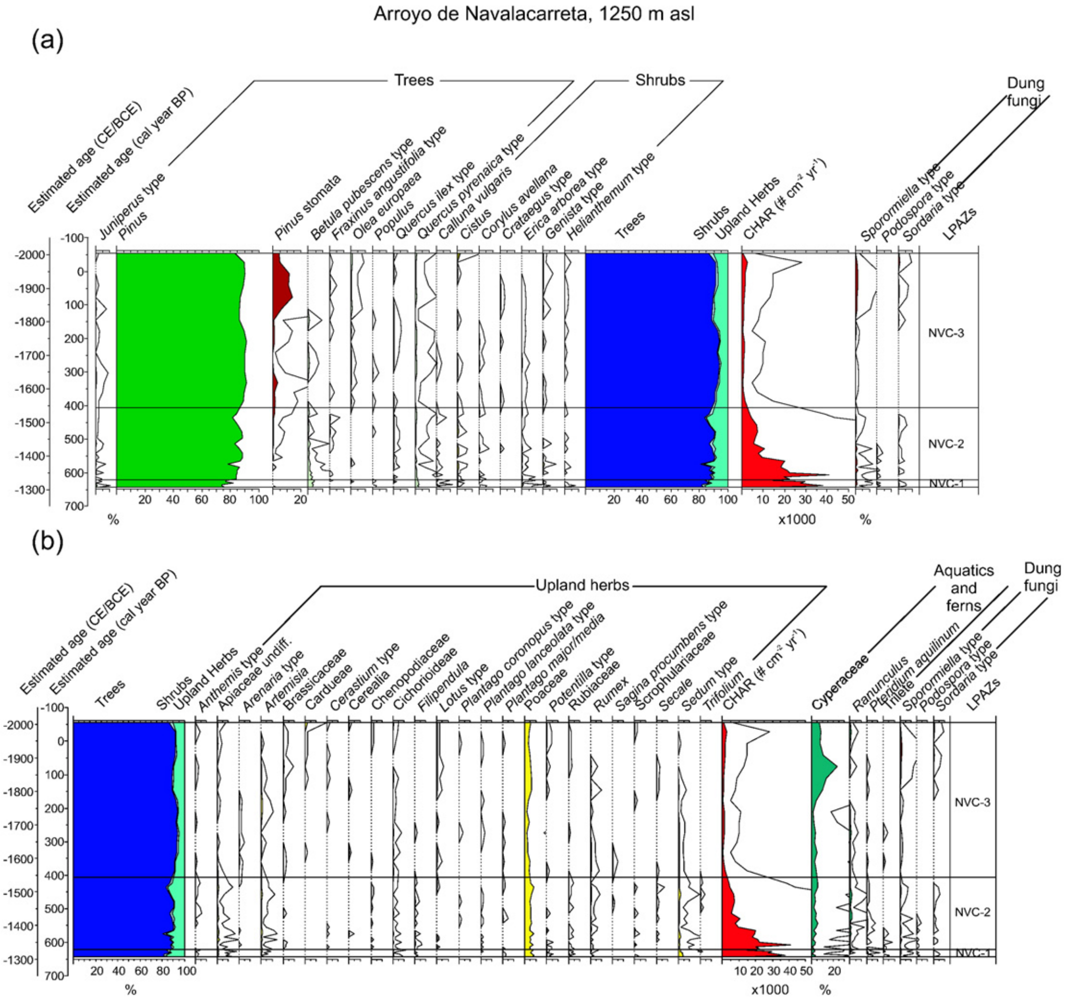

Fig. 4. Diagrams showing pollen percentages (selected types), obligate coprophilous fungi percentages and charcoal accumulation rates (CHAR) of the Navalacarreta sequence: (a) trees, shrubs, CHAR and dung fungi and (b) upland herbs, CHAR, aquatic and wetland plants, ferns and dung fungi. Empty curves represent 10 × exaggerations.

pine forest decline or even local extinction reported from several areas of central Spain (Franco-Múgica et al., 1998; Pardo and Gil, 2005; Rubiales et al., 2007; Morales-Molino et al., 2016). Moreover, the results of the PCA analysis highlight the outstanding stability of the floristic composition of the Sierra de Guadarrama pine forests through time, given the close proximity of all the Cárcavas and Navalacarreta pollen samples (Fig. 6a). The low suitability of this area for farming activities (acidic soils, cold climate and steep slopes) could explain the low historical human impact on the Guadarrama pine forests, in agreement with the almost complete absence of archaeological remains. These forests might have been relatively insensitive to both late Holocene climatic (Martín-Puertas et al., 2008; Dorado-Liñán et al., 2012; Fig. 7) and fire variability (Figs. 3, 4, 7). Our data suggest that *P. sylvestris* resisted the relatively wide range of fire variability in the Guadarrama Mountains during the last millennia, maybe because of the predominance of moderate-severity fires to which *P. sylvestris* is relatively resistant (Tapias et al., 2004; Fernandes et al., 2008). Unfortunately, our palaeodata cannot provide insights into the forecasted replacement of *P. sylvestris* with the more drought-tolerant *Q. pyrenaica* under increasing dryness (Gea-Izquierdo et al., 2014; Fernández-de-Uña et al., 2015) because: (1) the recent trend towards intensified summer drought is apparently unprecedented in the context of the last centuries (Ruiz-Labourdette et al., 2014); and (2) there is no available regional precipitation reconstruction for the time span covered by our longest record (Cárcavas) allowing quantitative assessments about similar situations in the past.

Our detailed palaeoecological Navalacarreta and Valdeconejos sequences allow more detailed, quantitative reconstruction of vegetation changes during the last centuries in forest ecosystems with quite different land-use histories, i.e. pine forest and pine-oak forest ecotone. It is worth noting here that different land-uses might also explain the quite lower microscopic CHAR values at Valdeconejos with respect to the pine forest sequences (Cárcavas and Navalacarreta): oak woodlands and pasturelands not only yield lower biomass but this biomass is also periodically harvested (i.e. firewood gathering, livestock raising). First, *P. sylvestris* forests have dominated around Navalacarreta since the onset of the sequence, i.e. since at least ca. 1300 CE (Figs. 4, 7e), with *Betula* (*B. pubescens*), *Corylus avellana*, *Salix* and probably *Populus* (*P. tremula*; Fig. 4) and *Ulmus laevis* (Fuentes-Utrilla et al., 2014) forming riparian communities along the River Eresma. Coupled fire and grazing caused several minor forest opening events between ca. 1300 and 1550 CE (Figs. 6b, 7c–e), also accounting for the transient oscillations detected in palynological richness (Fig. 7g). *Pinus sylvestris* was disfavoured by both disturbances (Fig. 6b) because of the sensitivity of its seedlings to browsing and its relatively low resistance to fire (Zamora et al., 2001; Fernandes et al., 2008), but its high rate of recovery (resilience) buffered the effects of disturbances. Increased fire activity and landscape opening might be associated to transhumant pastoral farming as elsewhere in the Iberian Central Range by that time (Franco-Múgica et al., 1998; López-Merino et al., 2009; López-Sáez et al., 2014), although warmer summer temperatures during the Medieval Climate Anomaly could also have resulted in more ignitions and fire

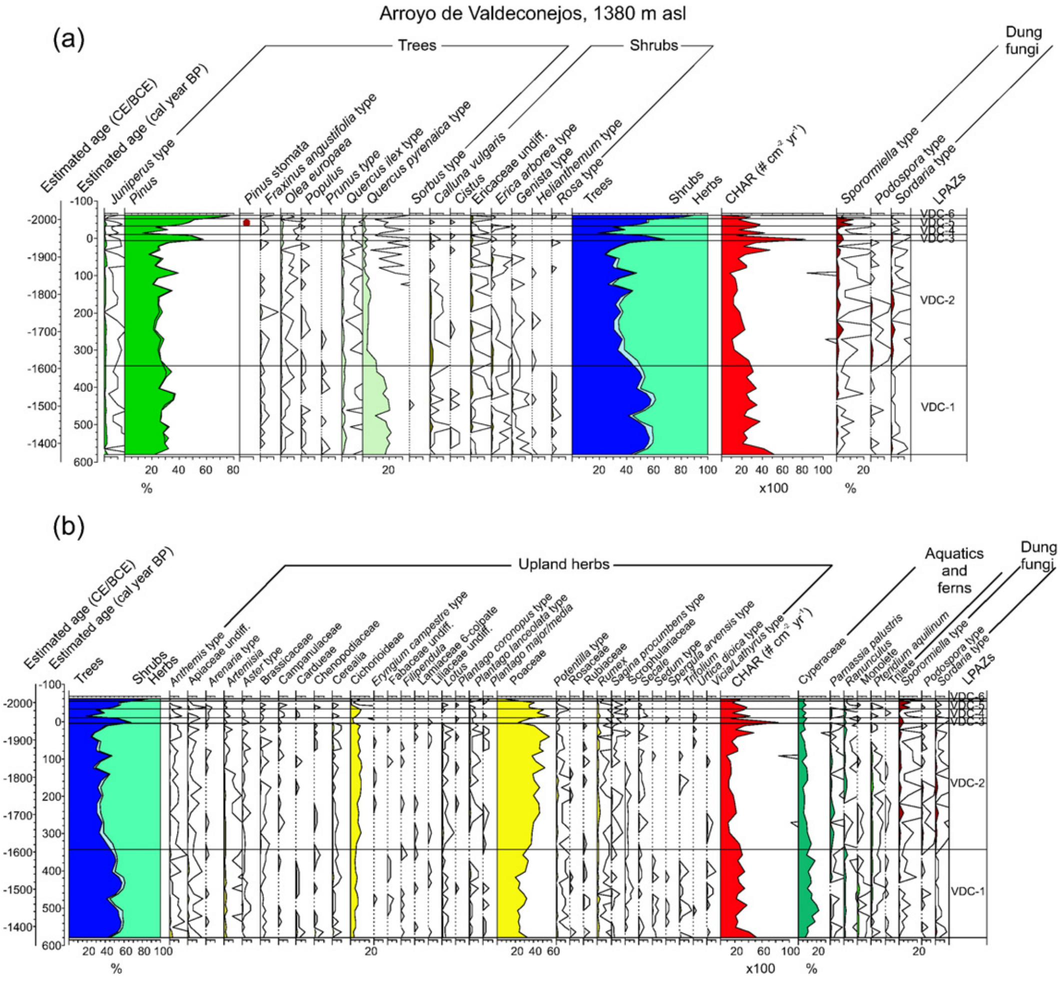

Fig. 5. Diagrams showing pollen percentages (selected types), obligate coprophilous fungi percentages and charcoal accumulation rates (CHAR) of the Valdeconejos sequence: (a) trees, shrubs, CHAR and dung fungi and (b) upland herbs, CHAR, aquatic and wetland plants, ferns and dung fungi. Empty curves represent 10 × exaggerations.

spread (Fig. 7b; Dorado-Liñán et al., 2012). However, the limited extent of the Valsaín pine forest transformation was probably related to the high value of timber during the Middle Ages and the Modern Period (Manuel-Valdés, 1997). Later on, pine forest remained stable for several centuries (ca. 1550–2014 CE) with very low fire and grazing disturbances (Fig. 7c–d) and low plant diversity typical of dense pine forests (Fig. 7g; Barbier et al., 2008). We may explain this multi-centennial persistence of relatively undisturbed pine forests during the Modern Period because the aristocracy, i.e. the Castilian Crown, protected them to preserve big game (for hunting) and timber supply (to build their palaces; Manuel-Valdés, 1997). Livestock grazing increased again since ca. 1900 CE (Fig. 7d) when Crown's control was reduced in the Valsaín area, but it did not cause pine forest opening probably because planned forest management had already started in 1890 CE (Manuel-Valdés, 1997).

More pronounced and abrupt vegetation changes occurred during the last ca. 700 years in the pine-oak forest ecotone according to the Valdeconejos pollen record (Fig. 5). Between 1350 CE and 1500 the vegetation around Valdeconejos was composed of open *Q. pyrenaica* and *P. sylvestris* woodlands, coppiced *Q. pyrenaica* stands, and/or a mosaic-like landscape with forest stands and grasslands under a relatively important fire activity (Figs. 5, 7c). Our data suggest that *Q. pyrenaica* woodlands were resilient to fire during this period, recovering after episodes of higher regional fire activity (Figs. 5, 7). The further decrease in *Q. pyrenaica*-t. pollen from 1500 to 1650 CE (from 20 to <5%; Fig. 7e) was probably caused by woodland clearance. When exploring the potential drivers of oak woodland decline, climatic oscillations and/or fire disturbance seem unlikely, as summer temperatures mostly remained warm (Fig. 7b; Dorado-Liñán et al., 2012) and fire activity did not experience significant changes (Figs. 5, 7c). Further, moderate-to-high fire activity should not have disfavoured *Q. pyrenaica*, a fire-resistant species able to vigorously re-sprout after disturbances (Fig. 6c; Calvo et al., 2003). A minor increase in grazing pressure reconstructed from our data (Figs. 5, 7d) might have contributed to oak reduction because *Q. pyrenaica* seems to be sensitive to browsing (Fig. 6c; Perea and Gil, 2014), but it is unlikely that a slight increase in grazing was able to cause such a heavy deforestation. One could then argue that the *Q. pyrenaica* decline was caused by intensified coppicing, which may have caused a "palynological silence" of the coppiced species (Waller et al., 2012). The assumption of coppicing is in agreement with the historically-documented increase of firewood production during the XVI-XVIIth centuries CE (Manuel-Valdés, 1997) and the age of the oldest radiocarbon-dated oak stools in the study area (Salomón et al., 2016). Historical archives also report the disappearance of several *Q. pyrenaica* stands in the XVIIth and XIXth centuries CE as a result of such intense exploitation (Fig. 7a; Manuel-Valdés, 1997). This heavy exploitation of the oak woodlands greatly contrasts with the simultaneous protection of the adjacent pine forests by the Crown and helps to understand the different legacies and in turn conservation conditions of the two forest ecosystems.

Under increasing grazing pressure pasturelands subsequently expanded at the expense of oak woodlands around Valdeconejos (increases in grazing pollen indicators –notably *P. lanceolata*-t.- and coprophilous fungi –*Sporormiella*, *Sordaria*, *Podospora*-; Figs. 5, 7d).

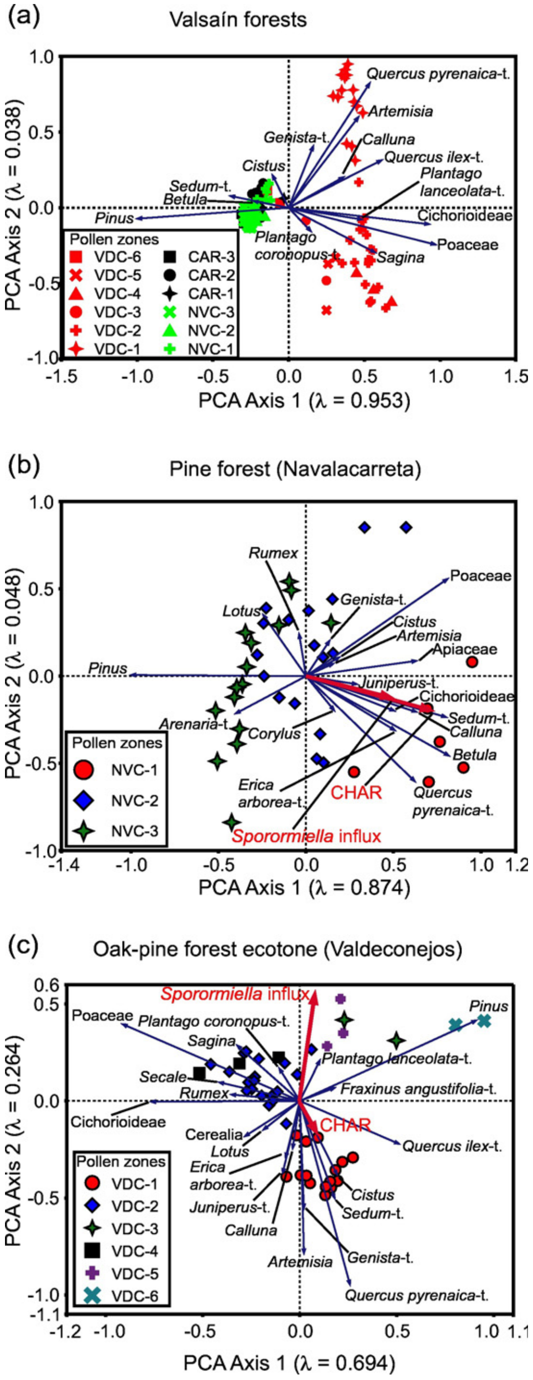

Fig. 6. Principal Component Analysis biplots of species (blue arrows) and samples (symbols) of the (a) Valsaín forests – which includes the Cárcavas (CAR), Navalacarreta (NVC) and Valdeconejos (VDC) sequences-, (b) Navalacarreta and (c) Valdeconejos pollen datasets. Two environmental variables (red arrows) were passively added: charcoal accumulation rate (CHAR) as a proxy for regional fire activity, and *Sporormiella* influx as a proxy for local grazing activities. Only the most relevant terrestrial pollen types for vegetation dynamics are shown. Samples are grouped according to the local pollen assemblage zones delimited for each sequence, which account for the main vegetation changes occurred around the study sites. The first PCA axis explains the 95.3%, 87.4% and 69.4% of the variance in the Valsaín forests, Navalacarreta and Valdeconejos pollen datasets, respectively, whereas the second PCA axis accounts for the 3.8%, 4.8% and 26.4%.

Quercus pyrenaica woodlands did not recover later from the increase in pasturing, suggesting that they are not resilient to heavy grazing. Enhanced grazing also caused a decrease in plant diversity (Fig. 7g), as it has been observed because of overgrazing by increasing populations of large mammals (Bakker et al., 2006). Later, between 1800 and 1860 CE two minor but noticeable increases in *Pinus* pollen occurred (Fig. 7e), indicating a certain trend towards pine forest spread that is reported in historical archives (Manuel-Valdés, 1997) and may have been advantaged by particularly cold temperatures during the Dalton Minimum of solar activity in the Little Ice Age (Fig. 7b; Dorado-Liñán et al., 2012).

Finally, pine expanded around Valdeconejos from ca. 1910 CE until today (Figs. 5, 7e), after planned forest management started in the Valsaín forests (1889–1890 CE; Fig. 7a). Indeed, PCA analysis has shown that the most recent Valdeconejos pollen spectra are very similar to those from closed pine forests such as Cárcavas and Navalacarreta (Fig. 6a). Pine stands spread towards lower and drier areas despite the increase in grazing activities around the site (Fig. 7d), perhaps because of the delimitation of regeneration and grazing areas within the forest. However, a transient decrease of *Pinus* pollen percentages is recorded at 1960–1980 CE, indicating a temporary decline of pine forest. This retreat was probably related to two wildfires which occurred in close proximity to Valdeconejos (1–1.5 km; personal communication, J. Donés) around 1940–1960 CE (important charcoal maximum in our record; Figs. 5, 7c), and/or to the extraordinary cuttings carried out in the Valsaín pine forest for two decades after the Spanish Civil War (i.e. approximately 1940–1960 CE) to accelerate country's economic recovery (personal communication, J. Donés). The later pine forest recovery could be attributed to the certain resilience of *P. sylvestris* to wildfires small-to-moderate in size and to heavy logging, but we must certainly consider that by that time forest management was already quite intense and surely support pine regeneration. A marked decrease in pollen evenness accompanied pine forest spread around Valdeconejos (Fig. 7f), which could account for the observed drop in PRI (Fig. 7g). DE-PRI corrects this bias by over-represented *Pinus*, showing that plant diversity changed in response to pine forest spreads and retreats following a decreasing trend towards relatively low-diversity pine forests (Fig. 7g). The final and unprecedented increase in *Sporormiella* and other coprophilous fungi (Figs. 5, 7d) reflects the increasing number of cattle favoured by the Common Agricultural Policy. Our record shows that current grazing pressure is well outside its range of variability of the last 700 years (Fig. 7d), seriously threatening the regeneration of *Q. pyrenaica* stands (Gómez et al., 2003; Perea and Gil, 2014).

Multi-decadal to centennial antagonisms between *P. sylvestris* and deciduous oaks (*Quercus pubescens*, *Q. petraea*, *Q. robur*) are also reported from the Rhone Valley (Valais, Swiss Alps), where pine is in an ecotonal position under relatively warm and dry conditions. There, the dominance of Scots pine was related to low human impact, due to the reduced resistance of this species to logging and fire disturbance (Bendel et al., 2006). This finding from a region which experiences similar climatic conditions (ca. 9–10 °C mean annual temperature, 600 mm mean annual precipitation) again suggests that under moderate to low disturbance, *P. sylvestris* has the potential to form natural or quasi-natural forests in competition with sub-Mediterranean and temperate oaks (Bendel et al., 2006). In this case, the millennial dominance or co-dominance of *P. sylvestris* reaches back to the early Holocene and is well-documented in the palynological record for periods (e.g. mid-Holocene) with summer conditions 1–2 °C warmer than today (e.g. Welten, 1982; Colombaroli et al., 2013).

5.2. Concluding remarks: implications of palaeoecological data for the management of the Sierra de Guadarrama NP

Our palaeoecological data show how land-use history played a crucial role in determining the composition and structure of forest vegetation in the Guadarrama Mountains. First, our data demonstrate that *P. sylvestris* stands have been naturally present at altitudes as low as 1250–1300 m a.s.l., thus contributing to clarify the long-lasting controversy about its potential lowermost altitudinal limit (see Introduction). We have also shown that both pine and oak stands were resilient to a

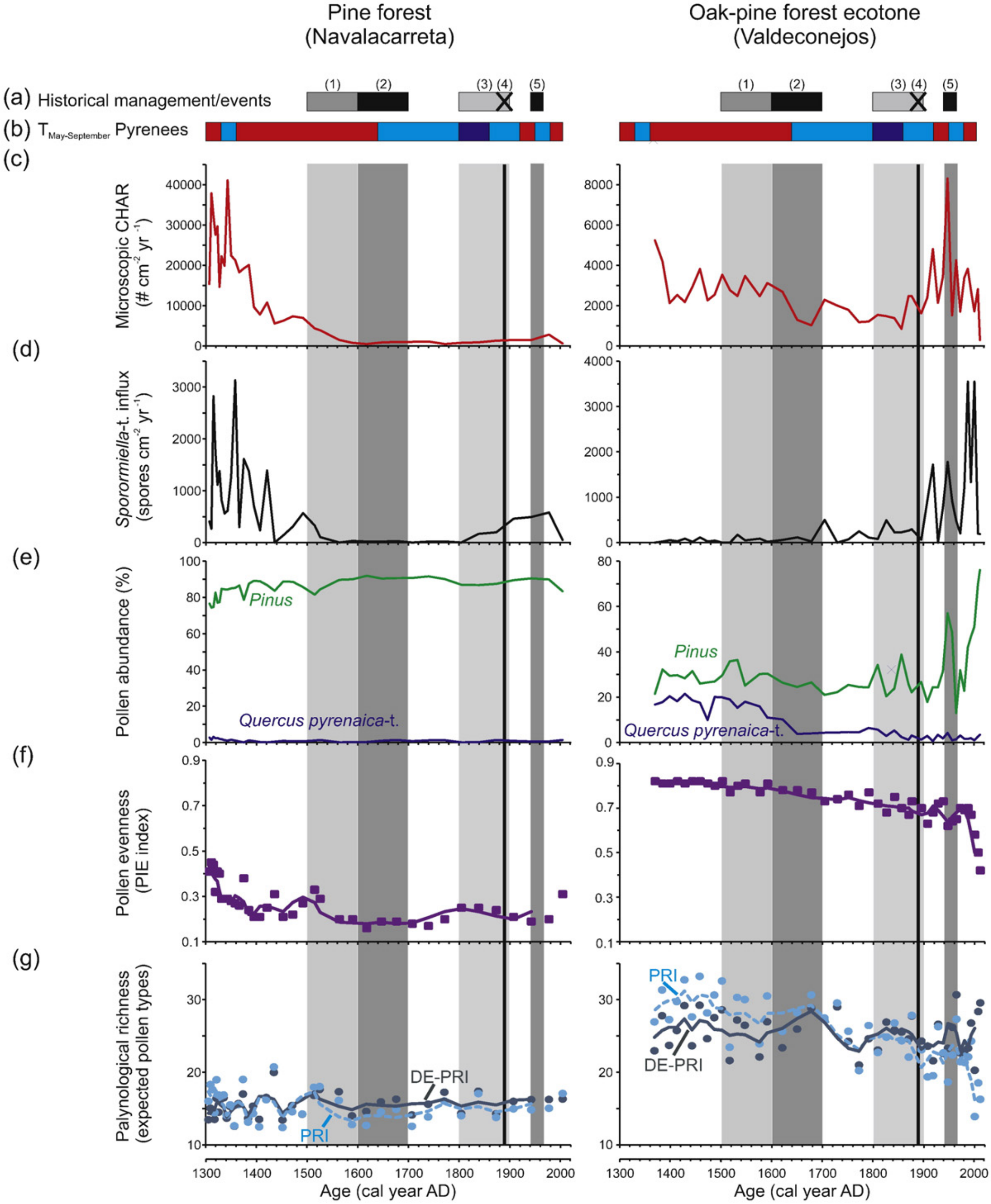

Fig. 7. Historical, climatic and ecological drivers of vegetation change in the Sierra de Guadarrama National Park forest ecosystems. The Navalacarreta site is currently located in a dense pine forest, while the Valdeconejos site lies within the oak-pine ecotone. (a) Historically-documented land-use- and management-related events (Manuel-Valdés, 1997). (1) Leasing of pastures and oak firewood; increasing presence of the Spanish Crown and subsequent population increase. (2) Disappearance of some oak stands. (3) Pine forest expansion at the expense of oak woodlands. (4) Start of planned forest management. (5) Documented fires near Valdeconejos and post-Spanish Civil War extraordinary cuttings. (b) Summer temperature anomalies in the Pyrenees reconstructed from conifer tree-rings (Dorado-Liñán et al., 2012): very cold (dark blue), cold (light blue) and warm (red). (c) Microscopic charcoal accumulation rate (CHAR) as a proxy for fire activity. (d) *Sporormiella* influx as a proxy for local grazing activities around the study sites. (e) Pollen percentages of the main trees in the Guadarrama Mountains, *Pinus* (green) and *Quercus pyrenaica*-t. (blue), as indicators of forest dynamics. (f) Pollen evenness as estimated by the probability of interspecific encountering (PIE), and (g) palynological richness (PRI, light blue) along with evenness-detrended palynological richness (DE-PRI, dark blue), as proxies for plant diversity. Palynological richness was in both cases estimated using rarefaction analysis with a constant pollen sum of n = 250 pollen grains. Three-point moving averages were drawn to discern the main temporal trends in pollen evenness and palynological richness. Note the different scales of Y axes in plots (c)–(e).

broad range of fire and grazing disturbance conditions, but intense coppicing and overgrazing caused degradation of *Q. pyrenaica* woodlands. This information is relevant to local ecosystem managers who aimed at understanding the origins and evolution of the ecosystems under their responsibility. Quantifying historical grazing pressure using coprophilous fungal spores has evidenced that current grazing pressure on oak woodlands is unprecedented and it should be diminished to allow *Q. pyrenaica* regeneration. Thus, our data have provided a much needed empirical support to forest managers' perception (based on historical data) that current grazing pressure in the Guadarrama

Mountains is excessive and should be diminished. Consequently, they have started to adopt measures to reduce the impact of cattle ranching on the Valsaín forests, either by reducing its number or by modifying its management. The final success of these measures will largely depend on harmonizing both conservation and socio-economic targets in the Sierra de Guadarrama NP.

Finally, our palaeovegetational records suggest that *Betula pubescens*, *Corylus avellana*, *Salix* and probably *Populus tremula* and *Ulmus laevis* formed riparian communities along the River Eresma, even under moderate levels of disturbance, thus underlining the role of intermediate disturbance conditions for ecosystem dynamics (e.g. Colombaroli et al., 2013). These novel results have brought guidance to ongoing and forecasted projects aimed at restoring the lost riparian vegetation of the Valsaín forest area (personal communication, M. Redondo), thus giving a further applied use to our palaeoecological records (e.g. Willis and Birks, 2006; Froyd and Willis, 2008). In summary, the use of a palaeoecological approach has proven to be of great interest for current ecosystem conservation and management, while direct collaboration with local ecosystem managers has provided a new practical dimension to the use of palaeoecological data in ecosystem conservation (Davies et al., 2014). Thus, an increasing use of palaeoecological tools to inform ecosystem conservation and management would be desirable in the near future, provided that suitable study sites (e.g. lakes, mires) are available and despite these techniques are relatively time consuming.

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