



# Late-glacial and Holocene shifts in the mountain landscapes of the Cantabrian range (northern Spain) in response to changing climate, fire occurrence and land use

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## ABSTRACT

A new well-dated (18 <sup>14</sup>C dates on short-lived terrestrial plant macrofossils, <sup>210</sup>Pb and <sup>137</sup>Cs dating) fine-resolution palaeoecological sequence (pollen, coprophilous fungi, conifer stomata, macrofossils, charcoal) from Lago de Isoba (1400 m a.s.l.) spanning the past c. 17,000 years provides novel insights into the long-term dynamics of the high-elevation Cantabrian landscape in response to climate variability and human activities. Vegetation changes were mainly climate-driven during the Late-glacial and the Early Holocene. Thus, steppe-like environments prevailed during the Greenland Stadial 2.1a (GS-2.1a ≈ 'Oldest Dryas'). Warmer and moister conditions during the Greenland Interstadial 1 (GI-1 ≈ 'Bølling-Allerød') enabled successive expansions of *Juniperus*, *Betula* and *Pinus*. Steppe-like vegetation re-expanded during the cooler and drier Greenland Stadial 1 (GS-1 ≈ 'Younger Dryas'). Afterwards, the Early Holocene warming triggered the rapid spread of mixed pine-broad-leaved deciduous mountain forests. Pollen, stomata and macrofossils indicate continuous, long-lasting (c. 10,850–1250 cal yr BP) local occurrence of *Pinus sylvestris* stands. The records of *Cerealia* and *Plantago lanceolata* pollen types (first Holocene occurrences dated at c. 5100 cal yr BP) evidence increased land use during the Late Holocene, which triggered substantial changes in forest ecosystems. Following a phase of intensified arable and pastoral farming, which involved the use of fire to create and maintain forest clearings, pinewoods expanded and reached their maximum development between c. 3600 and 3300 cal yr BP. *Pinus* probably out-competed temporarily other woody taxa thanks to its resilience to low-intensity disturbances. Later, pinewoods underwent a stepwise, human-induced decline ending in their final massive collapse after c. 1150 cal yr BP. The highest intensity of agricultural and pastoral farming took place during the Middle Ages, following maximum fire occurrence. We conclude that the present-day open landscape has been shaped by millennia of land use that partly blurred the impact of climate variability.

## 1. Introduction

As climate and land-use changes are modifying environmental conditions dramatically (IPCC, 2022), understanding future developments

of vegetation and biodiversity becomes more urgent. To achieve this goal, we need to improve our knowledge about the mechanisms driving vegetation change in the long term and how they operate (Alverson et al., 2003). In this regard, examining the incidence of the various

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ecological factors through time allows gaining a holistic view on ecosystem dynamism and functioning (Seddon et al., 2014). The two main long-term ecological drivers are natural forcing (mostly climate variability and natural disturbances) and anthropogenic activities. Palaeoecology's unique long-term perspective, which exceeds experimental and observational time series, is particularly valuable in this context (Lang et al., 2023a).

The Cantabrian Range in northern Spain constitutes an excellent setting to investigate long-term vegetation dynamics in response to changing climate and land use for two main reasons. Firstly, this mountain range lies in the transitional area between the Mediterranean and the Eurosiberian biogeographical regions, which results in outstandingly diverse extant flora and vegetation. Similarly, the Cantabrian Range marks the boundary between two different climates. On the north-facing slope, the climate is more oceanic, without marked thermal contrasts, neither seasonal nor daily, and with reduced summer drought. On the south-facing slope, the climate is continental mediterranean, therefore with strong thermal oscillations (both day-night and summer-winter) and a marked summer drought. This makes the Cantabrian Range highly sensitive to multi-decadal to millennial climate variability (Ramil-Rego et al., 1998). Secondly, this mountain area is characterised by a long history of intense exploitation of its resources via mainly agriculture, pastoralism (chiefly transhumant), and mining (Price, 2000; González-Álvarez et al., 2016; González-Álvarez, 2019).

The Cantabrian Range and its surroundings have been intensively investigated from a palaeoenvironmental point of view (Iriarte-Chiapusso et al., 2016 and references therein). Late-glacial climate and vegetation dynamics have been studied on lake sediments and peat deposits at sites spanning a wide range of environmental conditions (e.g., Allen et al., 1996; Muñoz Sobrino et al., 1997, 2001, 2007, 2013; Ramil-Rego et al., 1998; Sánchez-Morales et al., 2022), as well as in marine cores (Naughton et al., 2007, 2016). Similarly, several studies have investigated Holocene vegetation history in the region (e.g., Muñoz Sobrino et al., 1997, 2001; Jalut et al., 2010; Pérez-Obiol et al., 2016). Further, the Cantabrian region has been profusely studied from an archaeological perspective and numerous sites, mainly located on coastal and low-elevation areas but with an increasing focus on mountain areas, have been excavated, which allows framing the palaeoecological findings into a cultural context (e.g., Arias Cabal, 1990; Bernaldo de Quirós and Neira, 1993; Peña-Chocarro et al., 2005; Vidal et al., 2008; González-Álvarez, 2019; Fuertes-Prieto et al., 2023). However, despite all these progresses, our current understanding of the long-term drivers of vegetation change is still limited, partly because of the low number of multi-proxy records available so far (Moreno et al., 2011; Muñoz Sobrino et al., 2013). Even two proxies commonly used in palynological research in recent decades such as charcoal, for fire occurrence, and dung fungi, for grazing, are quite rarely present in Cantabrian palaeoecological records (García Antón et al., 1997; Pérez-Díaz et al., 2016; Pérez-Obiol et al., 2016). Studies integrating both proxies to provide a more general picture of vegetation change are even rarer (Carracedo et al., 2018; Morales-Molino et al., 2022; Sánchez-Morales et al., 2022). Therefore, significant gaps in the regional palaeoecological knowledge can still be bridged with new detailed and well-dated multi-proxy records.

One of the most remarkable features of the vegetation history of the Cantabrian Range is the extensive decline of montane-subalpine pine-woods (*Pinus sylvestris* L.) during the Late Holocene (e.g., Rubiales et al., 2008, 2012; Morales-Molino et al., 2022). As a result, native *Pinus sylvestris* stands currently cover only few hundred hectares in these mountains (Ezquerro and García-López, 2017). Prior to this, pine-woods were an important component of the mid-to-high-elevation Cantabrian vegetation from the Late-glacial to the Mid-Holocene (Iriarte-Chiapusso et al., 2016 and references therein). Several ecological processes may have been involved in the demise of these pine-woods. Some authors have suggested that increasingly oceanic climatic conditions during the Holocene, i.e. higher moisture availability throughout the year caused by decreasing insolation seasonality (Gomes et al., 2020), favoured the

spread of more shade-tolerant broad-leaved deciduous trees (Muñoz Sobrino et al., 1997, 2001; Rubiales et al., 2010). Anthropogenic forest clearance to promote pastoral farming, often involving the deliberate use of fire, has also been proposed as the mechanism responsible for the demise of Cantabrian high-elevation pine-woods (Rubiales et al., 2008, 2012; Carracedo et al., 2018; Morales-Molino et al., 2022). However, the above-mentioned scarcity of detailed charcoal and obligate coprophilous fungi records has so far hindered testing these competing hypotheses.

The main goal of this study is to investigate in-depth the processes controlling long-term dynamics of mountain vegetation in the Cantabrian Range, drawing on a new c. 17,000-year long palaeoecological record from Lago de Isoba. Its robust and detailed chronology (based on 18  $^{14}\text{C}$  dates on short-lived terrestrial plant macrofossils, as well as on precise  $^{210}\text{Pb}$  and  $^{137}\text{Cs}$  dating) and the integration of proxies for fire occurrence (microscopic charcoal) and grazing (dung fungal spores) allow partly overcoming the previous paucity of well-dated palaeoecological sequences. The specific aims are as follows: (i) to assess the patterns and timing of Late-glacial and Early Holocene vegetation succession in response to the climatic variability typical of the last deglaciation and the onset of the current interglacial; (ii) to reconstruct the natural fire regime and its changes through time; (iii) to investigate the impact of human activities on vegetation and fire occurrence in the different cultural periods; and, (iv) to track the dynamics of mountain pine-woods in the Cantabrian Range at multi-decadal to millennial timescales.

## 2. Material and methods

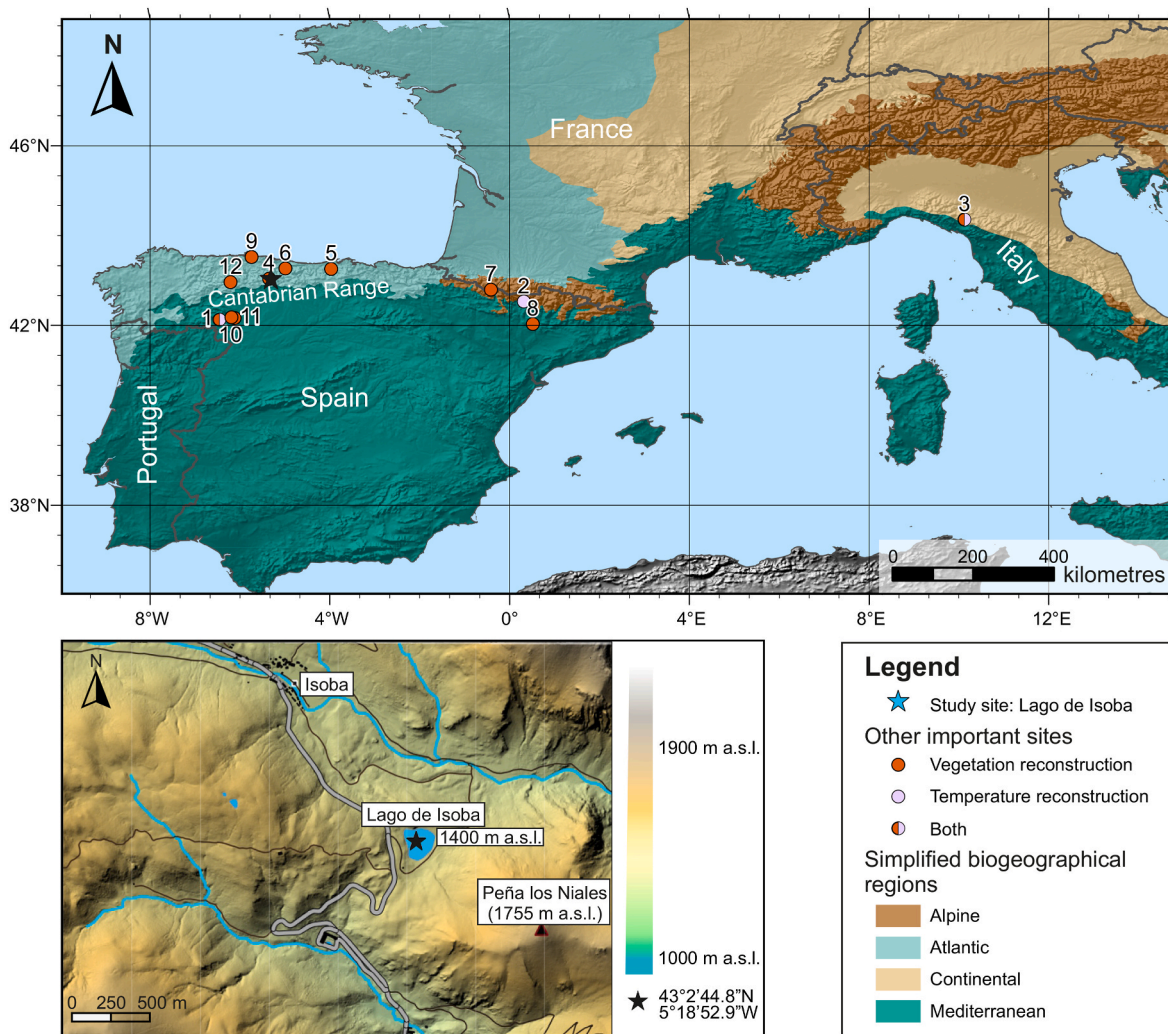
### 2.1. Study area

Lago de Isoba (43° 2' 44.8" N, 5° 18' 52.9" W, 1400 m a.s.l.) is a small (~ 3 ha) and shallow (maximum depth = 6 m) glacial-karstic lake located on the southern slopes of the Cantabrian Range (northern Spain; Fig. 1). The lake catchment is closed, with just small temporary inlet streams. The bedrock in the catchment is mostly limestone, but the lake lies on siliceous fluvio-glacial deposits (clay, sand). The climate is mountain oceanic (Dfb in the Köppen-Geiger classification). Mean annual temperature is ~ 6.5 °C ( $T_{\text{January}}$ : ~ 0 °C;  $T_{\text{July}}$ : ~ 15 °C; estimated from the Puerto de San Isidro weather station data series) and mean annual precipitation, ~ 1500 mm ( $P_{\text{July-September}}$ : ~ 180 mm; estimated from the Cofiñal weather station data series).

The lake catchment lies at the transition between the Atlantic and the Mediterranean biogeographical regions, therefore hosting a notable biodiversity. Today, the landscape is mostly treeless consisting of pastures and shrublands (e.g., *Genista*, *Erica*, *Cytisus*), with only few scattered individuals of *Pinus sylvestris*. The natural population of *Pinus sylvestris* is very fragmented in the region, with the strictly protected Pinar de Lillo, located c. 8 km away from Lago de Isoba, as the only remarkable exception. In the region, native forests and woodlands are mostly dominated by deciduous broad-leaved trees (*Fagus sylvatica* L., *Betula pubescens* Ehrh., *Quercus petraea* (Matt.) Liebl., *Q. pyrenaica* Willd. and *Q. faginea* Lam.). The Cantabrian Range has a long history of land use, with remarkable transhumant summer shepherding and cattle ranching occurring during the past few centuries (González-Álvarez et al., 2016).

### 2.2. Coring and dating

In September 2018, we retrieved two overlapping parallel cores from the deepest area of Lago de Isoba using a modified Streif-Livingstone piston corer (8-cm diameter; Merkt and Streif, 1970) operated from a floating platform. Additionally, we collected three short cores with a UWITEC gravity corer. The cores were split lengthwise in the laboratory and correlated according to their lithostratigraphy, resulting in a 682.5-cm long composite master core. To establish the chronology, we



**Fig. 1.** **Top.** Location of Lago de Isoba in the Cantabrian Range (northern Spain) and other relevant palaeoclimatic and palaeoecological sites discussed in the text. Palaeoecological sites: 1 Laguna de la Roya (Allen et al., 1996; Muñoz Sobrino et al., 2013), 2 Basa de la Mora (Tarrats et al., 2018), 3 Lago Verdarolo (Samartin et al., 2017; Morales-Molino et al., 2021), 4 Lago del Ausente (Morales-Molino et al., 2022), 5 La Molina (Pérez-Obiol et al., 2016; Sánchez-Morales et al., 2022), 6 Lago Enol (Moreno et al., 2011), 7 El Portalet (González-Sampérez et al., 2006; Gil-Romera et al., 2014), 8 Lake Estanya (González-Sampérez et al., 2017), 9 Monte Aro (López-Merino et al., 2010), 10–11 Vallefontado and Xan de Llamas, Teleno Mountains (Morales-Molino et al., 2011), 12 Vega de Viejos (Rubiales et al., 2008), Laguna del Castro and Laguna del Miro (Jalut et al., 2010). **Bottom left.** Detailed map of Lago de Isoba and its catchment.

used  $^{14}\text{C}$ ,  $^{210}\text{Pb}$  and  $^{137}\text{Cs}$  dating. Eighteen short-lived terrestrial plant macrofossil samples (Table 1) were radiocarbon-dated by Accelerator Mass Spectrometry (AMS) at the Laboratory for the Analysis of Radiocarbon with AMS (LARA) of the University of Bern (Switzerland; Szidat et al., 2014). We dated a particularly high number of samples around the two turbidites found at 391–377 and 288–271-cm depth (Table S1) to better understand the depositional dynamics. The radiocarbon ages were converted to calibrated years before present ('cal. yr BP'; present = 1950 CE) using the IntCal20 calibration curve (Reimer et al., 2020). The uppermost section of the master core was dated by gamma ray spectrometry on dry sediment samples, resulting in a series of 18  $^{210}\text{Pb}$  dates (Table S2; Gardoki et al., 2023). Additionally, this analysis allowed locating the 1963 CE maximum of  $^{137}\text{Cs}$  concentration associated with nuclear bomb testing fallout at 23.5-cm depth, which corroborates the robustness of the series of  $^{210}\text{Pb}$  dates (Gardoki et al., 2023). The age-depth relationship (Fig. 2) was modelled using a smoothing spline (95% confidence interval; 10,000 iterations; smooth = 0.6) with the package 'clam' (version 2.4.0; Blaauw, 2010). These and all the following analyses were performed using the software R (version 4.0.2; R Core Team, 2020) except when specified otherwise.

### 2.3. Palynological analysis

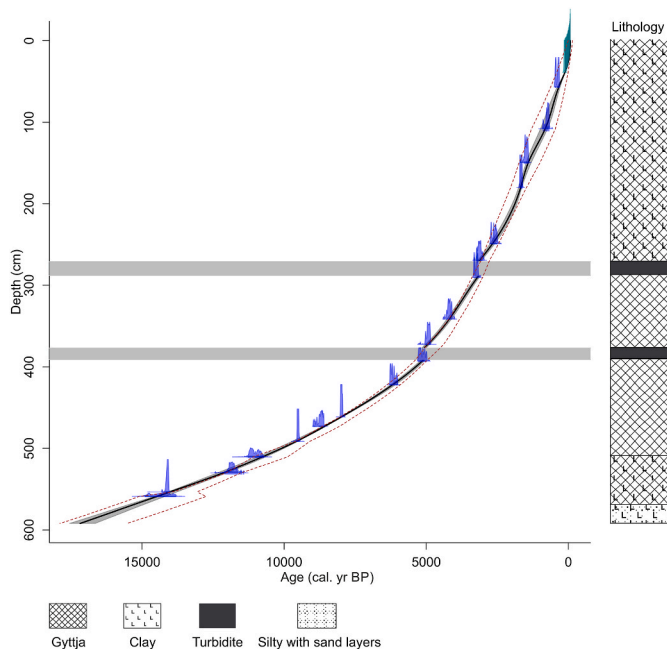
We treated 120 sediment samples ( $1\text{ cm}^3$ ), taken every 8 cm (592–560 and 200–0 cm depth) or 4 cm (560–200 cm depth), for palynological analysis (pollen, conifer stomata, spores, and microscopic charcoal). No sample was prepared between 682.5- and 592-cm depth because the inorganic glacial sediments contain very little pollen, and the pollen grains present were usually reworked and/or transported over long distances (Lang et al., 2023b). We treated the samples following standard protocols (Moore et al., 1991), adding a known amount of *Lycopodium* spores to estimate concentrations and influx (= accumulation rate; Stockmarr, 1971). Finally, we analysed the slides under a transmitted light microscope at  $400\times$  magnification, reaching a minimum of 500 pollen grains of terrestrial plants per sample. Identification of pollen, fern spores and fungal spores was achieved using dichotomic keys and photographic atlases (e.g., Moore et al., 1991; Reille, 1992; Beug, 2004). We must note that *Quercus robur* t. (t.: pollen type) comprises several species of deciduous *Quercus* in the study area, with *Q. pyrenaica* and *Q. petraea* as the most relevant and widespread (Costa et al., 2005). Spores of obligate coprophilous fungi are a proxy for the density of herbivores including pastoral farming (e.g., Gill et al.,

**Table 1**

Radiocarbon dates of the Lago de Isoba sedimentary sequence. Radiocarbon dates were calibrated using the IntCal20 calibration curve (Reimer et al., 2020) with the program Calib 8.20 (Stuiver and Reimer, 1993).

Laboratory code	Depth (cm)	Material	Radiocarbon age ( $^{14}\text{C}$ yr BP)	Calibrated age (cal. yr BP, 95% CI)	Calibrated age (cal. yr BP, median)
BE-18222	56–58	<i>Cytisus oromediterraneus</i> twigs	350 ± 20	316–479	386
BE-17841	105–111	<i>Betula</i> fruit, bud scales indet., bark, deciduous leaf fragment	820 ± 65	660–906	737
BE-17842	148–151	<i>Pinus</i> bud scale, conifer periderm, twig	1620 ± 40	1397–1586	1483
BE-11023	178–182	<i>Pinus</i> bud scales, conifer periderm	1780 ± 20	1612–1718	1655
BE-17843	248–250	<i>Pinus</i> bud scale, conifer periderm	2530 ± 40	2472–2748	2599
BE-11022	269–270	<i>Pinus sylvestris</i> t. needles, <i>Pinus</i> anthers, <i>Betula pubescens</i> t. female catkin scale	2960 ± 40	2967–3317	3122
BE-17844	290–291	<i>Pinus</i> bud scales, conifer periderm, bark	3030 ± 25	3158–3343	3234
BE-17845	341–342	<i>Pinus</i> bud scale, conifer periderm	3800 ± 40	4004–4396	4189
BE-17846	372–373	<i>Pinus sylvestris</i> t. dwarf shoot and needles, <i>Pinus</i> bud scales, conifer periderm	4360 ± 45	4839–5209	4932
BE-11021	392–394	<i>Pinus sylvestris</i> t. dwarf shoot, <i>Betula pubescens</i> t. fruits and female catkin scales	4470 ± 35	4974–5289	5149
BE-17847	421–423	<i>Betula pubescens</i> t. fruit, <i>Populus</i> catkin scale, conifer periderm, deciduous broad leaf fragment	5380 ± 45	6004–6286	6189
BE-17848	461–462	<i>Pinus</i> bud scale, <i>Betula</i> fruit, <i>Salix</i> bud scales, conifer periderm	7170 ± 30	7937–8022	7984
BE-11020	472–474	<i>Pinus</i> bud scales, <i>Betula pubescens</i> t. female catkin scales	7900 ± 40	8594–8981	8716
BE-17849	491–492	<i>Pinus</i> bud scale, hardwood periderm, conifer periderm	8530 ± 50	9447–9552	9512
BE-17850	509–512	<i>Pinus sylvestris</i> t. dwarf shoot, <i>Pinus</i> bud scale, <i>Betula</i> fruits, hardwood periderm, conifer periderm, deciduous broad leaf fragments	9700 ± 110	10,702–11,313	11,043
BE-17851	528–532	<i>Juniperus communis</i> needles, conifer bud scale, deciduous broad leaf fragments, twig	10180 ± 70	11,402–12,423	11,829
BE-11019	553–554	Twig	12210 ± 25	14,045–14,295	14,102
BE-17852	558–560	Deciduous broad leaf fragments, wood	12230 ± 160	13,795–14,920	14,267

CI = confidence interval; cal. yr BP = calibrated years before present (present = 1950 CE).



**Fig. 2.** Age-depth model of the Lago de Isoba sedimentary sequence, alongside its simplified lithology. The chronology is based on 18  $^{14}\text{C}$  dates (in blue) and 18  $^{210}\text{Pb}$  dates (in turquoise). The age-depth relationship was modelled using a smoothing spline (black line) with ‘clam’ (version 2.4.0; Blaauw, 2010). The 95% confidence interval of the age-depth model is shaded in grey. Additionally, the dashed brown line depicts the 95% confidence interval of a mixed-effect model (Heegard et al., 2005). The two horizontal grey bands represent turbidites (271–288 cm and 377–391 cm) that were excluded from the model.

2013; Baker et al., 2013, 2016). Conifer stomata, proxy for the local presence of conifer trees and shrubs (Ammann et al., 2014), were identified using Trautmann (1953) and Finsinger and Tinner (2020). Microscopic charcoal (>10  $\mu\text{m}$ ), widely used as a proxy for regional fire activity (Conedera et al., 2009; Adolf et al., 2018), was quantified

following Tinner and Hu (2003) and Finsinger and Tinner (2005). We applied optimal partitioning using the minimum sum-of-squares criterion (Birks and Gordon, 1985) and the broken-stick model (Bennett, 1996) to divide the pollen record into statistically significant local pollen assemblage zones (LPAZ).

#### 2.4. Macrofossil analysis

For macrofossil analysis, we took 83 sediment samples (6–28  $\text{cm}^3$ ). Adjacent 1–2-cm thick samples were taken in sections of 4–16-cm long, spaced at varying intervals (5–85 cm) across the sequence. We focused on these specific sections because of their particular interest in terms of sedimentological or vegetational change. For instance, we sampled the 590–552-cm depth section to assess and date the earliest presence of trees in the lake catchment. Similarly, the 72–56-cm depth section was selected to investigate in detail and date local pine extirpation. We first soaked the sediment samples in a 10% sodium hexametaphosphate solution for 24 h and then sieved them through a 200  $\mu\text{m}$  mesh. Finally, we identified the macrofossils under a stereomicroscope, aided by photographic atlases (e.g., Cappers et al., 2006) and the reference collection at the Institute of Plant Sciences of the University of Bern (Switzerland). Macrofossil concentrations were standardised to the average sample volume (13  $\text{cm}^3$ ).

### 3. Results and interpretation

#### 3.1. Lithology and chronology

We did not find any material suitable for radiocarbon dating below 560-cm depth, so the chronology of the bottom section is based on extrapolation and must therefore be taken with caution (Table 1, Fig. 2). However, both the pollen stratigraphy and the sedimentology (siliclastic deposits of clay, silt and sand intercalated; Table S1) are consistent with the age-depth model, indicating that the bottom of the record lies within the Greenland Stadial 2.1a (GS-2.1a, ~17,450–14,650 cal yr BP; Rasmussen et al., 2014). From the oldest radiocarbon date (~14,270 cal yr BP at 558–560-cm depth) to present-day, the chronology is very well constrained (Table 1, Fig. S2; Fig. 2). For most of the

Late-glacial and the Holocene, the sediment typically consists of ‘gyttja’ (organic-rich silts) with variable amounts of carbonates and the intercalation of some millimetre-thick clayey laminae (Table S1). However, the occurrence of two turbidites at 288–271- and 391–377-cm depth is remarkable. These were first visually assessed as massive fining-upwards sequences (ranging from silt to clay), with anomalously high quantities of plant remains at their base. Later, the mass-wasting origin of these layers was confirmed by the similar ages of the radiocarbon-dated samples at their edges (Table 1; Fig. 2) and the very similar pollen assemblages found throughout each of them. Pollen and macrofossil samples contained within the turbidites were eventually

excluded from further analyses and discussion. Following the first turbidite (~ 5100 cal yr BP), sediment accumulation rates increase as well as clay content (Table S1, Fig. 2), suggesting enhanced erosion in the catchment that likely favoured mass-wasting activity.

### 3.2. Vegetation, grazing, and fire history

The palynological record of Lago de Isoba is remarkably diverse and we identified up to 170 pollen types, one conifer stoma type and 15 spore types. We delimited seven statistically significant LPAZ (ISB-1 to ISB-7; Figs. 3 and 4), plus additional non-statistically significant

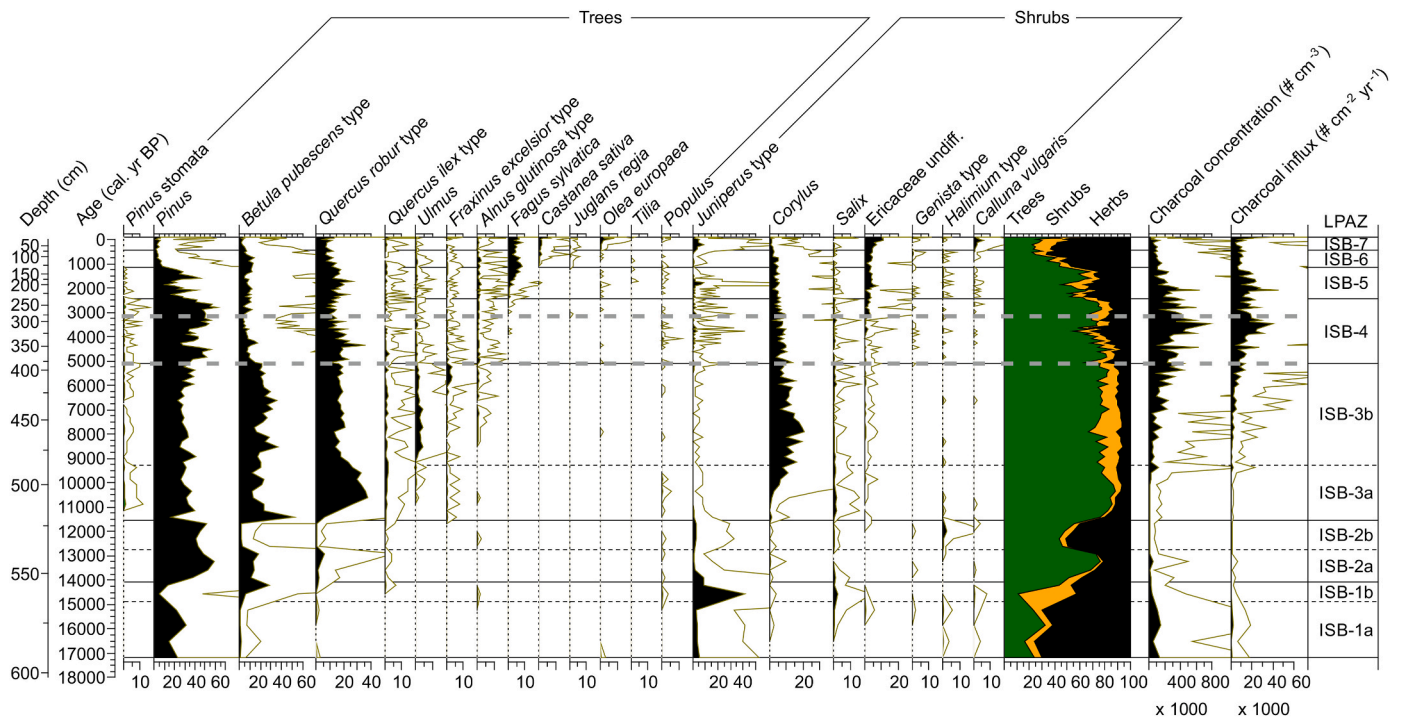


Fig. 3. Percentage pollen diagram of Lago de Isoba: selected tree and shrub pollen types, stomata and microscopic charcoal (concentration and influx). Hollow curves show 10× exaggeration. LPAZ: local pollen assemblage zone. Thick grey dashed lines indicate the position of the turbidites.

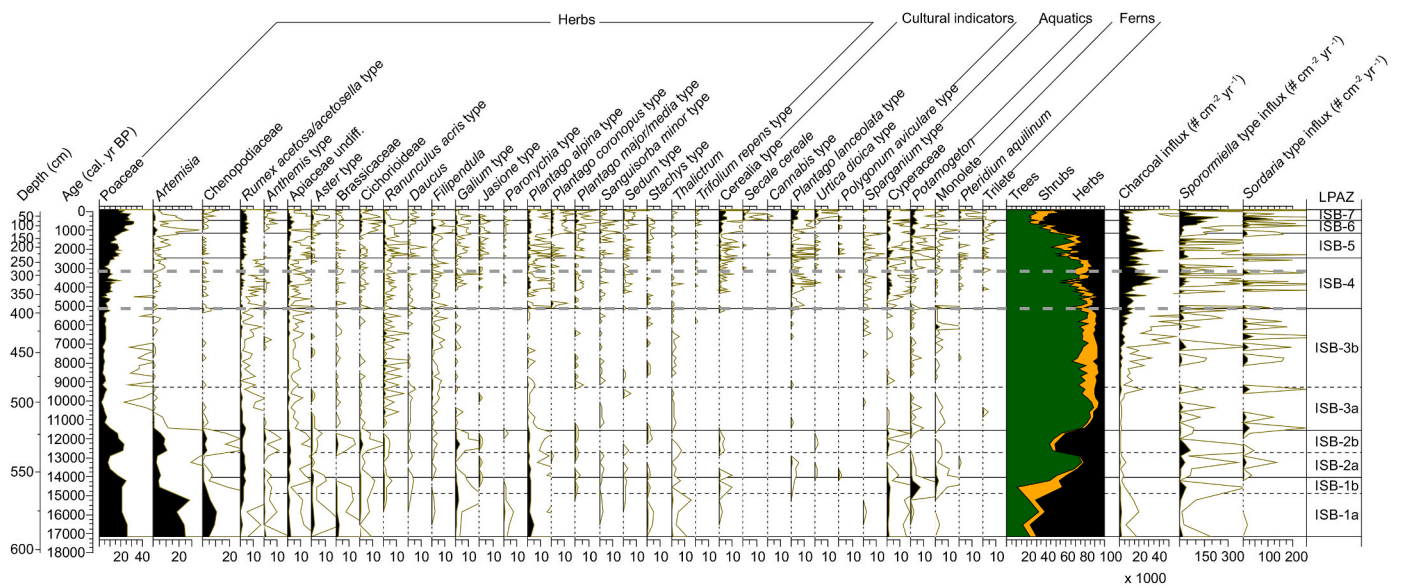
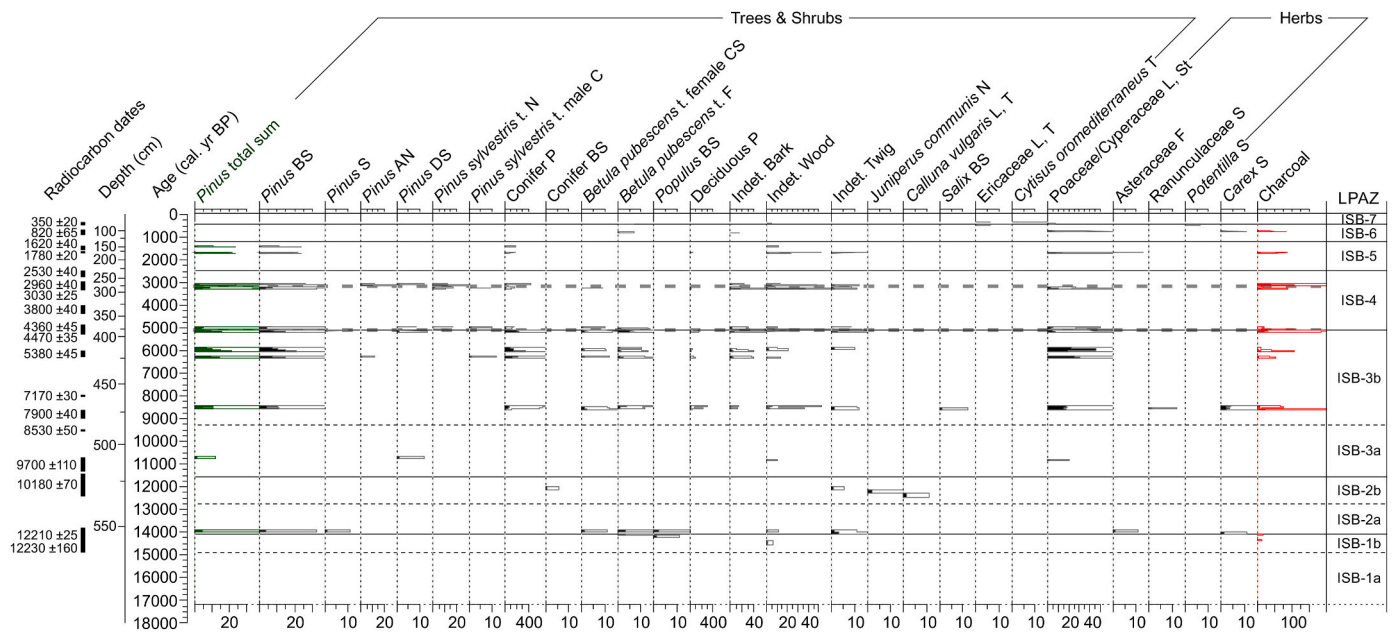


Fig. 4. Percentage pollen diagram of Lago de Isoba: selected upland and aquatic herb pollen types, fern spores, microscopic charcoal (influx), *Sporormiella* type (influx) and *Sordaria* type (influx). Hollow curves show 10× exaggeration. LPAZ: local pollen assemblage zone. Thick grey dashed lines indicate the position of the turbidites.



**Fig. 5.** Macrofossil diagram of Lago de Isoba (selected taxa). Macrofossil concentrations are referred to mean sample volume (13 cm<sup>3</sup> of sediment). Periderm and leaves are given as number of fragments. Abbreviations: AN anther, B bud, BS bud scale, C cone, CS catkin scale, DS dwarf shoot, L leaf, N needle, S seed, Sc scale, T twig, St stem, P periderm, LPAZ local pollen assemblage zones. Hollow grey bars show 10 × exaggeration. Thick grey dashed lines indicate the position of the turbidities.

subzones within ISB-1, ISB-2 and ISB-3 to refine our understanding of past vegetation dynamics.

Herb pollen dominates during ISB-1a (592–564 cm; ~17,150–14,900 cal yr BP), with Poaceae, *Plantago alpina* t., *Artemisia* and Chenopodiaceae as the most abundant taxa (Fig. 4). Scattered pollen grains of Cerealia t. occur from this subzone until ISB-2b (Fig. 4). Tree and shrub pollen abundances are consistently low (Fig. 3), mainly *Pinus*, *Betula pubescens* t. ('*Betula*' hereafter) and *Juniperus* t. ('*Juniperus*' hereafter). Neither *Pinus* stomata nor *Pinus* and *Betula* macrofossils were recorded (Figs. 3 and 5). Pollen evidence suggests that steppe-like vegetation covered the catchment, with trees growing at lower elevations (long distance pollen transport). Consistently low microscopic charcoal and *Sporormiella* t. (although fluctuating) influx suggests low regional fire occurrence and rare local herbivore presence (Figs. 3 and 4).

The pronounced peak of *Juniperus* at ~14,500 cal yr BP is the most prominent feature of ISB-1b (564–554 cm; 14,900–14,050 cal yr BP; Fig. 3). Later, at ~14,300 cal yr BP, herb pollen declines while *Betula* increases sharply (Figs. 3 and 4). The earliest macrofossils of tree *Betula* and *Populus* date to ~13,900 cal yr BP (Fig. 5). Pollen and macrofossil records indicate that early successional woody taxa such as *Juniperus*, *Salix* and *Betula* established close to Lago de Isoba within an open steppe-like vegetation (*Artemisia*, Chenopodiaceae, Poaceae). Microscopic charcoal influx values remain low, but *Sporormiella* t. influx slightly increases (Figs. 3 and 4), suggesting persistently low fire occurrence and moderate herbivory.

Tree pollen, mainly *Pinus* and *Betula*, significantly increases and later dominates throughout ISB-2a (554–538 cm; 14,050–12,750 cal yr BP; Fig. 3). Deciduous *Quercus* pollen slightly increases, whereas *Juniperus* declines alongside Poaceae, *Artemisia* and *Rumex acetosa/acetosella* t. (Fig. 4). *Pinus*, tree *Betula* and *Populus* macrofossils indicate that boreal trees established nearby (Fig. 5). These data point to the expansion of boreal woodland. Microscopic charcoal and *Sporormiella* t. influx remains low, pointing to low grazing and fire disturbance.

During ISB-2b (538–522 cm; 12,750–11,550 cal yr BP), tree pollen declines (Fig. 3). *Pinus* is by far the most abundant tree, whereas *Betula* and *Quercus robur* t. experience remarkable drops. Herb pollen rises, with Poaceae, *Artemisia* and Chenopodiaceae dominating the

assemblages (Fig. 4). Pollen influx values follow the same trends as pollen percentages (Fig. S1). In this subzone, plant macrofossils are less abundant: only a conifer bud scale and some *Juniperus communitis* and *Calluna vulgaris* remains are present (Fig. 5). Pine-birch woodlands opened and steppe-like vegetation re-expanded at their expense. Minimum microscopic charcoal influx suggests very low regional fire occurrence (Fig. 3). In contrast, peaking *Sporormiella* t. influx suggests high abundances of ungulates in the catchment (Fig. 4).

The expansion of *Pinus*, *Betula* and deciduous *Quercus* during ISB-3a (522–486 cm; 11,550–9250 cal yr BP) drive tree pollen to its maximum of the record. *Quercus ilex* t. features a continuous curve. Shrub pollen increases after c. 10,250 cal yr BP, associated with the expansion of *Corylus*, while herb pollen abundance is low. The continuous *Pinus* stomata record since 10,850 cal yr BP (Fig. 3) attests to the local presence of pines, which is further confirmed by the sole macrofossil sample in this subzone (Fig. 5). According to the pollen, stomata and macrofossil data, closed forests dominated by *Pinus*, *Betula* and deciduous *Quercus* thrived around Lago de Isoba. Microscopic charcoal influx is initially low and only increases slightly towards the end of ISB-3a, suggesting low regional fire occurrence. Lower *Sporormiella* t. influx values suggest declining grazing activities.

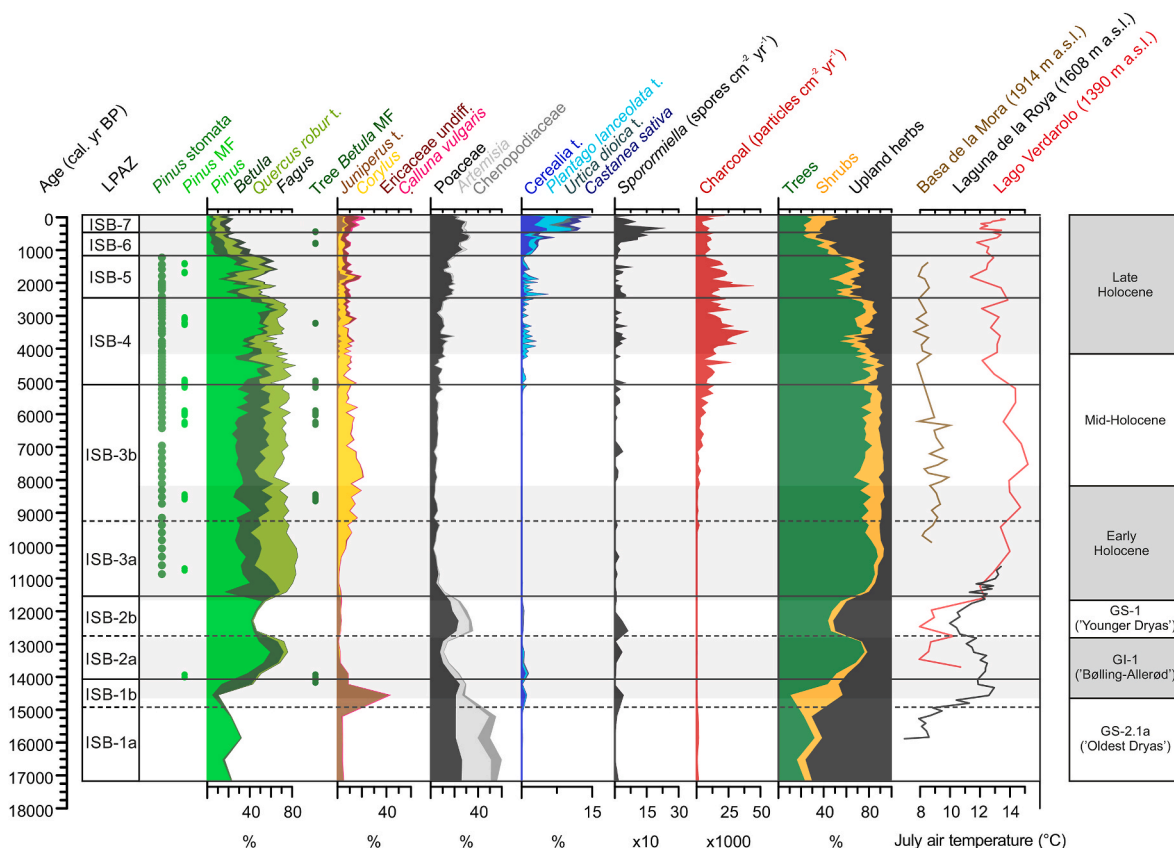
The pollen assemblages continue to be dominated by *Pinus*, *Betula* and deciduous *Quercus* during ISB-3b (486–384 cm; 9250–5100 cal yr BP; Fig. 3). Deciduous *Quercus* pollen percentages decrease, but pollen influx remains almost unchanged (Fig. S1). Notable increases in *Ulmus* and *Fraxinus excelsior* t. pollen percentages occur at c. 9000 and 6000 cal yr BP respectively. *Corylus* continues increasing to reach its highest value, with *Juniperus*, *Salix* and Ericaceae at lower abundances (Fig. 4). *Pinus* stomata are almost continuously recorded (Fig. 3). *Pinus*-, *Betula*- and deciduous *Quercus*-dominated forests, enriched with other deciduous trees and shrubs such as *Ulmus*, *Fraxinus excelsior*, and *Corylus* (likely in the understory) were widespread, with *Pinus* and tree *Betula* dominating in the catchment (Figs. 3 and 5). Microscopic charcoal influx gradually increases (Fig. 3), indicating rising regional fire occurrence. Macroscopic charcoal occurrence suggests that local fires took place (Fig. 5). The influx of *Sporormiella* t. remains low and discontinuous (Fig. 4), indicating limited grazing.

During ISB-4 (384–238 cm; 5100–2450 cal yr BP), tree pollen

initially follows a declining trend (minimum at c. 3750 cal yr BP) to later recover almost to previous values (Fig. 3). The first Holocene occurrence of *Cerealia* t. pollen dates to c. 5100 cal yr BP, and its curve becomes continuous after 4250 cal yr BP. *Plantago lanceolata* t. record is almost continuous. The abundance of cultural indicators (e.g., *Cerealia* t., *Plantago lanceolata* t., *Urtica dioica* t.), particularly since c. 4300 cal yr BP, is remarkable. *Corylus* decreases steadily while Ericaceae increase notably from c. 3800 cal yr BP onwards, a trend paralleled by Poaceae, *Rumex acetosa/acetosella* t., Apiaceae and *Plantago alpina* t. (Fig. 4). *Pinus* is particularly abundant between c. 2800–2600 cal yr BP, right before its decline, while deciduous *Quercus* pollen abundances are very similar to those in ISB-3b (Fig. 3, Fig. S1). In contrast, *Betula* features markedly lower pollen percentages than in ISB-3b (Fig. 3, Fig. S1). *Fagus* reaches the empirical limit (continuous curve) around 2750 cal yr BP, indicating its establishment in the Lago de Isoba area. *Pinus* stomata are almost continuously present, and their highest abundance coincides with the maximum in *Pinus* pollen percentages (Fig. 3). Macrofossil data confirms the local presence of *Pinus*, tree *Betula* and Poaceae/Cyperaceae (Fig. 5). Pine-dominated woodlands continued to prevail in the landscape but were cleared under increasing land use. Microscopic charcoal influx increases to reach the first notable peak of the series at c. 3750 cal yr BP (Fig. 3), when macroscopic charcoal is also abundant (Fig. 5). Therefore, regional fire occurrence was relatively high, and fires affected areas close to Lago de Isoba. The *Sporormiella* t. record is more continuous featuring intermediate values (Fig. 4) suggesting moderate pastoralism.

A further decrease in tree pollen followed by a slight recovery characterise ISB-5 (238–132 cm, 2450–1150 cal yr BP; Fig. 3). *Pinus* pollen abundances are moderately high but fluctuate markedly for most of this LPAZ and eventually decline at c. 1150 cal yr BP (Fig. 3, Fig. S1). Deciduous *Quercus* and *Betula* are less abundant than *Pinus* but still quite relevant. *Fagus* reaches its rational limit (steeper curve) at c. 1700 cal yr BP, indicative of its mass expansion. Among the shrubs, Ericaceae continue increasing whereas *Corylus* decreases further. The main herbs are Poaceae, *Rumex acetosa/acetosella* t., Apiaceae and *Plantago alpina* t. (Fig. 4). Cultural indicators follow an increasing trend interrupted by a transient decrease towards the end of the zone (Fig. 4). The *Pinus* stomata and macrofossil records mostly match the pollen curve (Fig. 3), with their most recent presence in the entire record at c. 1250 and 1400 cal yr BP, respectively (Fig. 6). Pinewoods collapsed stepwise, while heathlands and meadows expanded at their expense under increasingly heavier land use. Microscopic charcoal influx reaches its absolute maximum (Fig. 3), suggesting high regional fire occurrence. *Sporormiella* t. influx shows an almost continuous curve featuring moderate values (Fig. 4).

Herb pollen (mainly Poaceae, *Rumex acetosa/acetosella* t., *Artemisia*, Apiaceae and *Plantago alpina* t.) clearly dominates (Fig. 4) during ISB-6 (132–68 cm; 1150–450 cal yr BP) after the sustained drop in tree pollen (Fig. 3). *Pinus* pollen abundances are very low, and *Betula*, deciduous *Quercus*, *Fagus* and *Corylus* all decrease significantly (Fig. 3). *Castanea* has a continuous curve suggestive of its presence in the study area



**Fig. 6.** Proxies for vegetation dynamics at Lago de Isoba and their drivers. Dots denote presence of *Pinus* stomata, and *Pinus* and *Betula* macrofossils ('MF'), attesting to their local presence. Pollen percentages include the most relevant trees (*Pinus*, *Betula*, *Quercus robur* t., *Fagus*), shrubs (*Juniperus* t., *Corylus*, Ericaceae undiff. *Calluna vulgaris*), herbs (Poaceae, *Artemisia*, Chenopodiaceae), and anthropogenic indicator taxa (*Cerealia* t., *Plantago lanceolata* t., *Urtica dioica* t., *Castanea sativa*). *Sporormiella* t. influx (spores  $\text{cm}^{-2} \text{yr}^{-1}$ ) is used as a proxy for grazing activity. Microscopic charcoal influx (particles  $\text{cm}^{-2} \text{yr}^{-1}$ ) is a proxy for regional fire occurrence. The summary pollen diagram (total tree, shrub and upland herb pollen percentages) provides an overview of vegetation structure. Chronomid-based reconstructions of mean July air temperatures ( $^{\circ}\text{C}$ ) at three high-elevation sites of southern Europe: Basa de la Mora (Tarrats et al., 2018) in the central Pyrenees, Laguna de la Roya (Muñoz Sobrino et al., 2013) in the Sanabria Mountains of north-western Iberia and Lago Verdaro in the Northern Apennines (Samartin et al., 2017). LPAZ: local pollen assemblage zones of the Lago de Isoba pollen record. Chronostratigraphic division of the Late-glacial and the Holocene according to Rasmussen et al. (2014) and Walker et al. (2019), respectively.

(Fig. 3), and *Cerealia t.* and *Plantago lanceolata t.* show remarkable increases (Fig. 4). The most noticeable macrofossil finds are *Betula* fruits, Poaceae/Cyperaceae remains and the first fragments of Ericaceae (Fig. 5). All the evidence points to further woodland clearance and the expansion of pasturelands and heathlands. Microscopic charcoal influx decreases to moderate values suggesting lower fire occurrence, and higher *Sporormiella t.* abundances since c. 750 cal yr BP suggest heavier pastoral farming.

Herb pollen continues dominating during ISB-7 (68–0 cm; 450 cal yr BP—present), although with lower abundances (mainly Poaceae and *Rumex acetosa/acetosella t.*; Fig. 4). Meanwhile, shrub pollen (*Juniperus*, Ericaceae and *Calluna*) increases, and tree pollen (mainly deciduous *Quercus* and *Fagus*) remains stable until the significant rise of the past few decades (Fig. 3). *Castanea* continues spreading, *Olea* reaches the rational limit, indicative of its regional expansion, and *Cerealia t.* and *Plantago lanceolata t.* reach their highest abundances (Fig. 4). Only few shrub macrofossils were found (Fig. 5). The landscape was dominated by mountain meadows with sparse small woods and mountain scrub under intense farming, both arable and pastoral. Microscopic charcoal influx mostly remains low to moderate (Fig. 3). The high values during the past few decades seem an artefact due to unrealistically low deposition times at the top of the sequence. *Sporormiella t.* influx reaches its maximum (Fig. 4), suggesting heavy grazing.

## 4. Discussion

### 4.1. Abrupt and rapid vegetation changes in response to Late-glacial climate variability

The age-depth model, the lithology (i.e., highly inorganic sediment; Fig. 2) and the pollen stratigraphy (i.e., steppe-like vegetation; Figs. 4 and 6) together allow assigning the basal section of the Lago de Isoba pollen record to the Heinrich Stadial 1, which is usually named Oldest Dryas in terrestrial records (Naughton et al., 2009, 2016) and roughly corresponds to the GS-2.1a (Rasmussen et al., 2014). During the Oldest Dryas, the Lago de Isoba catchment was covered by steppe-like vegetation dominated by Poaceae and xerophytes, and the treeline was probably at lower elevation (Figs. 4 and 6). The occurrence of *Cerealia t.* pollen in the Late-glacial sediments of Lago de Isoba (from the Heinrich Stadial 1/Oldest Dryas to the Younger Dryas) is certainly not associated with agricultural activities, given the lack of other unambiguous cultural indicators in the corresponding pollen assemblages (Figs. 4 and 6) and taking into account that the regional archaeological record places the onset of Neolithic farming several millennia later, at c. 7500–7000 cal yr BP (Fano et al., 2015) and even more recently, at c. 6000–4500 cal yr BP, in the mountain areas (Peña-Chocarro et al., 2005; González-Álvarez, 2019). Thus, these Late-glacial *Cerealia t.* pollen grains could be assigned to wild grasses that share such pollen morphology like *Glyceria* and several wild relatives of the cultivated cereals (Beug, 2004), which thrive in wetlands and disturbed habitats, respectively. The rather high *Pinus* pollen abundances recorded during this period can be explained by upward long-distance transport from the foothills of the Cantabrian Range where pioneer trees like pines were already able to thrive (Houston Durrant et al., 2016). This is supported by previous studies on modern pollen—vegetation relationships that have documented the deposition of substantial amounts of pollen from lower vegetation belts transported by upslope winds (e.g., Andrade Olalla et al., 1994; Morales-Molino et al., 2020; Senn et al., 2022). Further, regional pollen signal is larger in sites lacking closed forest cover (no ‘screen effect’; Lang et al., 2023b), and *Pinus* pollen may also be overrepresented in lakes when the water table oscillates significantly (likelier under dry conditions; Castro-Parada and Muñoz Sobrino, 2022). Pollen-inferred vegetation reconstruction around Lago de Isoba suggests cold temperatures and reduced moisture availability during the Oldest Dryas. The chironomid-inferred summer temperature reconstruction from Laguna de la Roya, a glacial lake (1608 m a.s.l.) 160 km southwest of Lago de

Isoba (Fig. 1) also shows that cold conditions (up to 4 °C colder than during the subsequent Bølling-Allerød interstadial –GI-1) prevailed during the Oldest Dryas (Fig. 6; Muñoz Sobrino et al., 2013), as also depicted by other palaeoclimatic reconstructions from southern Europe (Moreno et al., 2010; Naughton et al., 2016; Samartin et al., 2017; Finsinger et al., 2019). Other palaeoecological records from northern Iberia revealed that steppe-like vegetation was the main feature in the landscape of the Cantabrian Range and adjacent mountains (Allen et al., 1996; Muñoz Sobrino et al., 1997, 2001, 2004, 2007; Sánchez-Morales et al., 2022), and the Pyrenees (Montserrat Martí, 1992; González-Sampérez et al., 2006, 2017; Gil-Romera et al., 2014) during this period. Interestingly, Oldest Dryas pollen assemblages from Lago de Isoba associated with steppe-like vegetation are very similar to those of present-day alpine grasslands in the Alps but with higher abundances of Chenopodiaceae and *Artemisia* pollen (Furlanetto et al., 2019). Marine records off north-western Iberia allowed subdividing the Heinrich Stadial 1 (= Oldest Dryas) in up to three different phases according to regional pollen-inferred vegetation shifts (Naughton et al., 2007, 2009, 2016). The conspicuous dominance of steppe taxa, the scarcity of Ericaceae and the moderate abundances of *Pinus* in the pollen assemblages of ISB-1a suggest that the bottom of the Lago de Isoba pollen record may correspond to the most recent phase of the Heinrich Stadial 1 according to Naughton et al. (2016), although the chronology at Lago de Isoba for this section is not sufficiently well constrained to be certain about this correlation.

At the onset of the Bølling-Allerød interstadial at c. 14,500 cal yr BP, *Juniperus* expanded significantly around the site, with *Betula* establishing shortly after (Fig. 6). The remarkable spread of *Juniperus* and *Betula* strongly points to notably warmer temperatures around Lago de Isoba at the onset of the Bølling-Allerød (≈ GI-1) interstadial (c. 14,650–12,850 cal yr BP; Rasmussen et al., 2014). The chironomid record from Laguna de la Roya allows quantifying the magnitude of such notable and rapid warming, indicating that summer air temperatures raised c. 2.5–4 °C with respect to the Oldest Dryas (Muñoz Sobrino et al., 2013). Sea surface temperatures also increased significantly in the region during the Bølling-Allerød interstadial (Naughton et al., 2016). Our pollen data also suggest that warming was accompanied by higher precipitation, which was probably key to triggering the spread of woody taxa on the southern slopes of the Cantabrian Range (Iriarte-Chiapusso et al., 2016). A similar *Juniperus* peak, both in pollen percentages and accumulation rates, occurred at Laguna de la Roya but c. 750 years earlier (Muñoz Sobrino et al., 2013). The location of Laguna de la Roya in the Galician-Duero Mountains, probably closer to the glacial refugia for trees and with a milder more oceanic climate, might have enabled an earlier expansion of woody taxa. Nonetheless, we cannot exclude that the uncertainties inherent to the Late-glacial chronologies (often spanning several centuries) may result in the temporal mismatch of the *Juniperus* peak between these two sites. Most palaeoecological sites investigated so far in northwestern Iberia did not feature any significant spread of *Juniperus* during the Bølling-Allerød interstadial (Muñoz Sobrino et al., 1997, 2007; Ramil Rego et al., 1998; Iriarte-Chiapusso et al., 2016). However, the Laguna del Miro and Laguna del Castro pollen records represent a remarkable exception, as they both feature a major expansion of *Juniperus* during the last deglaciation (Jalut et al., 2010). Unfortunately, the chronologies of these two sequences for this period are based on pollen stratigraphy, which prevents comparing the timing of such *Juniperus* spreads to Lago de Isoba (Fig. 1). In the Pyrenees, a slight *Juniperus* spread occurred at sites located across an elevation transect spanning from Lake Estanya (670 m a.s.l.; González-Sampérez et al., 2017) to El Portalet mire (1802 m a.s.l.; González-Sampérez et al., 2006; Gil-Romera et al., 2014). Further north, primary succession involving a *Juniperus* mass expansion followed by *Betula* is typical of the Central European lowlands north of the Alps, where it occurs nearly synchronously at c. 14,600–14,500 cal yr BP (e.g., Lotter, 1999; Ammann et al., 2013; Rey et al., 2017). Altogether, these data suggest that the *Juniperus* expansion was more marked in areas probably still featuring relatively strong

continentality during the Bølling-Allerød interstadial, like the southern slopes of the Cantabrian Range where Lago de Isoba is located. That would also explain the much slighter expansion of *Juniperus* at lower-elevation sites located in more oceanic mountains of north-western Iberia. Certainly, this will become clearer as more well-dated and detailed Late-glacial records from the Cantabrian Mountains become available. Following the abovementioned expansion of *Juniperus*, a boreal-like forest spread started at c. 14,000 cal yr BP, involving *Betula* first and *Pinus* soon after, which benefitted from the warmer temperatures and higher water availability of the Bølling-Allerød interstadial to migrate upwards (Fig. 6). Macrofossil evidence indicates that both birch and pine woods reached the elevation of Lago de Isoba, although quite low pollen influx points to these occurring at low densities (sparse individuals or small stands; Fig. S1). Findings of *Populus* macrofossils support the presence of *Populus tremula* in these woods (Fig. 5). At lower elevation, oak woodlands expanded. Regional pollen records show that this pattern of forest succession was widespread across northwestern Iberia (Muñoz Sobrino et al., 2007; Naughton et al., 2016).

Pine-birch woodlands opened, and steppe-like vegetation re-expanded around Lago de Isoba at c. 12,750–11,550 cal yr BP (Figs. 3, 4 and 6), suggesting a return to cold and dry conditions. These vegetation shifts perfectly match the Younger Dryas stadial in most European records (c. 12,800–11,600 cal yr BP; Mangerud, 2021), which corresponds to the Greenland Stadial 1 (GS-1, c. 12,850–11,650 cal yr BP; Rasmussen et al., 2014). Regional palaeoclimatic reconstructions using lake and speleothem proxies also showed that significantly cooler (summer temperatures 2–2.5 °C lower than in the Bølling-Allerød) and drier conditions prevailed during this phase (Muñoz Sobrino et al., 2013; Baldini et al., 2015, 2019). The replacement of boreal woodlands with steppe vegetation during the Younger Dryas was a widespread phenomenon in the mountains of Southern Europe and much of Central and Western Europe (e.g., Muñoz Sobrino et al., 2007; Iriarte-Chiapusso et al., 2016; Rey et al., 2017; Morales-Molino et al., 2021; Sánchez-Morales et al., 2022; Lang et al., 2023c). It is worth noting that *Pinus* was much less affected than *Betula* by the Younger Dryas climatic reversal, not only around Lago de Isoba (Fig. 6) but in other sites of north-western Iberia (e.g., Allen et al., 1996; Muñoz Sobrino et al., 2004; Sánchez-Morales et al., 2022), probably because of *Pinus*' higher tolerance to frost and drought (Costa et al., 2005; Houston Durrant et al., 2016).

#### 4.2. Early and Mid-Holocene mixed pine-broad-leaved deciduous mountain forests under warmer climate and low human impact

Well-developed mixed pine-broad-leaved deciduous mountain forests spread around Lago de Isoba at the onset of the Holocene (Figs. 3, 5 and 6), suggesting warmer and moister conditions. These mountain forests were probably mosaic-like, with *Pinus*, *Betula* and deciduous *Quercus* (co-)dominating depending on the local micro-environmental conditions (e.g., aspect, soil development and water holding capacity, soil pH, air moisture and temperature) and disturbance occurrence. Nevertheless, these main tree species could also have formed truly mixed woodlands, as it happens today (Costa et al., 2005). The regular finds of *Pinus* stomata and macrofossils when pollen abundances are ~35% support the presence of pine trees in the Lago de Isoba catchment and show that moderate *Pinus* pollen abundances can be associated with local pine occurrence and are not the result of long-distance transport (Fig. 6). Similarly, rather high deciduous *Quercus* pollen accumulation rates (1000–2500 grains cm<sup>-2</sup> yr<sup>-1</sup>) point to the presence of deciduous oaks near or even within the lake catchment, probably growing at the warmest and relatively dry microsites (Lotter, 1999; Tinner et al., 2009). Rapid afforestation involving mostly *Betula*, deciduous *Quercus* and *Pinus* was widespread in northern Iberia at the onset of the Holocene (Muñoz Sobrino et al., 1997, 2007; Ramil-Rego et al., 1998; Iriarte-Chiapusso et al., 2016; Sánchez-Morales et al., 2022). Deciduous

*Quercus* and *Betula* dominated since the beginning of the Holocene in oceanic settings of the Cantabrian Range and adjacent areas, usually with *Quercus* further expanding during the Early Holocene (Allen et al., 1996; Muñoz Sobrino et al., 1997, 2001, 2007, 2012; Sánchez-Morales et al., 2022). Meanwhile, *Pinus* persisted as dominant or co-dominant in woodlands located at higher elevation and more continental areas (Fombella et al., 2001; Muñoz Sobrino et al., 2004; García-Rovés, 2007; Jalut et al., 2010; Rubiales et al., 2010; Carrión et al., 2022). Another remarkable feature of Early Holocene vegetation dynamics at Lago de Isoba is the *Corylus* spread around 10,500 cal yr BP (Figs. 3 and 6). A delayed and/or limited expansion of *Corylus*, compared to Central and Western Europe (Lang et al., 2023c), occurred over vast areas of the Cantabrian Range (e.g., Allen et al., 1996; Jalut et al., 2010; Muñoz Sobrino et al., 2012; Iriarte-Chiapusso et al., 2016; Sánchez-Morales et al., 2022) and the southern Alps (Finsinger et al., 2006; Giesecke et al., 2011). Harsh winters might have hindered *Corylus avellana* expansion at the onset of the Holocene in these areas.

Around 11,650 cal yr BP (Younger Dryas-Holocene transition; Walker et al., 2019), numerous palaeoclimatic reconstructions based on various proxies also documented significant warming all over Europe (e.g., Samartin et al., 2012; Muñoz Sobrino et al., 2013; Rasmussen et al., 2014; Heiri et al., 2015; Tóth et al., 2015; Gomes et al., 2020; Bernal-Wormull et al., 2023). Specifically, chironomid-inferred summer air temperature increased ~2 °C at the beginning of the Holocene at Laguna de la Roya in northwestern Iberia (Fig. 6; Muñoz Sobrino et al., 2013), and a warming of similar magnitude was reconstructed at Lago Verdaro (~1.5–4 °C) in the Northern Apennines (Fig. 6; Samartin et al., 2017). Interestingly, such large warming meant reaching pre-industrial summer temperatures between 11,000 and 10,500 cal yr BP. Concerning the hydroclimate, regional studies on speleothems, lake levels and pollen suggest that precipitation increased during the Early Holocene, particularly in winter (Smith et al., 2016; Morellón et al., 2018; Rossi et al., 2018; Baldini et al., 2019).

Closed forests mainly consisting of *Pinus*, *Betula* and deciduous *Quercus*, likely with well-developed *Corylus* thickets in the understory continued dominating the vegetation in the Lago de Isoba area for several millennia during the Mid-Holocene (Fig. 6). Macrofossil and stomata evidence allows specifying that *Pinus* and *Betula* were present in close proximity to the lake (Figs. 5 and 6). The seemingly long gap in *Pinus* macroscopic remains between c. 8400 and 6250 cal yr BP (470–424-cm depth) is an artefact created by the lack of macrofossil samples in this section, hence it does not mean that *Pinus* was absent (Figs. 5 and 6). In fact, the almost continuous record of *Pinus* stomata during this period attests to the continued local presence of pine stands or forests in the catchment (Figs. 3 and 6). In continental settings of northern Iberia, pine- and birch-dominated forests persisted for millennia well into the Mid-Holocene and even the Late Holocene, according to the available pollen (Fombella et al., 2001; Muñoz Sobrino et al., 2004; García-Rovés, 2007; Jalut et al., 2010; Morales-Molino et al., 2011, 2017, 2022; Carrión et al., 2022) and macrofossil records (Rubiales et al., 2008, 2010; Ezquerro et al., 2019). Since c. 9250 cal yr BP, regional and local fire occurrence followed a gentle but steady increasing trend (Fig. 6), in a context of enhanced summer drought as suggested by the spread of *Corylus* at the expense of deciduous *Quercus* (Sánchez Goñi et al., 2018). The multi-proxy record of Lago Enol, on the northern slope of the Cantabrian Range, also suggests a tendency towards drier summer conditions during the Mid-Holocene (Moreno et al., 2011), which might have promoted wildfire occurrence and spread around Lago de Isoba during this period. Agriculture started in the Cantabrian region around 7700–6800 cal yr BP (Fano et al., 2015), but reached the uplands of the Cantabrian Range only around 5500 cal yr BP (González-Álvarez et al., 2016; González-Álvarez, 2019). The first clear palynological evidence of farming at Lago de Isoba (i.e., unambiguous cultural indicators assemblages) dates to c. 5100 cal yr BP (Fig. 6). Therefore, the increase in fire occurrence during the Mid-Holocene at Lago de Isoba may first have been primarily associated with favourable

climatic conditions (enhanced summer drought), and it was only at a later stage that human agency took over as the main cause of fire ignition and spread.

#### 4.3. Anthropogenic impact and deforestation during the Late Holocene

The transition from the Middle to the Late Holocene (c. 5100–4250 cal yr BP) featured crucial ecosystem changes around Lago de Isoba. Fires became more frequent and the gradual increase in both primary and secondary cultural indicators since c. 5100 cal yr BP indicates that anthropogenic disturbance increased during the Neolithic (Fig. 6). Additionally, faster deposition of more clayey sediment indicates enhanced runoff and erosion in the lake catchment caused by the beginning of anthropogenic forest clearance (Fig. 2; Table S1). Despite the latter, rather closed forests continued dominating, albeit with substantial changes in their composition (Fig. 6). Overall, *Pinus sylvestris* expanded at the expense of *Betula* and *Corylus*, following the usual secondary succession path in the cool-temperate mountains of northern Iberia (Costa et al., 2005) associated with the higher shade-tolerance of *Pinus sylvestris* (Beck et al., 2016; Enescu et al., 2016). Fires occurring during the Mid-to-Late Holocene transition were apparently of low severity because they did not trigger notable changes in vegetation composition and structure (Fig. 6). These wildfires detected in the microscopic charcoal record may therefore have corresponded to surface fires, which would have promoted *Pinus sylvestris* dominance because: (i) *Pinus* seedling recruitment is favoured by removing the litter and competition by the herbaceous layer, and (ii) adult trees withstand these fires thanks to their thick bark, thus maintaining an understory too shaded for *Betula* and *Corylus* to regenerate (Agee, 1998; Tapias et al., 2004). Alternatively, or rather complementarily, fires could have affected more severely the sites where *Betula* was dominant. The ecosystem changes described above were probably driven mostly by anthropogenic impact, more specifically by the establishment of Neolithic farming in the Lago de Isoba area. Neolithic farming spread in the highlands of the Cantabrian region between c. 6000–4500 cal yr BP according to the first archaeological evidence of agricultural and pastoral farming, and even later at the highest elevation sites, where Neolithic is usually associated with megalith construction (Peña-Chocarro et al., 2005; González-Álvarez et al., 2016; González-Álvarez, 2019; Fano and Cubas, 2021). Further, previous research has also shown that the first Neolithic farming communities introduced the use of fire to clear forests and establish and maintain pastures in the Cantabrian Range (Carracedo et al., 2018). However, we cannot discard that decreasing seasonality during the Middle and Late Holocene (driven by the decreasing difference between summer and winter insolation; Laskar et al., 2004) played a role in some of the vegetation changes observed. Proxy data like the chironomid-inferred July air temperatures from Basa de la Mora and Lago Verdadero indeed show a cooling trend during the Late Holocene (Fig. 6; Samartin et al., 2017; Tarrats et al., 2018).

The influence of climate on the Late Holocene vegetation dynamics at Lago de Isoba was blurred by the more prominent impact of human activities. The first remarkable forest opening, which started at c. 4250 cal yr BP, was synchronous with increasing wildfire occurrence and farming (both arable and pastoral; Fig. 6). The palaeoecological record of Lago de Isoba therefore indicates that during the Bronze Age (c. 4000–2900 cal yr BP in the Cantabrian Range; González-Álvarez, 2019) increased land use involved the use of fire to clear forests and establish agricultural fields and pasturelands (Fig. 6; Arias Cabal, 1999; Blas Cortina, 2014). The relatively limited transport of *Sporormiella* dung fungal spores (e.g., Gill et al., 2013; Baker et al., 2016) indicates that pastoral activities, probably transhumance, occurred locally during this period. Recent palaeoecological research places the beginning of pastoralism and agriculture in northern Spain around 7300 and 6700 cal yr BP respectively (López-Merino et al., 2010; Iriarte-Chiapusso et al., 2016; Sánchez-Morales et al., 2022), much earlier than previously

assumed (Zapata et al., 2004). The lag of about 2000 years between these early indications of farming in the region and our findings could be related to the lower suitability of the Lago de Isoba area for agriculture because of the relatively cold temperatures. In line with this, Carracedo et al. (2018) interpreted the asynchronous patterns of fire occurrence at different sites in the Cantabrian Range as reflecting the spatial heterogeneity of land-use intensity in the region. Following this moderate deforestation phase, pinewoods recovered between c. 3600 and 3300 cal yr BP benefitting from lower land-use intensity and reduced wildfire occurrence (Fig. 6). Pinewood dominance in the landscape around Lago de Isoba lasted until c. 2500 cal yr BP (Fig. 6, Fig. S1). *Pinus sylvestris* was probably able to recolonise the forest openings and took advantage of its adaptation to surface fires and cooler summers (Houston Durrant et al., 2016). Ericaceae underwent their first minor expansion in parallel to pinewoods, probably establishing in the understory (Fig. 6).

Forests were again cleared using fire to develop farming activities at c. 2500 cal yr BP, during the Iron Age (c. 2900–2300 cal yr BP; Fig. 6). Deforestation affected particularly pinewoods, whereas *Betula* slightly expanded (Fig. 6). The Iron Age in the Cantabrian region (c. 2900–2300 cal yr BP) was characterised by the construction of hillforts (locally known as ‘castros’), that is, permanent highly fortified settlements on prominent and usually highly visible sites (Celis and Muñoz, 2015). One of these hillforts was less than 2 km away from Lago de Isoba (Vidal, 2015). Additionally, secondary temporary settlements were built up in the mountains to be used in summer, associated with the increasing development of valley-transhumance (González-Álvarez et al., 2016). Partial woodland recovery occurred a couple of centuries later, at c. 2200 cal yr BP, during the transition between the Iron Age and the Roman Period. Historical sources report lower population density in the Lago de Isoba area resulting from the Roman conquest of this territory (Peralta Labrador et al., 2019; Menéndez Blanco et al., 2020). During the peak of the Roman period (c. 1800 cal yr BP, 150 CE), pinewoods were again cleared using fire, but in this case mountain shrublands (Ericaceae, *Juniperus*) established and *Betula* did not spread (Fig. 6, Fig. S1). This vegetation shifts strongly suggest higher-intensity wildfires during this period, probably crown fires that hampered the recruitment of a non-serotinous pine such as *Pinus sylvestris*. In contrast, deciduous *Quercus*, probably inhabiting lower elevation areas, were largely unaffected by increasing land use and fire occurrence during this period, and even spread slightly (Fig. 6, Fig. S1). *Quercus* species thriving in the region, particularly *Quercus pyrenaica*, are excellent resprouters (Calvo et al., 2003; Huerta et al., 2022) that may have withstood quite well and even benefitted from anthropogenic disturbance. The local establishment and initial expansion of *Fagus sylvatica* started shortly after, at c. 1700 cal yr BP (250 CE; Figs. 3 and 6). The Late Holocene spread of *Fagus* in northern Iberia was synchronous with episodes of deforestation and heathland expansion (García Antón et al., 1997; Muñoz Sobrino et al., 2009; Carracedo et al., 2018). *Fagus* is very sensitive to late frost and drought, so decreasing seasonality in temperature and the resulting higher water availability may have favoured its spread (Ascoli et al., 2013; Maringer et al., 2016). Additionally, under such favourable climatic conditions, the great recruitment capacity of *Fagus sylvatica* could have enabled it to colonise the openings left in the forests by previous wildfires. Actually, in the Northern Apennines *Fagus* spread during the Late Holocene under similar conditions, that is, anthropogenic fire disturbance and cooler and wetter summers (Morales-Molino et al., 2021).

Between c. 1600 and 1150 cal yr BP (400–800 CE), a noticeable forest recovery involving mostly pinewoods occurred around Lago de Isoba, probably related to decreased human impact following the collapse of the Western Roman Empire and the Migration Period (e.g., Martín-Chivelet et al., 2011; Helama et al., 2017). After this wooded stage, *Pinus sylvestris* and deciduous *Quercus* woodlands declined rapidly at c. 1150 cal yr BP (800 CE), during the Early Middle Ages (Fig. 6, Fig. S1). Heavy land use involving both agriculture and pastoralism nearly led to the regional extirpation of pinewoods (Fig. 6). Several

studies hypothesised that mountain pinewoods disappeared from vast areas of the Cantabrian Range as a result of human activity, fire and grazing (Muñoz Sobrino et al., 2004; Rubiales et al., 2008; Jalut et al., 2010; Ezquerro et al., 2019). The high-resolution palaeoecological record from the close Lago del Ausente (3 km west of Lago de Isoba at 1740 m a.s.l.) supported the previous hypothesis based on the evidence provided by proxies for fire and grazing (Morales-Molino et al., 2022). Further, Morales-Molino et al. (2022) proposed that recurrent crown fires set deliberately by the local shepherds triggered the pinewood demise. At the time of the final *Pinus* demise (c. 1050–850 cal yr BP; 900–1100 CE) around Lago del Ausente, temperatures were quite warm and thus favourable for fire spread (Medieval Climate Anomaly; Moreno et al., 2012; Abrantes et al., 2017) even if pastoral activities were not peaking (Morales-Molino et al., 2022). Our data from Lago de Isoba also suggest that intense wildfires alongside high grazing pressure drove the *Pinus* demise (Fig. 6).

In the Teleno and the Sanabria Mountains (~100–150 km southwest of Lago de Isoba; Fig. 1) pinewoods drastically declined after c. 3200 and 3000 cal yr BP respectively (Allen et al., 1996; Morales-Molino et al., 2011), earlier than at Lago de Isoba. The main regional vegetation changes were therefore neither synchronous nor parallel, which further supports local anthropogenic forcing. Woodlands were replaced with meadows, mountain scrub (Ericaceae, *Juniperus*) and crops (Cerealia, *Cannabis*, *Castanea*), while more disturbance-tolerant trees (*Fagus*) expanded (Fig. 6). During the Middle Ages, the highest development of pastoral and agricultural farming was not accompanied by increasing fire activity (Fig. 6). The limited number of regional fire history reconstructions based on sedimentary charcoal hint at site-specific asynchronous developments (e.g., García Antón et al., 1997; Carracedo et al., 2018; Morales-Molino et al., 2022; Sánchez-Morales et al., 2022). Since the Middle Ages, metal mining arose in northern Iberia, impacting the landscapes by overexploitation of forests to serve steel, coal and naval industries (Ceballos Cuerno, 2001; Arias Cabal, 2005; Blas Cortina, 2014; Carracedo et al., 2018). In summary, present-day vegetation at our study site established quite recently although as an endpoint of millennia of intense human impact.

## 5. Conclusions

We found rapid landscape changes around Lago de Isoba in response to the Late-glacial and Early Holocene abrupt climate changes: local steppe during the Heinrich Stadial 1/Oldest Dryas, boreal forest expansion during the Bølling-Allerød interstadial, steppe re-expansion during the Younger Dryas and local afforestation at the onset of the Early Holocene. An unexpectedly marked *Juniperus* expansion occurred at the onset of the Bølling-Allerød interstadial in response to climate warming and increasing water availability, strongly resembling central European lowland records (Lotter, 1999; Ammann et al., 2013; Rey et al., 2017).

Limited fire occurrence throughout the Late-glacial and Early Holocene shifted to higher levels only when humans began to use fire as a tool to open forests around 5000 years ago. During the Mid-Holocene, mixed pine-birch mountain forests with hazel established and persisted for several millennia. From c. 5100 cal yr BP onwards, the role of climate in shaping the mountain landscapes of the Cantabrian Range progressively decreased in importance as human impact gained. Available evidence strongly suggests that the deforestation, the intensification of fire occurrence, the substantial changes in taxonomic composition, the higher grazing activity and the increased erosion documented by the Lago de Isoba palaeoecological record were mainly caused by the intensification of land use during the past few millennia.

*Pinus sylvestris* was a key component of the regional vegetation since the beginning of the record and was locally present from c. 10,850–1250 cal yr BP. *Pinus* slightly benefitted from anthropogenic influence when this released low-intensity disturbances (e.g., c. 3600–3300 cal yr BP), but later (after c. 1150 cal yr BP) underwent a

rapid decline to near local extirpation when farming intensified causing widespread forest clearance.

Millennia of anthropogenic activity have largely altered the landscape and explain why the present-day vegetation (fairly open with pasturelands and shrublands) is so different from its potential natural state (Morales-Molino et al., 2022). Our data thus highlight the relevance of taking into consideration the impact of historical land use on vegetation when planning ecosystem restoration, as pre-disturbance communities can be almost completely missing in the target area today (e.g., mountain pinewoods in the Cantabrian Range). Moreover, the high degree of disturbance that features the present-day vegetation around Lago de Isoba makes it difficult to predict how the surrounding landscape will respond to ongoing climate change. Future research might aim at filling this gap using high-resolution analyses that include quantitative temperature reconstructions to develop species response curves (e.g., Colombaroli et al., 2010; Morales-Molino et al., 2021) and dynamic vegetation modelling to better assess past and future ecosystem responses to climate change and disturbance (e.g., Henne et al., 2015; Schwörer et al., 2024).

## CRediT authorship contribution statement

**Anouk van der Horst:** Investigation, Formal analysis, Visualization, Writing – original draft. **Willy Tinner:** Conceptualization, Funding acquisition, Writing – Review and editing. **F. Javier Ezquerro:** Writing—Review and editing. **Erika Gobet:** Investigation, Writing – Review and editing. **André F. Lotter:** Investigation, Writing – Review and editing. **Mario Morellón:** Investigation, Funding acquisition, Writing – Review and editing. **Castor Muñoz Sobrino:** Writing—Review and editing. **Carole Niffenegger:** Investigation, Writing – Review and editing. **Christoph Schwörer:** Investigation, Writing – Review and editing. **Sönke Szidat:** Investigation, Writing – Review and editing. **César Morales-Molino:** Conceptualization, Supervision, Investigation, Visualization, Data curation, Project administration, Writing – original draft.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

The data will be made available upon acceptance in the European Pollen Database, a constituent database of Neotoma Palaeoecology Database (<https://www.neotomadb.org/>)

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## Appendix A. Supplementary data

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