RESEARCH ARTICLE

Millennial land use explains modern high-elevation vegetation in the submediterranean mountains of Southern Europe

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Abstract

Aim: Pinewood decline and scrubland expansion are major features of Late Holocene vegetation history in the Cantabrian Range. However, the drivers of this remarkable vegetation shift remain to be investigated. Here, we aim at disentangling the role of past land use and climate in shaping the high-elevation Cantabrian landscape during the past two millennia.

Location: Cantabrian Range (northern Iberia).

Taxa: *Pinus sylvestris*, *Betula*, Ericaceae, *Juniperus*, Poaceae.

Methods: We conducted high-resolution multiproxy palaeoecological analyses (pollen, plant macrofossils, microscopic charcoal and dung fungi) on lake sediments from Lago del Ausente to reconstruct vegetation, fire occurrence and grazing through time. The chronology is based on ^{14}C (terrestrial plant macrofossils) and ^{210}Pb dating, and Bayesian age-depth modelling ('rbacon'). We carried out cross-correlation analysis to quantify vegetation responses to fire.

Results: Between 250 and 900 CE, the vegetation above 1700 m a.s.l. consisted of subalpine scrubland and scattered *P. sylvestris* trees/stands. Pinewoods with *Betula* were widespread at slightly lower elevation. This vegetation was resilient to moderate fire disturbance associated with limited pastoral activities. In contrast, enhanced fire occurrence alongside heavier pastoralism led to the demise of pinewoods and their replacement with *Betula* stands, subalpine scrublands, and meadows between 900 and 1100 CE. Later, the subalpine scrubland-birch tree line did not respond to Little

Ice Age cooling. However, further intensification of transhumant herding between 1300 and 1860 CE ('La Mesta') triggered birch decline and the establishment of the modern treeless landscape.

Main conclusions: The extant high-elevation vegetation of the Cantabrian Range is largely the legacy of intensive land use starting more than one millennium ago. Recurrent and severe fires to promote pasturelands led to the regional extirpation of the previously widespread *Pinus sylvestris*. Future management should aim at preserving the valuable cultural open landscape of mountain scrubland and meadows and also at restoring patches of ancient pine-birch woodlands.

KEYWORDS
charcoal, cultural landscapes, heathlands, human impact, palaeoecology, *Pinus sylvestris*, plant macrofossils, pollen, Spain, transhumance

1 | INTRODUCTION

High-mountain ecosystems like the upper forest line (or timberline), the tree line ecotone, and the subalpine meadows and scrublands are particularly sensitive to changes in both climate and land use (Ameztegui et al., 2016; Camarero & Gutiérrez, 2004; Gehrig-Fasel et al., 2007; Steinbauer et al., 2018). Investigating their dynamics over long time-scales, in response to both changing climatic conditions and human activities, is therefore highly relevant to assess their current status, predict their future developments, and adapt their management if needed. In this regard, the Late Holocene constitutes an ideal period to explore long-term vegetation change because of the notable climatic variability (Büntgen et al., 2011; Mann, 2007; Martín-Chivelet et al., 2011) and the significant socio-economic changes occurred (Deza-Araujo et al., 2020). In line with this, previous palaeoecological research in the mountains of Central and Southern Europe has highlighted the importance of accounting for long-term interactions between climate, land use and vegetation to understand present-day landscapes (Feurdean & Willis, 2008; Morales-Molino et al., 2021; Schwörer et al., 2015).

Spatially precise reconstructions of tree line dynamics require plant macrofossil analysis (Birks & Birks, 2000). The remarkable paucity of macrofossil-stratigraphic records from the mountains of Southern Europe (Allen et al., 1996; Cagliero et al., 2021; Leunda et al., 2019; Morales-Molino et al., 2021; Sánchez Goñi & Hannon, 1999; Tinner et al., 2016; Turner & Hannon, 1988) has seriously hampered tracking forest and tree line shifts through time in response to environmental and anthropogenic forcing. Moreover, although recent research has underlined the usefulness of integrating pollen, plant macrofossils, conifer stomata, charcoal and coprophilous fungi to investigate the timing and impact of transhumant herding and fire on the high-elevation landscapes of Southern Europe, studies applying the multiproxy approach are still notably rare (e.g., Cagliero et al., 2021; Leunda et al., 2019; López-Merino

et al., 2009). Additionally, most available palaeoecological records from the mountains of Southern Europe do not have sufficiently precise chronologies for the Late Holocene because they often focused on older periods (see Table 1). All in all, there is significant room for improving our current knowledge of the dynamics of southern European mountain vegetation during the past centuries and millennia and thus reinforcing our understanding of the origins of the modern landscapes.

The Cantabrian Range, in northern Iberia, is particularly well suited to investigate the impact of climate change and land use on long-term vegetation dynamics for the following reasons: (i) its location on the oceanic-Mediterranean boundary near the North Atlantic makes it particularly sensitive to climate change, and (ii) the long history of exploitation of its high-elevation pastures with various transhumant herding systems (González-Álvarez et al., 2016). Indeed, for the past few decades the Cantabrian Range has been one of the areas in Southern Europe most intensively studied from a palaeoecological point of view. The numerous pollen records published have notably improved our knowledge about the postglacial vegetation dynamics in the area (e.g., Allen et al., 1996; Muñoz Sobrino et al., 2001; Sánchez-Morales et al., 2022; Figure 1). However, most available studies have focused on the responses of vegetation to the Lateglacial and Early Holocene climatic oscillations (e.g., Jalut et al., 2010; Muñoz Sobrino et al., 2007, 2013), and detailed well-dated multi-proxy records focusing on Late Holocene landscape changes are rare (García-Antón et al., 1997; Morales-Molino et al., 2011). Finally, palaeoecological research drawing on specific proxies for fire (charcoal) and pastoralism (dung fungi) is almost lacking in the region (but see Carracedo et al., 2018; García-Antón et al., 1997; Morales-Molino et al., 2011; Pérez-Díaz et al., 2016), despite fire and transhumance are commonly considered major modellers of today's high-elevation Cantabrian landscape (Ezquerra & Rey, 2011). This knowledge gap is particularly relevant because the combined impact of fire and heavy pastoral farming has been

TABLE 1 *Pinus* pollen declines and/or *Pinus sylvestris* (or *P. sylvestris* type) macrofossil evidence during the Late Holocene (from *c.* 2250 BCE to present) in the upper montane and subalpine vegetation belts of the Cantabrian Range (northern Iberia)

Site name (no. in Figure 1)	Latitude (N)	Longitude (W)	Elevation (m a.s.l.)	Pinus pollen decline (P)/ macrofossil presence (M)[a]	References
Lago del Ausente[b] (1)	43°02′36″	5°21′11″	1740	700 CE (P) 900 CE (P) 850 CE (M)	This study
Lago de la Baña (6)	42°15′11″	6°45′17″	1450	50 BCE (P)	Janssen (1996)
Xan de Llamas[b] (10)	42°18′15″	6°19′17″	1500	1250 BCE (P)	Morales-Molino et al. (2011)
Laguna del Castro/ Villaseca (11)	42°56′59″	6°15′37″	1310	100 BCE(?) (P)	Jalut et al. (2010)
Laguna del Miro/La Mata (13)	42°58′04″	6°13′31″	1500	100 BCE (P) 500 CE(?) (P)	Jalut et al. (2010)
Lago de Ajo (14)	43°02′27″	6°08′21″	1570	1200 BCE(?) (P)	Allen et al. (1996)
Laguillín (16)	42°52′51″	6°02′25″	1780	2100 BCE (P) 900 BCE(?) (P)	García-Rovés (2007); Carrión et al. (2012)
Puerto de San Isidro (20)	43°03′25″	5°23′00″	1650	1100 BCE(?) (P) 200 BCE(?) (P)	Fombella et al. (2001); Carrión et al. (2012)
Lillo-II[b] (21)	43°04′34″	5°16′00″	1500	1100 CE (P)	Muñoz Sobrino et al. (2003)
Pinar de Lillo[b] (22)	43°03′39″	5°15′42″	1360	1100 CE (P) 1200 CE (P)	García-Antón et al. (1997)
Puertos de Riofrío (25)	43°02′12″	4°41′49″	1760	300 BCE (P) 500 CE(?) (P)	Menéndez Amor and Florschütz (1963)
Cueto de la Avellanosa (26)	43°06′50″	4°21′55″	1340	1000 BCE (P)	Mariscal (1983); Carrión et al. (2012)
Zalama[b] (27)	43°08′06″	3°24′35″	1330	1000 BCE (P)	Pérez-Díaz et al. (2016)
Pobladura de la Sierra (8)	42°24′39″	6°28′12″	1550	630 BCE (M) 970 BCE (M)	Ezquerra et al. (2019)
Vega de Viejos (12)	42°57′57″	6°14′00″	1300	1040 BCE (M) 220 BCE (M)	Rubiales et al. (2008)
Mena de Babia (15)	42°55′18″	6°07′15″	1650	570 CE (M)	Rubiales et al. (2012)
Aralla de Luna (17)	42°53′44″	5°50′02″	1530	390 CE (M)	Rubiales et al. (2012)
Valle de Riopinos (18, 19)	43°02′52″ 43°02′08″	5°25′00″ 5°26′00″	1650 1430	900 BCE (M) 60 BCE (M)	Sánchez-Hernando et al. (1999) Rubiales et al. (2012)
Llánaves de la Reina (23)	43°02′52″	4°46′59″	1450	550 CE (M)	Sánchez-Hernando et al. (1999)
Valle de Pineda (24)	42°59′00″	4°37′57″	1450	50 BCE (M)	Ezquerra (2015)

[a](?) denotes uncertain ages due to poorly constrained age-depth models.

[b]Palaeoecological records with two or more absolute dates for the past approximately two millennia.

hypothesised to be the main driver of the Late Holocene decline of Cantabrian mountain pine forests (Rubiales et al., 2008, 2012), but empirical data to test this hypothesis are largely missing.

In this article, we present a new high-resolution, well-dated and multiproxy palaeoecological record (pollen, fern spores, dung fungi spores, conifer stomata, plant macrofossils and microscopic charcoal) from Lago del Ausente (northern Iberia) that spans the past *c.* 2000 years. We reconstruct vegetation, fire and land-use history at high elevation in the Cantabrian Range with the following aims: (i) disentangling the legacy of historical land use from the impact of past climatic variability on today's landscape and (ii) refining the knowledge of the long-term ecology of high-elevation Cantabrian

vegetation, with particular focus on the striking decline of mountain pinewoods.

2 | MATERIALS AND METHODS

2.1 | Study site

Lago del Ausente (43°02′36.0″N, 005°21′10.9″W, 1740 m a.s.l.) is a small (~3.5 ha) glacial lake (maximum water depth 13.4 m) located in the headwaters of the River Porma on the southern slope of the Cantabrian Range (northern Spain; Figure 1). The hydrological lake
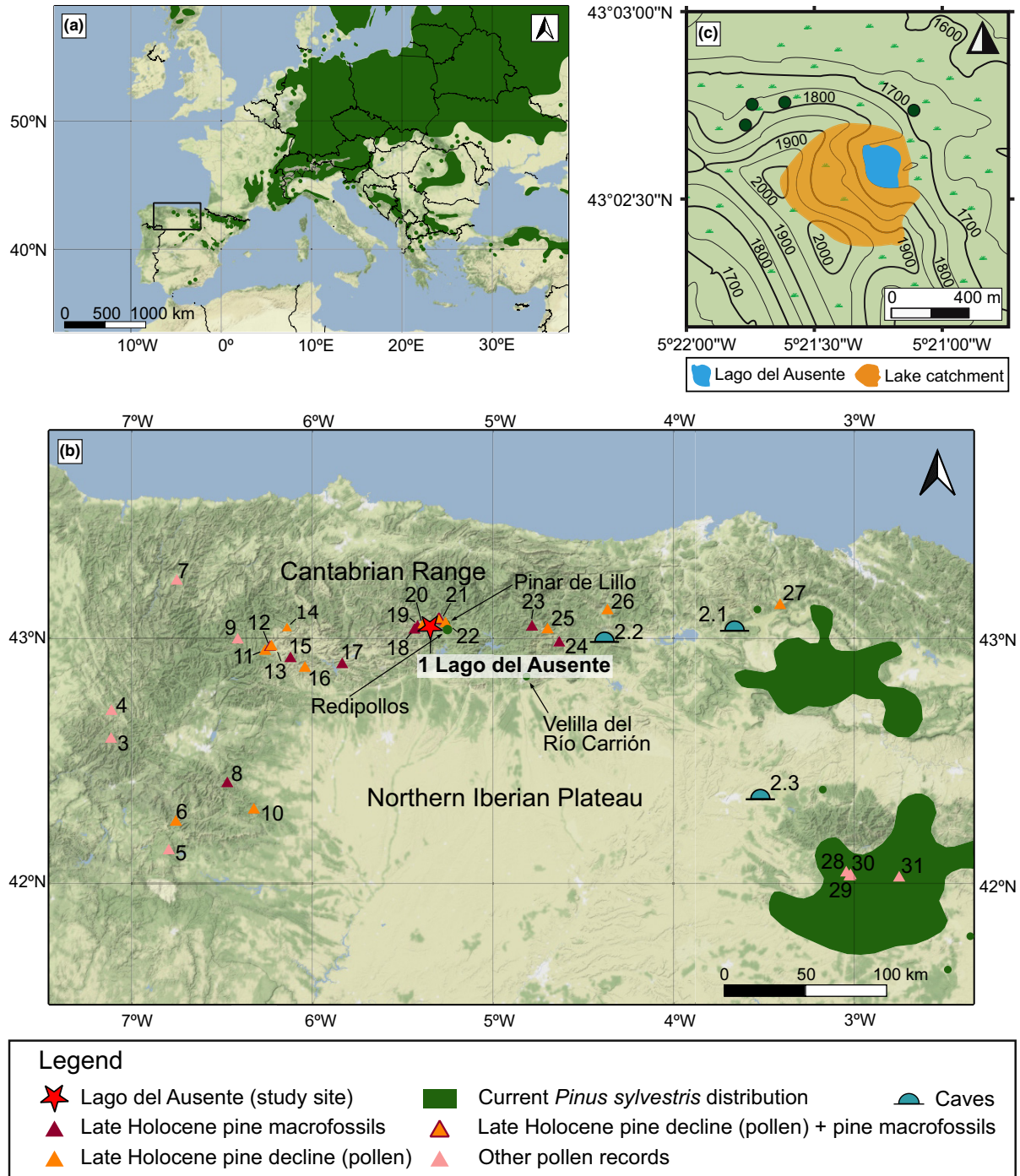
FIGURE 1 (a) Current distribution of natural *Pinus sylvestris* stands in southwestern Eurasia (Caudullo et al., 2017), and situation of the study area in north-western Iberia. (b) Location of the study site (1 Lago del Ausente) and other palaeoclimatic/palaeoecological sites in the Cantabrian Range, the Galician Mountains (southwest) and the Northern Iberian Range (southeast). The current natural distribution of *P. sylvestris* in northern Iberia is also shown. (c) Detailed elevation map of Lago del Ausente, its catchment, and the location of isolated natural *P. sylvestris* trees (Ezquerra & García, 2017). Sites: 1 Lago del Ausente (this study), 2 caves: 2.1 Kaite Cave, 2.2 Cueva del Cobre, 2.3 Cueva Mayor (Martín-Chivelet et al., 2011), 3 Lagoa de Lucenza (Muñoz Sobrino et al., 2001), 4 Pozo do Carballal (Muñoz Sobrino et al., 1997), 5 Laguna de la Roya (Allen et al., 1996), 6 Lago de la Baña (Janssen, 1996), 7 Pena Velosa (Muñoz Sobrino et al., 2012), 8 Pobladura de la Sierra (Ezquerra et al., 2019), 9 Puerto de Leitariegos (Carrión et al., 2012; García-Rovés, 2007), 10 Xan de Llamas (Morales-Molino et al., 2011), 11 Laguna del Castro (Jalut et al., 2010), 12 Vega de Viejos (Rubiales et al., 2008), 13 Laguna del Miro (Jalut et al., 2010), 14 Lago de Ajo (Allen et al., 1996), 15 Mena de Babia (Rubiales et al., 2012), 16 Laguillín (Carrión et al., 2012; García-Rovés, 2007), 17 Aralla de Luna (Rubiales et al., 2012), 18–19 Valle de Riopinos (Rubiales et al., 2012; Sánchez-Hernando et al., 1999), 20 Puerto de San Isidro (Carrión et al., 2012; Fombella et al., 2001), 21 Lillo-II (Muñoz Sobrino et al., 2003), 22 Pinar de Lillo (García-Antón et al., 1997), 23 Llánaves de la Reina (Sánchez-Hernando et al., 1999), 24 Valle de Pineda (Ezquerra, 2015), 25 Puertos de Riofrío (Menéndez Amor & Florschütz, 1963), 26 Cueto de la Avellanosa (Carrión et al., 2012; Mariscal, 1983), 27 Zalama (Pérez-Díaz et al., 2016), 28 las Pardillas Lake (Sánchez Goñi & Hannon, 1999), 29 Quintanar de la sierra (Peñalba, 1994), 30 Laguna Grande (Ruiz-Zapata et al., 2002), 31 Hoyos del Iregua (Gil-García et al., 2002). Map projection: WGS84.

catchment extends over *c.* 45 ha, spanning an elevation range between 1740 and 2041 m a.s.l., and there is no relevant inlet stream (Figure 1). The bedrock is siliceous, comprising Ordovician quartzite, conglomerate, slate and sandstone. The climate is mountain oceanic, corresponding to the Dsc type (cold with dry and cool summer) of the Köppen-Geiger classification. At the Puerto de San Isidro weather station (1540 m a.s.l.), located *c.* 3 km away from Lago del Ausente, mean annual temperature, $T_{January}$ (coldest month) and T_{July} (warmest month) are 5.7, 0 and 13.4°C, respectively. Mean annual precipitation amounts to 1290 mm and $P_{July-September}$ to 172.6 mm (P_{August} 48.4 mm), so there is no summer drought. Extant vegetation in the catchment is treeless, dominated by subalpine scrublands (*Cytisus oromediterraneus*, *Erica* spp., *Daboecia cantabrica*, *Calluna vulgaris*, *Halimium lasianthum* subsp. *alyssoides*, *Vaccinium myrtillus*, *Juniperus communis* subsp. *alpina*) and meadows (Figure S1). The broader high-elevation landscape around Lago del Ausente is also largely deforested and dominated by scrublands and grasslands. Trees are restricted to some sparse stands of *Betula pubescens*, few scattered natural *Pinus sylvestris* trees (Figure 1), and pine reforestations (mainly *P. sylvestris*) carried out from *c.* 1970 CE onwards. Regionally, natural high-elevation forest vegetation consists of *Fagus sylvatica* (up to 1700 m a.s.l.), *B. pubescens* (reaching 1800–2100 m a.s.l.), *P. sylvestris* (up to 1900 m a.s.l.), *Quercus petraea* (up to 1600 m a.s.l.) and *Q. robur* (up to 1850 m a.s.l.) stands. Natural occurrences of *P. sylvestris* in the central Cantabrian Range are highly fragmented and limited to three major relict pinewoods (Pinar de Lillo—~300 ha-, Redipollos—~20 ha-, and Velilla del Río Carrión—~40 ha-, located ~7, 9, and 50 km away from Lago del Ausente, respectively), as well as few smaller stands and scattered individuals mostly in the River Porma headwaters (Figure 1; Ezquerra & García, 2017).

2.2 | Coring, dating, and age-depth modelling

On September 2018, we retrieved four short cores from the deepest part of Lago del Ausente using a UWITEC gravity corer. All the cores were correlated according to their lithostratigraphy to produce a ~60-cm long master core. In the field, we extruded the core AUS18-SA and subsampled it in 1-cm thick slices for ^{210}Pb and ^{137}Cs dating, which was carried out at the St Croix Watershed Research Station (Science Museum of Minnesota, USA). Lead-210 dates were obtained from the unsupported ^{210}Pb activity profile using the Constant Rate of Supply model (Appleby, 2001). Additionally, we radiocarbon-dated four terrestrial plant macrofossil samples from the core AUS18-SB using accelerator mass spectrometry (AMS) at the Laboratory for the Analysis of Radiocarbon with AMS (LARA) of the University of Bern. Radiocarbon dates were calibrated using CALIB 8.2 (Stuiver et al., 2022) and the IntCal20 calibration curve (Reimer et al., 2020). Based on the ^{210}Pb and ^{14}C dates, we modelled the age-depth relationship using the Bayesian approach implemented in the package 'rbacon' 2.5.5 (Blaauw & Christen, 2011) running in R (R Core Team, 2021) with the following settings: 'acc.mean' = 30, 'acc.shape' = 1.5, 'mem.mean' = 0.5, 'mem.strength' = 15, and 'thick' = 1.

2.3 | Pollen, spore, charcoal and macrofossil analyses

Sixty 1-cm thick contiguous sediment subsamples of 1 cm^3 were treated for palynological analyses in the laboratory according to standard protocols (Moore et al., 1991). We added a known amount of *Lycopodium* spores to estimate pollen, spore, and microscopic charcoal concentrations (Stockmarr, 1971). Influx values were then calculated dividing concentrations by the sediment deposition times obtained from the age-depth model. To reconstruct local-to-regional vegetation dynamics and land use through time, we identified pollen and spores up to a terrestrial pollen sum (i.e., excluding pollen of aquatic and wetland plants) of >500 pollen grains, using a transmitted light microscope at 500× magnification. For pollen and spore identification, we used dichotomous keys (Beug, 2004; Moore et al., 1991; Punt et al., 1976–2009), photographic atlases (Reille, 1992), and the reference collection at the Institute of Plant Sciences of the University of Bern. Although 'Ericaceae undiff.' contains some *Vaccinium* pollen grains, the vast majority of the pollen included within this pollen type corresponds to *Erica*. We will therefore usually name this type '*Erica*' hereafter. Likewise, '*Quercus robur* type' embraces pollen not only of *Quercus robur* but also of *Q. petraea* and *Q. pyrenaica*, so we will usually refer to it as 'deciduous *Quercus*' hereafter. Normally, we will express pollen data as percentages calculated with respect to the previously defined terrestrial pollen sum. Dung fungal spores (e.g., *Sporormiella* type, *Sordaria* type, *Podospora* type), a proxy for local grazing activities (Baker et al., 2016; Gill et al., 2013), were also identified according to van Geel and Aptroot (2006). We quantified microscopic charcoal particles, a proxy for regional fire activity (Adolf et al., 2018; Tinner et al., 1998), in the same slides used for palynological analyses, following the recommendations by Tinner and Hu (2003) and Finsinger and Tinner (2005). To track local vegetation changes around Lago del Ausente, we took contiguous 2-cm thick sediment subsamples of 8–16 cm^3 (average ± standard deviation: 12 ± 2 cm^3) and sieved them through a 200-μm mesh. Then, we identified the plant macrofossils under a stereomicroscope at 8–50× magnification using botanical illustrations (Castroviejo, 1986–2021; Eggenberg & Möhl, 2020) and reference material collected in the study area. Macrofossil concentrations were then standardised to the median sample volume of 12 cm^3.

2.4 | Numerical analyses

First, we delimited statistically significant local pollen assemblage zones ('pollen zones' or 'AUS-' hereafter) using the optimal splitting by sums-of-squares method (Birks & Gordon, 1985) and the broken-stick model (Bennett, 1996). Pollen percentage data were square-root transformed prior to the analysis. The zonation of the pollen sequence was also applied to the plant macrofossil record. Second, we used cross-correlation analysis to investigate long-term fire ecology in more detail (Gil-Romera et al., 2014; Tinner et al., 1999) using

the software MYSTAT 12 (Systat, 2007). Cross-correlations were calculated on pollen percentage and microscopic charcoal influx data (see Schwörer et al., 2015). Cross-correlation coefficients were calculated at ±5 lags (approximately ±150 years, as each lag corresponds to 30.9 ± 3.9 years) during the interval spanning the decline of pine (59–30 cm; ~250 to 1150 CE). Prior to the cross-correlation analysis, we detrended linearly the pollen percentage and the charcoal influx data series to extract the main temporal trends (and thus reduce temporal autocorrelation, see Colombaroli et al., 2007).

3 | RESULTS

3.1 | Lithology and chronology

The sedimentary sequence is quite homogeneous throughout. The sediment mostly consists of brown organic-rich siliciclastic silts with diatoms, with few thin lighter-coloured bands of coarse silts and sands intercalated (Figure 2). Only the uppermost 6 cm of the sedimentary sequence contained unsupported ^{210}Pb that allowed assigning them a date (Table S1). Sediment accumulation rate has therefore been rather slow during the past two centuries. Nevertheless, the near-exponential curve of the ^{210}Pb activity profile indicates a high reliability of the ^{210}Pb dates. The slow sedimentation prevented detecting the 1963 CE ^{137}Cs maximum peak related to thermonuclear bomb testing. The age-depth model fitted to lead-210 (Table S1) and radiocarbon dates (Table S2) provides an age of ~250 CE for the bottom of the studied sedimentary sequence and indicates a rather constant sediment accumulation rate (Figure 2).

3.2 | Plant macrofossil, pollen and charcoal

During the pollen zone AUS-1 (59–37.5 cm; ~250 to 950 CE), plant macrofossil assemblages are dominated by subalpine shrubs (*Calluna vulgaris*, *Erica*, *Vaccinium myrtillus*, *Cytisus oromediterraneus*, *Juniperus communis* subsp. *alpina*), with some *Pinus* remains (Figure 3 and Figure S2). The pollen assemblages are dominated by trees (50%–70%), with arboreal pollen (trees+shrubs, 'AP') reaching maxima ~80%. *Pinus* (~30% to 45%) and deciduous *Quercus* (~10% to 20%) are the main taxa, with *B. pubescens* type and *Fagus sylvatica* at lower abundances (Figure 3 and Figure S3). A notable reduction in *Pinus* pollen percentages (from >40% to ~25%) occurs at ~700–800 CE, followed by a slight recovery to ~30% at ~800 to 900 CE (Figure 3). *Betula* and *Fagus* increase their abundances slightly but significantly at the time of the transient decline of *Pinus* (Figure 3 and Figure S3). Pollen concentrations and influxes corroborate the robustness of these patterns (Figure S4). *Erica* and *Corylus* (usually ~5% each) are the most relevant shrubs (which amount to ~10% to 15% in total; Figure 3 and Figure S3). Poaceae (~10% to 20%) are the most abundant upland herbs (~20% to 30% in total) followed by *Artemisia*, *Rumex acetosa/acetosella* type, *Plantago alpina* type, and *Plantago lanceolata* type (usually around 1%–2% each; Figure 3 and
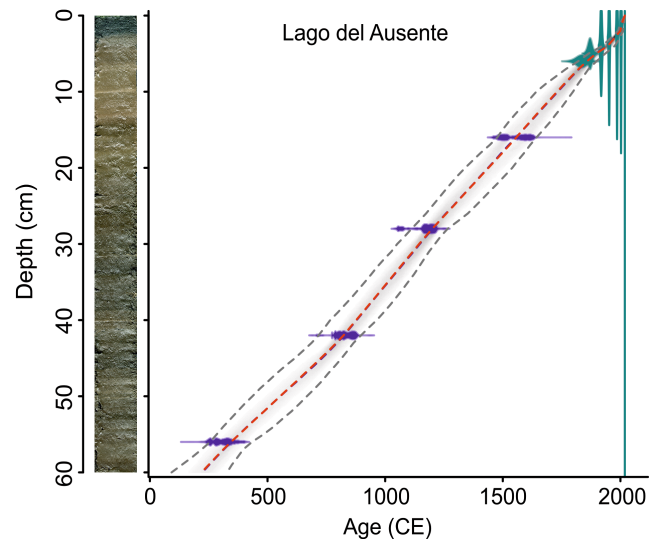
FIGURE 2 Chronology of the Lago del Ausente sedimentary sequence (Cantabrian Range, northern Iberia). Left: Picture of the sedimentary sequence. Right: Age-depth model built using 'rbacon' 2.5.5 (Blaauw & Christen, 2011), where turquoise and blue areas represent the probability distribution of the ^{210}Pb and ^{14}C dates (calibrated) respectively, the red dashed line shows the median age, and the dashed black lines delimit the 95% confidence interval.

Figure S3). Between *c.* 700 and 800 CE upland herb pollen increases (~30% to 35%), mainly driven by Poaceae (~20% to 25%; Figure 3 and Figure S3). It is worth noting that Cerealia type pollen also increases notably during this period, consistently showing values ~1% (Figure 3). *Sporormiella* type and *Sordaria* type are the most important dung fungi throughout the Lago del Ausente palaeoecological record (Figure S3), featuring moderate abundances (both influxes and concentrations) during AUS-1, with maxima at *c.* 350 and 800 CE (Figure 3 and Figures S3, S4). Charcoal influx (and concentration) shows mostly moderate values (~5000 to 10,000 # cm^{-2} year^{-1}; '#' = 'no. of charcoal particles') with a prominent peak at the beginning of the record (>20,000 # cm^{-2} year^{-1}, *c.* 250 CE), a marked increase at ~700 to 750 CE (maximum ~15,000 # cm^{-2} year^{-1}), and a final abrupt increase towards a large peak at the transition to AUS-2 (~27,000 # cm^{-2} year^{-1}, *c.* 950 CE; Figure 3 and Figure S4).

Pinus macrofossils are absent in the pollen zone AUS-2 (37.5–15.5 cm; ~950 to 1570 CE), where the only (rare) tree macrofossils correspond to tree *Betula* (Figure 3 and Figure S2). *Calluna vulgaris* and *Erica* continue dominating the plant macrofossil assemblages, although concentrations are usually lower than in AUS-1 (Figure 3). The decline of *Pinus* pollen continued during this pollen zone (from ~30% at ~900 CE to <5% at ~1100 CE), driving an overall decrease in tree pollen (~30% to 40%) and a less pronounced in AP (~45% to 60%; Figure 3 and Figure S3). In contrast, *Betula* pollen abundances follow an increasing trend until ~1200 CE (>10% between 1200 and 1300 CE) before starting an overall decreasing tendency particularly steep since ~1500 CE (Figure 3 and Figure S3). Meanwhile, both deciduous *Quercus* and *Fagus* maintain their representation (~10% to 15% and ~5%, respectively; Figure S3). Pollen concentration and
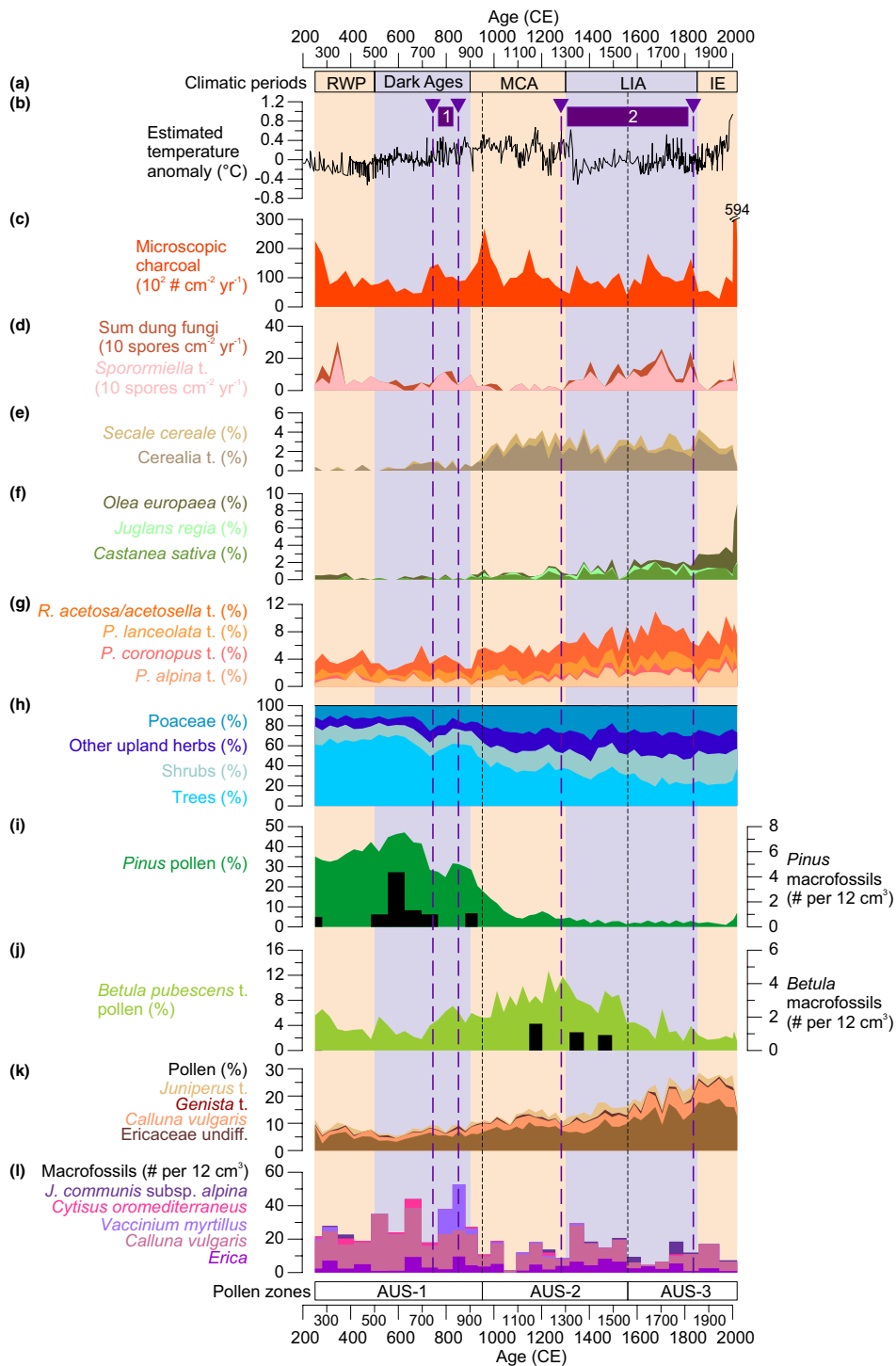
FIGURE 3 High-elevation vegetation dynamics in the Cantabrian Range (northern Iberia) during the past two millennia as inferred from the Lago del Ausente palaeoecological record. (a) Main climatic periods delimited according to Moreno et al. (2012): Cool periods shaded in blue and warm in orange. RWP = 'Roman Warm Period', MCA = 'Medieval Climate Anomaly', LIA ='Little Ice Age', IE ='Industrial Warming'. (b) Estimated temperature anomaly from the mean of the 380–1280 CE period (Martín-Chivelet et al., 2011). Standard error of temperature reconstruction: ±0.26°C. (c) Microscopic charcoal influx, proxy for regional fire occurrence. (d) Spore influxes of *Sporormiella* type and the sum of obligate coprophilous fungi (*Sporormiella* type, *Sordaria* type, *Podospora* type), proxy for pastoral farming. (e, f) Pollen percentages of the main regional herbaceous (Cerealia type, *Secale cereale*) and tree (*Castanea sativa*, *Olea europaea*, *Juglans regia*) crops. (g) Pollen percentages of the most relevant disturbance-tolerant and rock-dwelling herbs, probably favoured by human activities. (h) Main pollen diagram showing the percentages of trees, shrubs, Poaceae, and other upland herbs. (i, j) pollen percentages and macrofossil concentrations of the main high-elevation tree taxa around Lago del Ausente. (k, l) pollen percentages and macrofossil concentrations of the most important subalpine shrubs present in the region. (1) and (2), delimited by purple dashed lines, represent periods of intensified transhumant herding in the Cantabrian Range according to historical sources (e.g., (2) corresponds to 'La Mesta').

influx data attest to the demise of pine around Lago del Ausente as well as to its partial replacement by birch (Figure S4). Shrub pollen rises slightly (~15% to 25%) with *Erica* (usually ~10%), *Corylus* (~4% to 8%) and *Calluna* (~2% to 5%) as the main taxa, and *Juniperus* type following an increasing stepwise trend (from <1% to ~5%; Figure 3 and Figure S3). Nevertheless, shrub pollen concentrations and influxes remain unchanged during this pollen zone (Figure S4). The abundance of upland herbs is significantly higher (~40% to 50%): mainly Poaceae (~20% to 35%), disturbance-tolerant or rock-dwelling taxa (mainly *Rumex*, but also *Plantago lanceolata* type and *Plantago alpina* type to a lesser extent), and cereals (Cerealia type ~1% to 3%, *Secale* continuous curve and even >1%; Figure 3 and Figure S3). Coprophilous fungal spores are rare and even lacking until they increase to moderate values at ~1300 CE (Figure 3, Figures S3 and S4). Charcoal influxes drop at the beginning of this zone following the large peak at ~950 CE, and then stay at generally moderate values (~5000 to 10,000 # cm^{-2} year^{-1}) punctuated by peaks at ~1150 CE (~20,000 # cm^{-2} year^{-1}), 1350 CE (~14,000 # cm^{-2} year^{-1}) and 1520 CE (~12,000 # cm^{-2} year^{-1}).

Finally, plant macrofossil assemblages consist of *Calluna vulgaris*, *Erica* and *Juniperus communis* subsp. *alpina* during AUS-3 (15.5–0 cm; ~1570 to 2018 CE), without any tree macrofossil (Figure 3 and Figure S2). Concerning the pollen record, trees decrease further (~20% to 25% until the final rise to >35%), shrubs increase significantly (~25% to 30%, so AP continued ~50% to 55%), and upland herbs stay stable (~45% to 50%; Figure 3). Deciduous *Quercus* (although <10%) and *Fagus* (~5%) are the main trees (Figure S3), whereas *Betula* and *Pinus* are almost absent (Figure 3). In contrast, *Castanea sativa* reaches higher values (often 1% to 2%), and *Olea europaea* experiences a notable increase during the past ~200 years (to >5%), particularly steep for the past few decades (Figure 3). *Erica* (~10% to 20%), *Calluna* (~4% to 8%) and *Juniperus* type (~1% to 5%) are the commonest shrubs, particularly during the last ~150 years (Figure 3), and *Corylus* undergoes a reduction (Figure S3). The composition of the herbaceous pollen assemblages does not show relevant changes compared to the AUS-2 pollen zone (Figure 3 and Figure S3). Charcoal influx usually features moderate values (~5000 to 10,000 # cm^{-2} year^{-1}) with two maxima at *c.* 1650 (~18,000 # cm^{-2} year^{-1}) and 1830 CE (~16,000 # cm^{-2} year^{-1}; Figure 3). Dung fungal spore influxes show overall moderate values until ~1860 CE, with two major increases at *c.* 1700 and 1830 CE (Figure 3), to become later relatively low till present (Figure 3). The huge peak in charcoal influx (~60,000 # cm^{-2} year^{-1}) close to the top is an artefact created by the age-depth model, given that the peak does not parallel the trends observed in charcoal concentration and is shared by all the pollen and spore types (Figure 3 and Figure S4).

3.3 | Cross-correlation analyses

The results of cross-correlation analyses show significant negative correlations between *Pinus* pollen percentages and microscopic charcoal influxes at lags 0 to +2 (i.e., 0–60 years following the peak in microscopic

charcoal influx; Figure 4). In contrast, *Erica* and *Rumex acetosa/acetosella* type pollen percentages are significantly positively correlated with microscopic charcoal influxes at lag 0 (i.e., right after the charcoal peak; Figure 4). Poaceae and *Calluna* also bear positive correlations with microscopic charcoal at lag 0, although not significant (Figure 4). Finally, *Betula* pollen percentages present rather high positive correlations with microscopic charcoal influxes (significant at lag −2—i.e., ~60 years before charcoal peaks—almost significant at lags −1 and 0 –i.e.,~30 years preceding the charcoal peak and at the time of this; Figure 4).

4 | DISCUSSION

4.1 | The high-elevation landscape of the Cantabrian Range prior to medieval land-use intensification

The Lago del Ausente macrofossil record shows that the tree line ecotone was the dominant vegetation at high elevation (>1700 m a.s.l.) on the southern slope of the Cantabrian Range on siliceous bedrock between *c.* 250 and 900 CE (Figure 3). This tree line ecotone consisted of scattered *Pinus* trees/stands, perhaps 'krummholz', within subalpine scrublands (*Erica*, *Calluna vulgaris*, *Vaccinium myrtillus*, *Juniperus communis* subsp. *alpina*, *Cytisus oromediterraneus*; Figure 3). The regional macrofossil evidence (cones; Rubiales et al., 2008) and the modern distribution range (Caudullo et al., 2017; Figure 1) suggest that *P. sylvestris* was the main pine species involved. Further, according to studies investigating modern vegetation-pollen relationships in the Iberian Peninsula (e.g., Morales-Molino et al., 2020), the Lago del Ausente pollen record strongly suggests that the upper forest limit was close to the elevation of the lake. Pollen evidence indicates that the lower subalpine and upper montane forests were dominated by *Pinus* (Figure 3). *Betula*, and deciduous *Quercus* and *Fagus* probably played a secondary role in these mountain forests (Figure 3). Regional pollen records and macrofossil finds show that *P. sylvestris* forests persisted as the dominant high-elevation forest vegetation on the inner slopes of the Cantabrian Range and adjacent mountains for most of the Holocene (Figure 1, Table 1). In some sites, these were mixed with *Betula* or were alternating as dominant forests. In such settings, pinewoods benefitted from the more continental and submediterranean climate with respect to the seaward slopes (Rubiales et al., 2010). Even more continental and drier climatic conditions, alongside widespread poor soils, would have favoured the persistent dominance of pinewoods on the southern slopes of the Northern Iberian Range until today (Gil-García et al., 2002; Peñalba, 1994; Ruiz-Zapata et al., 2002; Sánchez Goñi & Hannon, 1999; Figure 1). This pattern markedly contrasts with the early replacement of pinewoods with deciduous broadleaved forests (usually dominated by *Quercus*) observed in more oceanic settings at the onset of the Holocene or even during the Lateglacial interstadial (Allen et al., 1996; Muñoz Sobrino et al., 1997, 2001; Rubiales et al., 2010; Figure 1). A maximum in microscopic charcoal followed by an increase in dung fungal spores suggest the use of fire to promote pasturelands during late Roman Times (Figure 3), which agrees
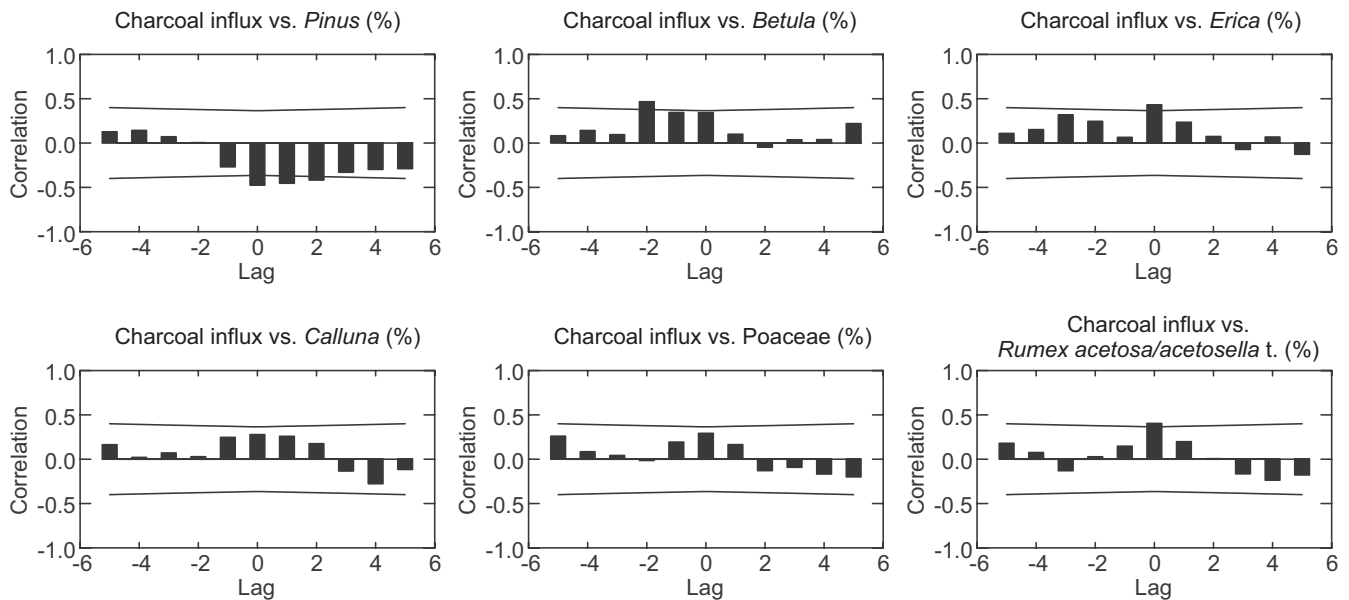
FIGURE 4 Cross-correlation analysis of microscopic charcoal influx (# cm^{-2} year^{-1}) versus several selected pollen types of the Lago del Ausente (Cantabrian Range, northern Iberia) palaeoecological sequence during the *Pinus* decline (*c.* 250–1150 CE). 1 lag = 31 ± 4 year. Solid black lines indicate *p* < 0.05.

with the archaeological evidence of transhumance since the Neolithic in the region (González-Álvarez et al., 2016). Pastoral burning peaking at ~250 to 300 CE may also be responsible for the slight pine forest retreat occurred between *c.* 300 and 450 CE, suggested by the lower pollen abundances and lack of macrofossils of *Pinus* (Figure 3). One of the main Roman roads crossing the Cantabrian Range used the San Isidro pass (1520 m a.s.l.), located ~3 km away from our study site (González-Álvarez, 2011), which supports local land use at that time. Cooler temperatures in the Cantabrian region at the end of the Roman Warm Period (Martín-Chivelet et al., 2011; Figure 3) might have also contributed to triggering the downslope shift of the tree line. Following this minor deforestation event, subalpine pine forests recovered and expanded. Indeed, pine trees recolonised the surroundings of Lago del Ausente during the Dark Ages (~500 to 700 CE), a period of socioeconomic and demographic collapse in northern Iberia following the fall of the Western Roman Empire (Bonassie et al., 2001). *Pinus* woodlands were partially replaced with grasslands and *Betula* stands later, between *c.* 700 and 800 CE (Figure 3). Despite the pine retreat was limited according to pollen and macrofossil evidence, pinewoods never completely recovered afterwards. Cereal cultivation started increasing at ~600 CE, probably on south-facing slopes and in the adjacent lowlands (Figure 3). Afterwards, a substantial rise in fire activity occurred at ~700 to 750 CE, followed by a rise in pastoral activities at ~800 CE (Figure 3). Our new data suggest that coupled fire and grazing caused the moderate pine forest retreat observed around Lago del Ausente, with warmer temperatures at the end of the Dark Ages (Martín-Chivelet et al., 2011) probably favouring fire spread. Increased farming activities could be related to the historically documented migration of people from the Northern Iberian Plateau to the Cantabrian Range at ~750 to 850 CE fleeing the Muslim invasion (Figure 3; Bonassie et al., 2001; Ezquerra & Gil, 2004).

4.2 | Anthropogenic high-elevation pinewood decline mediated by fire

The final demise of pinewoods as well as the near disappearance of pine trees from the tree line ecotone around Lago del Ausente occurred from *c.* 900 to 1100 CE. The latter low *Pinus* pollen representation (2–4%) could be associated with: (i) the persistence of scattered trees or small stands in the catchment (Ezquerra & García, 2017), (ii) the long-distance transport of pollen from the close Valle de Riopinos (where several medieval toponyms refer to pine occurrence) and the Pinar de Lillo and (iii) the reforestations accomplished in the 20th century CE. *Betula* stands replaced to some extent the declining pinewoods (Figure 3), alongside mountain scrubland (Ericaceae, *Calluna vulgaris*, *Genista* type, *Juniperus* type), and disturbance-tolerant upland herb communities (mainly Poaceae and *Rumex acetosa/acetosella* type, but also several *Plantago* pollen types; Figure 3). The replacement of *P. sylvestris* with *Betula*, in some cases with an intermediate stage of heathlands, was widespread on the most continental slopes of the Cantabrian Range and adjacent mountains during the Late Holocene (Fombella et al., 2001; García-Antón et al., 1997; Jalut et al., 2010; Janssen, 1996; Morales-Molino et al., 2011; Muñoz Sobrino et al., 2003). Several authors had argued that human activities, more specifically fire and grazing, triggered the demise of mountain pinewoods on the Cantabrian Range (Ezquerra et al., 2019; Jalut et al., 2010; Muñoz Sobrino et al., 2004; Rubiales et al., 2008), but empirical evidence supporting this hypothesis was still quite limited (García-Antón et al., 1997).

The new palaeoecological record from Lago del Ausente has allowed testing this hypothesis because it includes proxies for fire (charcoal) and pastoral activities (dung fungi), in addition to the more usual cultural indicator pollen types. First, a further increase

in fire occurrence started at ~900 CE (peaking at ~950 CE), and fire activity remained rather high until ~1200 CE (Figure 3). This strongly suggests that fire played a relevant role in the decline of *P. sylvestris* around Lago del Ausente. The results of cross-correlation analysis corroborate the high sensitivity of *Pinus* to fire (Figure 4). Considering that adult *P. sylvestris* trees are resistant to surface fires, because of their thick bark, but not adapted to crown fires (Tapias et al., 2004), one can hypothesise that the episode/s triggering the Cantabrian pine decline were crown fires. In fact, multi-decadal monitoring of postfire regeneration in *P. sylvestris* forests of northeastern Iberia has also highlighted the inability of this species to recover after crown fires (Vilà-Cabrera et al., 2012). On the contrary, our results strongly suggest that *Betula*'s resprouting capacity and high recruitment ability enabled successful post-fire recovery of birch (Figure 4; Costa et al., 2005; Connor et al., 2012; Gil-Romera et al., 2014). Spreading from fire refugia on peatlands and scree slopes, birches probably encroached the pasturelands, thus motivating further pastoral burning (Figure 4). Similarly, *Erica* and *Rumex* responded very positively to fire (Figure 4), as previously observed at other sites located in the mountains of Iberia (Connor et al., 2012; Morales-Molino et al., 2011; Sánchez Goñi & Hannon, 1999). Warm climate during the Medieval Climate Anomaly (Martín-Chivelet et al., 2011; Moreno et al., 2012; Figure 3) must certainly have favoured fire spread, but evidence concerning the cause of such fires is not conclusive. On the one hand, pollen data indicate that arable farming increased notably in the region synchronously with the decline of *P. sylvestris* (Figure 3), suggesting that forests were burnt to obtain open land for arable farming in the lowlands. Pollen-inferred rising land use agrees with the increasing human population density on the Cantabrian Range and adjacent lowlands (on the Northern Iberian Plateau) associated with people fleeing from the Christian-Muslim border (Isla, 2019). On the other hand, relatively low dung fungal spore abundances suggest that pastoral activities were not particularly heavy near Lago del Ausente at that time (Figure 3) despite some powerful monasteries from the Northern Iberian Plateau, like the Benedictine Monastery of Sahagún, were expanding their summer-pasturing areas close to the study site (Orden, 2013). Climatic forcing for the observed pine demise seems quite unlikely because the warmer temperatures reconstructed for the Medieval Climate Anomaly in the region should have favoured pine recruitment and therefore woodland densification in the Lago del Ausente catchment, and not the other way round.

4.3 | The deforested landscapes of the Cantabrian Range as legacy of intensified transhumant herding

Following the pine decline, high-elevation vegetation was fundamentally open around Lago del Ausente, characterised by the increasing dominance of grasslands, disturbance-tolerant/rock-dwelling vegetation (Poaceae, *Artemisia*, *Rumex*, *Plantago*), and heathlands (Figure 3). More specifically, the macrofossil evidence allows inferring the local presence of a quite open tree line ecotone with heathlands and

scattered *Betula* trees between *c.* 1100 and 1500 CE (Figure 3). Our palaeobotanical data show that trees (*Betula*) were able to continue growing at least at the elevation of Lago del Ausente (1700 m a.s.l.) after the abrupt cooling occurred at the beginning of the Little Ice Age (Martín-Chivelet et al., 2011; Figure 3). Therefore, the decline of *Betula* since ~1300 CE (particularly marked after ~1500 CE) and the synchronous spread of heathlands and grasslands (with increasing abundances of disturbance-tolerant/rock-dwelling species) cannot be explained satisfactorily on purely climatic grounds (Figure 3). Instead, the coprophilous fungi record strongly suggests that grazing activities increased around the lake since ~1300 CE and continued until ~1860 CE, whereas microscopic charcoal point to the regular occurrence of fires in the region (Figure 3). The Late Holocene replacement of high-elevation *Betula* stands with heathlands and pasturelands was widespread in the Cantabrian Range (Jalut et al., 2010; Morales-Molino et al., 2011; Muñoz Sobrino et al., 1997) and elsewhere in Atlantic Iberia (Morales-Molino et al., 2013; van der Knaap & van Leeuwen, 1995). Our data suggest that this process may have been related to the high sensitivity of *Betula* to excessive browsing (Morales-Molino et al., 2019). Concerning the abovementioned period of high grazing and burning activity, this corresponds unequivocally to the 'Honrado Concejo de La Mesta' or 'La Mesta' (1273–1836 CE) and the more intensive use of the summer pastures owned by the Sahagún and Eslonza monasteries (Gutiérrez-Álvarez, 2008). 'La Mesta' was an organisation established to promote a herding system involving the long-distance transhumance of huge flocks of merino sheep between low-elevation warmer and drier regions (winter pastures) and high-elevation cooler and moister areas (summer pastures; González-Álvarez et al., 2016). The southern slope of the Cantabrian Range experienced a particularly intense use as summer farming area (González-Álvarez et al., 2016), although areas with acidic soils were less heavily exploited than those on limestone because of the worse grazing quality of their pastures (Rodríguez-Pascual, 2011). These results highlight the relevance of transhumance in driving vegetation change in the mountains of southern Europe (Brown et al., 2013; García-Ruiz et al., 2020; López-Sáez et al., 2014). The further spread of mountain scrublands (*Erica*, *Calluna*, *Juniperus*) and development of *Castanea sativa* cultivation are the most remarkable vegetational shifts that occurred since ~ 1550 CE around Lago del Ausente (Figure 3). Finally, it is worth noting the prominent pollen reflection that the relatively recent expansion of olive cultivation in the Iberian Peninsula generated on the remote Lago del Ausente (Figure 3). This phenomenon has also been observed in other Iberian fossil pollen records (e.g., Leunda et al., 2017; Pérez-Sanz et al., 2013) and surface samples (Leunda et al., 2017; Morales-Molino et al., 2020) located far away from the main olive cultivation areas.

DATA AVAILABILITY STATEMENT
The data that supports the findings of this study are available in the supplementary material of this article

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BIOSKETCH

César Morales-Molino is a palaeoecologist investigating the long-term ecology of terrestrial ecosystems in response to climate change, human activities, fire and herbivory. He is particularly interested in the dynamics of conifer forests in the mountains around the Mediterranean basin. The research team consists of palaeoecologists, palaeoclimatologists and forest ecologists with broad interests in the environmental history of southern Europe.

Author contributions: C.M.-M. conceived the research, produced the palaeoecological data and conducted the numerical analyses; W.T. and M.M. acquired the funding; C.M.-M. led the writing with contributions of the rest of authors, particularly of M.L. and W.T.; all authors approved the final version of the manuscript.

SUPPORTING INFORMATION

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