1   **Grazing activities in the southern central Pyrenees during the last millennium as deduced from**

2   **the non-pollen palynomorphs (NPP) record of Lake Montcortès**

3   Encarni Montoya[1,2,*], Valentí Rull[1,2], Teresa Vegas-Vilarrúbia[3], Juan Pablo Corella[4], Santiago

4   Giralt[2] and Blas Valero-Garcés[5]

5   [1] Botanic Institute of Barcelona (IBB-CSIC-ICUB), Passeig del Migdia s/n, 08038 Barcelona (Spain)

6   [2] Present address: Institute of Earth Sciences Jaume Almera (ICTJA-CSIC) Lluis Sole i Sabaris s/n,

7   08028 Barcelona (Spain)

8   [3] University of Barcelona, Av. Diagonal 645, 08028 Barcelona (Spain)

9   [4] Institute of Physical Chemistry Rocasolano (IQFR-CSIC), c. Serrano 119, 28006 Madrid (Spain)

10   [5] Pyrenean Institute of Ecology (IPE-CSIC), Av. Montañana 1005, 50059 Zaragoza (Spain)

11   * Corresponding author: emontoya@ictja.csic.es

12

13   **Abstract**

14   Human activities during the last millennium have shaped most of the present-day landscapes.

15   During this time, in the southern central Pyrenees several climate periods and phases of variable

16   human disturbance have driven varied landscape responses. In previous studies of the sediment

17   deposits in Lake Montcortès (southern central Pyrenees) several climatic shifts (including the

18   Medieval Climate Anomaly and the Little Ice Age), as well as forest clearance by fire, agriculture

19   and cattle raising as the main human impacts were recorded since Medieval times. In this work

20   we use non-pollen palynomorphs (NPP) on the same sequence to reconstruct the different

21   human activities, with a special focus on grazing, at an average resolution of around 30 years

22   per sample. Independent NPP proxies for fire and forest clearance were found, supporting

23   former studies. Moreover, the NPP record shows four periods of high abundance of

24 coprophilous fungi: 1) 830 - 865 CE); 2) 1120 - 1290 CE, 3) 1530 - 1795 CE; and 4) 1865 - 1880

25 CE. These four periods correspond to phases of increased livestock farming, as reported in

26 historical documents. Comparison of pollen, historical documents, and NPP records show that

27 the impact on landscape dynamics during the last millennium have been mostly related to

28 variable human population density controlled by historical, political and cultural changes in the

29 Pyrenean mountains. Moreover, the use and comparison of several independent proxies have

30 highlighted the strength of the indicator value obtained.

31 **Keywords:** fires; forest clearance; human disturbance; livestock; non-pollen palynomorphs;

32 Pyrenees.

33

34 **1. Introduction**

35 During the last decades, the study of past vegetation history has been highlighted as essential

36 for the understanding of current and future biodiversity and ecosystem dynamics (Willis et al.

37 2007; Rull 2012 IPCC 2013). These studies have provided information about past community

38 trends, allowing identification of the main drivers involved in vegetation changes as a response

39 to internal and external pressures (e.g., Vegas-Vilarrúbia et al. 2011, Pérez-Sanz et al. 2013).

40 Among these forcings, climate change and human activities have been the main factors

41 responsible for the shaping of current landscapes during the last millennia. However, the

42 coupled action of these drivers and their interactions often make it difficult to untangle the

43 climatic from anthropic signals in paleorecords. This handicap is especially problematic in studies

44 based on one or few related proxies due to eventual circular reasoning (Rull et al. 2011). The

45 analysis of microfossil remains of biological origin other than pollen and pteridophyte spores

46 present in palynological slides, known as non-pollen palynomorphs (NPP), has proved to be a

47 useful tool to disentangle the nature of the forcings involved (Loughlin et al. 2018). NPP provide

48 additional information due to their independent nature in relation to other proxies (van Geel

49   2001; Montoya et al. 2012). In this sense, NPP studies have been able to efficiently record the

50   human footprints on landscapes, mostly at local scales (deforestation, fire practices or grazing),

51   which can remain unnoticed using the usual proxies (van Geel et al. 1983, 2003).

52   NPP studies developed so far in the European mountains have demonstrated the intense human

53   management of these landscapes (Argant et al. 2006; Menozzi et al. 2010). In the Pyrenees (SW

54   Europe), where the present study is located, efforts have been focused on the reconstruction of

55   the human impact on vegetation changes during the last millennia. These studies have revealed

56   a wider range of activities than previously thought, including grazing, deforestation, agriculture,

57   hemp retting or mining (Riera et al. 2006; Cugny et al. 2010; Ejarque et al. 2009, 2010; Miras et

58   al. 2007, 2010; Rull and Vegas-Vilarrúbia 2014; Rull et al. 2011). According to these studies,

59   human activities are noticeable in the highlands since the start of Neolithic (ca. 6000 BCE). The

60   maximum level of human impact occurred during the last millennium (González-Sampériz et al.

61   2017). Moreover, the comparison among records has revealed asynchronies in human impact

62   between different study areas, and in some cases, even within the same study area. In these

63   cases, the local-scale information provided by the NPP (Ejarque et al. 2010; Miras et al. 2010)

64   highlighted the key role of social changes (cultural, political, and/or demographical) in shaping

65   the present-day landscapes.

66   The present paper is focused on the NPP analysis of the Lake Moncortès record (southern central

67   Pyrenees) during the last millennium. Previous studies of the lake sediment have provided

68   detailed understanding of the lake sedimentological, geochemical, paleolimnological and

69   paleoecological evolution during the last centuries (Corella et al. 2011, 2012, 2014, 2015, 2016,

70   2017; Rull and Vegas-Vilarrúbia, 2014, 2015; Rull et al. 2011; Scussolini et al. 2011, Vegas-

71   Vilarrúbia et al. 2018, Trapote et al. 2018). These studies revealed a complex interplay between

72   climate and human activities, sometimes in a synergistic fashion, in shaping modern landscapes.

73   A decisive advantage of the Montcortès sequence is the high chronological resolution provided

by their varved (annually laminated) sediments, which have led to a robust age model (Corella et al. 2012, 2014, 2016). A comprehensive review of historical documents (Rull et al. 2011; Rull and Vegas-Vilarrúbia, 2015 and literature therein) has also provided a detailed account of political, social and economic changes in the region. The aim of this paper is to obtain independent and complementary evidence for regional landscape management, with emphasis on grazing, pasture and fire history at a local scale based on the analysis of NPP. Also, the comparison of NPP data with other proxies contributes to clarify the interplay among the different drivers involved and, hence, to elucidate the human role in shaping the landscape.

2. Study Area

2.1. Geographic location

Lake Montcortès, thereafter LM (42°19'N - 0°59'E, 1027 m elevation), is a karstic lake located in the Pallars region (Catalonia), in the southern flank of the central Pyrenees, NE Spain (Figure 1). The lake is situated in a small catchment characterized by Triassic limestones, marls and evaporites, and Oligocene carbonatic conglomerates (Rosell 1994; Gutiérrez et al. 2012). LM has roughly a circular shape of 400-500 m diameter and a maximum water depth around 30 m near the center, which is fed mainly by groundwater, with intermittent smalls creeks and scattered springs (Camps et al. 1976; Modamio et al. 1988). The lake is located within the sub-Mediterranean bioclimatic domain, in a transitional climatic area with a strong rainfall gradient (Rull et al. 2011, 2017; Corella et al. 2012). Mean temperatures range from 1.9°C in January to 20.3°C in July (Annual average: 10.6°C). Total annual precipitation is 860 mm, being March (46.6 mm) and May (99.2 mm) the driest and wettest months respectively (Corella et al. 2011). The lake lies near the altitudinal boundary between the Mediterranean lowlands and the Middle Montane belt (Vigo 2008) and it is surrounded by three major forest communities: (i) Evergreen oak forests; (ii) Deciduous oak forests; and (iii) Conifer forests (Folch 1981). An exhaustive

4

99   floristic inventory of LM surroundings has been performed by Mercadé et al. (2013). Regarding

100   human occupation, the area is nowadays underpopulated compared to former periods and the

101   main economic activities are tourism and related services. Agricultural land uses are minor,

102   limited to cereal cultivation and livestock pastures (Rull et al. 2011).

103   2.2. Previous works on LM

104   Although detailed explanations of the different proxies used to date have been published

105   elsewhere (Table 1), a brief summary of the main environmental events inferred is provided

106   here in order to frame the interpretation of the results obtained in this study (Figure 2). During

107   the last two millennia, several intervals of low clastic inputs have been recorded and related to

108   the Iberian-Roman Humid Period (500 BCE – 400 CE), the Little Ice Age (LIA; c. 14th – 19th

109   centuries) and the last century, whereas periods of high clastic inputs have been related to the

110   Medieval Climate Anomaly (MCA, 9th – 13th centuries), and the end of the LIA (late 19th century).

111   Both intervals of high sediment delivery to the lake coincided with periods of intense farming

112   and high human pressure in the watershed. The anthropogenic impact on the landscape during

113   these periods was also revealed by the pollen record (Rull et al. 2011), and during the last 500

114   years, some of the anoxic processes registered at the lake were also linked to human activities

115   (Vegas-Vilarrúbia et al. 2018). Based on a detailed pollen analysis with species identification

116   thanks to an exhaustive botanical survey (Mercadé et al. 2013), two main phases of agricultural

117   development were registered, centered at 9th-14th (A1) and 16th-19th centuries (A2) (Fig. 2).

118   These two periods differed both in the cultivated species of interest and in the land use system

119   (such as fire clearance or rotation) (Rull and Vegas-Vilarrúbia 2015). Regarding climate, the

120   scarcity or absence of diatoms between 800 and 1250 CE has been considered indicative of low

121   lake levels during these periods (Scussolini et al. 2011). Since 1250 CE onwards, diatom

122   assemblages indicate a lake level recovery, with the occurrence of a short-lived drier and cooler

123   phase dated to 1335-1390 CE (Scussolini et al. 2011). In this sense, the detailed analysis of the

124 sediments evidenced two main periods of extreme multiple rainfall events centered at 927 to

125 1398 CE and 1844-1894 CE that coincided with historical floods from the nearby Segre River

126 (Corella et al. 2014, 2016). The pollen analysis of sediments corresponding to the last millennium

127 also record two major climatic shifts based on the vegetation dynamics: (i) a warmer and likely

128 drier climate (or higher rainfall seasonality) during MCA (1185-1375 CE); and (ii) a colder and

129 moister LIA (1375-1580 CE) (Rull et al. 2011). Minor climatic changes were possibly masked by

130 the consequences of human impact. A high resolution study of microfacies performed by Corella

131 et al. (2012) identified several intervals such as 1446-1598 CE, 1663-1711 CE and 1759-1819 CE

132 as colder periods, whereas 555-738 CE, 825-875 CE, 1010-1322 CE and 1874 CE -present day

133 where characterized by warmer conditions. Moreover, this study suggested the decoupled

134 action of human practices and climate upon landscape during the last two centuries, when

135 anthropogenic activities decreased despite a warmer and more favorable climate (Corella et al.

136 2012).

137

138 **3. Methodology**

139 The coring and sampling methodologies have been explained in detail in Corella et al. (2011) and

140 Rull et al. (2011); here, a summary will be provided. The NPP reported in this paper were

141 analyzed in the same palynological slides of Rull et al. (2011). For palynological analysis, samples

142 were taken from the core MON04-1A-1K (obtained with a Kullenberg coring platform), every 10

143 cm from the upper 3.6 m, roughly corresponding to the last millennium (Table 1). Pollen and

144 geochemical data from Rull et al. (2011) and Corella et al. (2011) respectively were obtained in

145 the same composite sequence and they will be used to compare with the NPP record (Table 1).

146 Palynological samples consisted of ~3-5 g of sediment that were processed using standard

147 methods, including NaOH, HCl and HF digestions and density gradient centrifugation (Bennet

148 and Willis 2001). Two Lycopodium tablets (Lund University: batch n° 483216: 18,583

6

149   spores/tablet) were added to each sample prior to chemical treatment, and the final slides were

150   mounted in glycerine jelly. NPP abundance was expressed as percentage with respect to the

151   pollen sum, including all pollen taxa except aquatic and semi-aquatic plants (Rull et al. 2011):

152   Cyperaceae, *Cladium, Myriophyllum, Pinguicula, Potamogeton, Ranunculus, Typha/Sparganium-*

153   type and *Utricularia*. NPP identifications were based on Bell (2005), Cugny et al. (2010), Ellis

154   (1971, 1976), Gelorini et al. (2011), Hooghiemstra and van Geel (1998) and references therein,

155   López-Vila et al. (2014), Montoya et al. (2010) and Revelles and van Geel (2016). Whenever

156   possible, unidentified NPP have been assigned to previously described morphotypes using the

157   codes of several already existing classifications (University of Amsterdam, University of Ghent,

158   Botanic Institute of Barcelona, and University of Toulouse-le Mirail) (Table 2). New morphotypes

159   have been described for the first time and named using a code from our institution (IBB-) and a

160   sequential number (Appendix A). Diagrams were plotted with Psimpoll 4.27

161   (http://chrono.qub.ac.uk/psimpoll/psimpoll.html) and zonations were performed by "Optimal

162   Splitting by Information Content" (OSIC), using the broken stick method to determine the

163   significant zones (Bennett 1996). The age model used in this work is based on 210^{Pb} dating and

164   varve counting recently published (Corella et al. 2014, 2016) that revisited the former age-depth

165   model based on radiocarbon dating (Corella et al. 2011). The most recent chronology of the lake

166   sediments only differs 7% with respect to previous ones (Corella et al. 2014). In this work, new

167   dates have been assigned to the former palynological samples published in Rull et al. (2011) (See

168   Corella et al., 2014, 2016 for further details about the age-depth model). In this sense,

169   comparison with other proxies from previous studies have been made using the new chronology

170   unless it is specified otherwise. A final summary figure of selected proxies was plotted by age in

171   R version 3.82 using the package "rioja" (Juggins 2017), which included log10 data

172   transformation of the charcoal influx values.

173

4. Results

A total of 58 morphotypes were found considering fungal spores (36), algal remains (8), zoological remains (6), pteridophyte spores (4), pollen from aquatic/semi-aquatic plants (3) and bryophyte spores (1). NPP often present low abundances or even single appearances in the paleoecological records, which decreases the strength of the potential indicator value of the remain found; here, to make them visible in the diagram, only NPP that appear in more than one sample with percentages respect to the total abundances per sample higher than 7% have been plotted in the diagrams (Figures 3 and 4). As the NPP percentages have been calculated based on the pollen sum, the significant zones shown in the diagrams (Figures 3 and 4) are those previously defined for the pollen analysis in Rull et al. (2011) that represents the vegetation dynamics of LM including the updated chronology.

4.1. Zone MON-1 (360-325 cm, 828-915 CE, 4 samples)

The base of the zone is characterized by high values of *Chaetomium, Glomus, Sordaria*-type, *Neurospora crassa, Delitschia* Types I and II, *Sporormiella*, UG-1118 and the new morphotypes IBB-47 and IBB-40 (Figure 3). At the middle part of the zone there is a peak of *Coniochaeta cf. ligniaria* (hereafter *Coniochaeta*), followed by a decreasing trend until the top of the zone (Fig. 3). Regarding aquatic or semiaquatic organisms (Figure 4), Cyperaceae and *Concentricystis* (also known as *Pseudoschizaea*) show the highest values. Monolete fern spores show an increase, although other spores are present as well. Acari and Chironomidae remains show higher values compared to the following zones. Bryophyte spores peak at the middle of the zone.

4.2. Zone MON-2 (325-203 cm, 915-1185 CE, 12 samples)

Most of the morphotypes already mentioned follow the same trends initiated in Zone MON-1, such as IBB-47, *Chaeotomium, Coniochaeta, Sordaria*-type, *Sporormiella* and UG-1118, though in slightly lower abundances (Fig. 3). *Glomus* disappears at the beginning and reappears at the middle of the zone, just after the peaks of *Entorrhiza, Gelasinospora* and *Kretzschmaria deusta*

8

199 (formerly known as *Ustulina deusta*; hereafter *Kretzschmaria*). At the end of the zone there is a

200 general increasing trend in the taxa that were dominant at the base of the zone, as well as in

201 IBB-3, IBB-29, IBB-46, IBB-47, and IBB-44 (Fig. 3). At the beginning Cyperaceae show lower

202 percentages than in the previous zone, followed by an increasing trend since around 300 cm (ca.

203 950 CE) (Fig. 4). Bryophyte and pteridophyte spore abundances decrease, whereas algal remains

204 show the opposite trend, with an abrupt peak of *Tetraedron* (and to a minor extent, of

205 *Spirogyra*), at the base of the zone and another of *Botryococcus* at the mid/upper part of the

206 zone. At the top of the zone, *Pediastrum* values increase. *Concentricystis* and Acari are

207 characterized by lower percentages than in the former zone (Fig. 4).

208 4.3. Zone MON-3 (203-112 cm, 1185-1373 CE, 9 samples)

209 The beginning of Zone MON-3 is marked by high percentages of several morphotypes including

210 *Chaetomium, Coniochaeta, Glomus, Sordaria*-type, *Sporormiella* and UG-1118 and, to a minor

211 extent, IBB-3, IBB-29, IBB-31*, Podospora, Kretzschmaria*, IBB-46, Sordariales, IBB-18 and IBB-44.

212 These abundances reflect in many cases an increasing trend that started at the top of the

213 previous zone (Fig. 3). IBB-47 also peaks at the beginning and completely disappears afterwards.

214 Indeed, after the high values that characterize the bottom part of the zone, there is a general

215 decreasing trend and the disappearance of some of the taxa around the middle of the zone.

216 Despite the decreasing trend, *Chaetomium* and *Sordaria*-type show the highest abundances at

217 the top of the zone (Fig. 3). Concerning taxa related to aquatic environments (Fig. 4), bryophyte

218 spores (and Monolete fern spores) and *Typha/Sparganium* also show an increase at the

219 beginning of the zone, followed by, in the case of the spores, a decreasing trend, and the

220 disappearance until the upper part regarding *Typha/Sparganium*. On the contrary, *Cladium*-type

221 appears in the middle of the zone and retains its abundance until the top. Algal remains display

222 different trends: *Tetraedron* has a single peak at the middle zone, *Concentricystis* shows higher

223 abundances than in the previous zone, whereas *Spirogyra, Botryococcus* and *Pediastrum* mimic

9

the decreasing trend of bryophyte spores and *Typha/Sparganium*. Acari remains are present with low and discontinuous values during the lower half of the zone and then disappears upwards for the rest of the sedimentary record.

4.4. Zone MON-4 (112-72 cm, 1373-1590 CE, 4 samples)

This zone is marked by the general disappearance of almost all fungal taxa except for UG-1118, which appears again during this zone, though in lower abundances than in previous zones. *Delitschia* Type I shows two minor peaks. At the middle of the zone, around 95 cm (ca. 1450 CE) firstly *Chaetomium*, and then *Sordaria*-type and *Sporormiella* are characterized by an increasing trend (Fig. 3). *Cladium*-type slightly increases at the beginning but declines from the middle part of the zone upwards (Fig. 4). Bryophyte spores are absent. Concerning algal remains, *Spirogyra* and *Botryococcus* show slightly higher abundances, and *Concentricystis* percentages decrease compared to the previous zone. Chironomidae remains peak at the middle zone, and Cladocera remains and *Centropyxis*-type appear for the first time in the record, though with very low values, at the end of this zone.

4.5. Zone MON-5 (72-20 cm, 1590-1865 CE, 5 samples)

A general increase in fungal spores' abundances is observed throughout this zone, especially marked for *Chaetomium, Sporormiella* and UG-1118 (Fig. 3). *Sordaria*-type shows a percentage increment at the bottom, but it decreases in the upper half of the zone. Other taxa such as *Glomus*, IBB-29, IBB-6, IBB-46, IBB-40 and *Arthrinium muelleri*-type (Ellis, 1971) peak in the middle part of the zone. Cyperaceae percentages are higher than in MON-4 and remain constant during the bottom part of this zone, slightly decreasing at the top. *Typha/Sparganium* shows an abrupt peak at the beginning of the zone, and a decreasing trend afterwards. Minor peaks at the beginning are observed in *Cosmarium* and *Plumatella* abundances (Fig. 4). *Cladium*-type disappears prior to the peak of *Typha/Sparganium*, without further recovery. *Concentricystis*

248 and *Spirogyra* present slightly higher values than in MON-4, and *Botryococcus* shows a

249 decreasing trend. *Pediastrum* reappears in this zone but with low values.

250 4.6. Zone MON-6 (20-5 cm, 1865-1881 CE, 2 samples)

251 The top zone is marked by the high values of fungal spores, especially from *Sporormiella*, but

252 also *Chaetomium* and *Sordaria*-type (Fig. 3). Minor contributions come from *Coniochaeta,*

253 *Glomus*, IBB-3, IBB-29, *Delitschia* (Types I and II), UG-1118, *Bispora*-type, and IBB-45, among

254 others. Bryophyte spores, Cyperaceae, Monolete fern spores, *Concentricystis* and Chironomidae

255 also increase. On the contrary, *Typha/Sparganium, Spirogyra* and *Botryococcus* show lower

256 values than in MON-5 (Fig. 4).

257

258 **5. Interpretation and Discussion**

259 5.1. Land use changes from palynological records and documentary sources

260 The oldest section of the record (9th century) was characterized by the occurrence of forest fires

261 as inferred from the charcoal curve (particles >5 μm). Fungal spores related to local fire events

262 (*Neurospora crassa*) and the presence of decayed and/or charred wood fed spores (*Coniochaeta*

263 and *Gelasinospora*) (van Geel and Aptroot 2006) are in agreement with the occurrence of fires

264 in the catchment prior to the 10th century (Fig. 3). These fungal spores are assumed to come

265 from a nearby area due to their low dispersion capacity, whereas charcoal particles could be

266 transported from fires up to almost 20 km far from the coring site (Whitlock and Larsen 2001).

267 The practice of fire with agricultural purposes was common in the Pallars region especially aimed

268 to provide pastures and hence avoid the long-distance winter transhumance (Marugan and

269 Oliver 2005). This practice was abolished in the region in 948 CE, and it can be clearly observed

270 as a decrease in the charcoal record and by the disappearance of the fungus *Neurospora* that it

271 is linked to local fire (Fig. 5). However, the increase in forest fires during the 12th-13th centuries

272 previously observed in the charcoal record (Rull et al. 2011; Rull and Vegas-Vilarrúbia 2015) does

273 not correspond with any increase of these fungal spores, which could be interpreted as an

274 increase in the fire incidence at a regional scale not affecting the lake catchment (Figures 3 and

275 5). Synchronous to the charcoal curve, the abundance of *Glomus* at the beginning of the record

276 suggests erosional processes due to the human land management (Anderson et al. 1984), in

277 agreement with high values of Ti (Fig. 5). Besides erosion, its ensuing decrease could be

278 explained by the coeval decrease of *Pinus* owing to fire, with which *Glomus* likely maintained

279 symbiotic relationships (Rull et al. 2011; Zhou et al. 1997). Therefore, *Glomus* abundances could

280 be related not only to erosion, but also to changes in coniferous forest cover. Remains from

281 aquatic and semi-aquatic organisms like bryophyte spores, *Concentricystis*, and Acari suggest

282 low lake levels until the second half of 10th century (Fig. 4), in agreement with previous

283 sedimentological and geochemical – based reconstructions (Corella et al. 2012).

284 The periods between the 10th - 14th and 16th – 19th centuries have been defined as intervals of

285 agricultural development around LM, where a wide range of cultivars were used (Fig. 5). Within

286 the first agricultural interval, the 11th and 13th centuries witnessed a significant increase in

287 human population around LM, and also a shift to more controlled and permanent land use

288 (Marugan and Oliver 2005). In a detailed analysis of the pollen of weeds and crops present in

289 the sediments of LM during the last millennium, Rull and Vegas-Vilarrúbia (2015) suggested the

290 establishment of a rotation system of the land in mosaics alternating between crops and

291 pastures. Among NPP the increase in *Glomus* abundance points to increased erosional processes

292 derived from a more intense soil disturbance, again matching with an increase in Ti reflecting

293 higher erosion and runoff rates in the watershed (Fig. 5; Corella et al. 2011). More abundant

294 algal remains (Fig. 4) favor the hypothesis of higher lake level phases during 11th and 12th

295 centuries as previously interpreted (Corella et al. 2011; Rull et al. 2011; Scussolini et al. 2011).

296   A significant crisis leading to a population decline occurred during 14th and 15th centuries,

297   coinciding with wars and the Black Death at the cooling onset of the LIA. The NPP record shows

298   the almost total disappearance of fungal spores related to human activities (Zone MON-4, Figs.

299   2 and 5). Slightly higher lake levels were inferred on the basis of a *Botryococcus* increase (Fig. 3;

300   Rull et al. 2011). A return of human activities around LM occurred during the second half of 16th

301   century (Bringué 2005), manifested in the paleoecological record by: i) an increase in fire

302   incidence, ii) the eutrophication of the lake inferred from the dramatic *Typha/Sparganium* peak

303   (Rull et al. 2011; Scussolini et al. 2011), iii) the increment of sediment delivery to the lake (Corella

304   et al. 2011, 2012) and, in the NPP record, iv) by the increasing trend of *Chaetomium* and the

305   return of *Glomus* coeval to the second phase of agricultural development (Fig. 5).

306   The isolation of the Pallars region during the 18th -19th centuries due to the absence of a well-

307   developed road system led to a subsistence economy, with some diversification in order to

308   increase self-sufficiency. During this period, the southern lowlands and the mountains to the

309   north were substantially different from a socio-economic point of view (Farràs 2005), and LM is

310   located in an intermediate area between both. Based on the NPP record, from c. 1865 to 1880

311   CE *Glomus* abundance reflected some erosional processes by likely land management, in

312   agreement with the Ti curve (Corella et al. 2011, Fig. 5). Although the charcoal record did not

313   show any significant change (Fig. 4), fire-related spores such as *Coniochaeta* and *Neurospora*

314   slightly increased (Fig. 3 and 5). However, during this interval the pollen record pointed to a

315   forest recovery, mainly manifested by an increase in *Pinus* percentages (Fig. 5). Pine species are

316   widely known for having huge pollen production with long distance dispersal capacity (Cañellas-

317   Boltà et al. 2009). On the other hand, the different behavior between charcoal and Ti curves

318   (proxy for runoff produced just in the catchment) along the record also points to a mixed source

319   area of charcoal, obtaining particles from close or far locations, or from both at the same time

320   (Fig. 5). Taking these evidence into account altogether, this interval could be interpreted as the

321   occurrence of patchy local fires in a regional context of reforestation, but the NPP results do not

322   point to agricultural fire practices as the main economic activity in the area as we will explain

323   below.

324   The paleoecological studies in nearby Pyrenean locations on human activities' trends generally

325   agree with LM´s reconstruction, although they also highlight great heterogeneity in land use

326   through time and space. The near Lake Estanya (Fig. 1) showed high levels of erosion based on

327   *Glomus* abundances from 820 until 1075 CE, with clear indicators of grazing and fires (Riera et

328   al. 2006). The 11th–13th centuries were characterized in the catchment area of Lake Estanya by

329   low abundances of anthropogenic disturbances' indicators (for erosion, grazing, fires), opposite

330   to LM and interpreted as a change from extensive grazing to arable activities. This asynchrony

331   could be due to: (i) the different altitude of both sites, with higher human pressure in LM during

332   MCA due to more favorable climatic conditions in the high lands (Corella et al. 2011; Rull et al.

333   2011); (ii) some taphonomic influence, due to the location of the records within the lake basins

334   (littoral en Estanya; distal in Montcortès) (Raper and Bush 2009; Parker and Williams 2011); or

335   (iii) chronological uncertainties based of different age models: radiocarbon (centennial to

336   decadal resolution) *vs*. varve counting (annual resolution). On the contrary, LIA was

337   characterized in both lakes by very low abundances of fungal spores; this decrease was not

338   recorded in the Pradell fen (Ejarque et al. 2009). This high altitude location (1975 m asl; Fig. 1)

339   reflected multiple human practices (e.g., mining, smelting, grazing, cropping, charcoal and

340   tupertine production and tree felling), with a maximum human impact during the 1600-1900 CE

341   interval, and woodland recovery and farming retreat during the 1330-1550 CE economic and

342   demographic crises (Ejarque et al. 2009). Such heterogeneity in land use was also observed

343   spatially in the Madriu Valley, eastern Pyrenees (Ejarque et al. 2010). In this work, Ejarque et al.

344   (2010) studied past human management at a micro-regional scale (three records within ca. 1700

345   ha), and concluded that landscape variability is not always necessarily linked to topographic or

346   climatic parameters, highlighting the role of social, economic and cultural trends in the land-use

347   organization and landscape shaping since Prehistory.

348 Outside the Pyrenees, the Lake Arreo record (Fig. 1) shows some parallel trends with Lakes

349 Estanya and Montcortès, e.g., a high fire frequency interval around 800 CE interpreted as caused

350 by Arab incursions in the area (Corella et al. 2013). A high anthropogenic pressure was also

351 suggested by the occurrence of human impact indicators and higher clastic inputs to the lake

352 until 10th century, synchronous to the first medieval settlements. In Arreo, fires and erosion

353 events seem to be closely related, given the parallel curves of charcoal particles and *Glomus*. As

354 in LM, the most intense land use period in Lake Arreo occurred between 890 and 1180 CE, with

355 deforestation and farming activities likely triggering an increase in the clastic run-off, followed

356 by a period of land abandonment, and a further recolonization from 1600 CE onwards (Corella

357 et al. 2013).

358 5.2. Cattle raising around Montcortès: the coprophilous fungi record

359 The curves of total coprophilous fungi show the trends of *Sordaria*-type, *Podospora*-type and

360 *Sporormiella* altogether, expressed in percentage and concentration values (Fig. 3). Although

361 there is a debate regarding the morphotypes that should be included as proxies for grazing

362 (Baker et al. 2013), we have only used already known obligate coprophilous fungi and well

363 defined spore types (Cugny et al. 2010, Ejarque et al. 2011). These curves show an almost

364 continuous presence of coprophilous taxa along the record (except for the zone MON-4, coeval

365 to LIA), suggesting grazing pressure to some extent. The NPP record is in agreement with the

366 documentary archives, which have highlighted the historically importance of livestock in the

367 Pallars region, with vertical transhumance being practiced since antiquity (Bringuè 2005), and

368 the abandonment of the practices very recently after the 19th century land confiscation.

369 Moreover, given the geographical location of LM, use of the livestock had an essential

370 communication and transport function. Based on the coprophilous fungi abundance, four

371 periods of pasture activities around LM can be suggested (Fig. 4):

372   (i)   830-865 CE: The smaller intensity of this peak could be related to the increase in

373   population caused by the northward Muslim expansion (Marugan and Oliver 2005)

374   and the recovery of isolated livestock practices during the Visigoth epoch until the

375   arrival of the Carolingians. Since the 9th century long-distance transhumance was

376   practiced although not extensively, leaded by the religious monasteries that were

377   also the owners of the available summer pasturelands (Marugan and Oliver 2005).

378   During the 9th and 10th centuries, the equine livestock was crucial for the

379   communication trades, and also had a political value given the military function

380   (Marugan and Oliver 2005). Documentary sources indicate an increase of the

381   mineral trade in the region mainly for horseshoes. The isolated peak in the

382   coprophilous concentration curve at around 940 CE (306 cm depth) corresponds to

383   a sample from a thick turbidite and consequently it is not coherent with any taxa

384   percentages (Fig. 2);

385   (ii)   1120-1290 CE: This interval of high dung indicators' values is coeval with the highest

386   population density documented in the area (11th-13th centuries), when the

387   expansion of cattle farming and the beginning of large vertical and horizontal sheep

388   transhumance occurred (Marugan and Oliver 2005). Documentary evidences also

389   show the onset of manure demands as fertilizer since the 12th century parallel to

390   agriculture expansion (Fig. 2) (Marugan and Oliver 2005);

391   (iii) 1530-1795 CE: Previous studies based on the pollen record did not show conclusive

392   evidence about increase in pastureland during the 16th-18th centuries despite the

393   occurrence of an agricultural development phase (Fig. 5; Rull and Vegas-Vilarrúbia

394   2015). However, the regional increase in pastures reported in the historical records

395   during this period is coherent with the high percentages of coprophilous taxa in the

396   Montcortés record. Also a new route with the nearby Montsec area was established

397   in 1687 CE (Fig. 2), which promoted an increment in the number of muleteers in the

398   region. At the end of the 18th century, the use of manure as fertilizer reached a peak

399   due to the high cattle and sheep populations in these montane locations.

400   (iv)   1865-1880 CE: This interval shows the highest levels of coprophilous fungi (Fig. 3)

401   and it coincides with the subsistence economy carried out during the pre-capitalism

402   period in the area, when animal husbandry markets were crucial for the inhabitants

403   (Farràs 2005). It has been reported that more than 88,000 sheep were in

404   transhumance in 1860 CE in the area (Farràs 2005). The palynological data indicate

405   that LM watershed was managed as a mountain area, with forestry and grazing as

406   main activities (Fig. 5), although some *Secale* and *Cannabis* cultivation also occurred

407   (Fig. 5; Rull and Vegas-Vilarrúbia 2015). The increase in grazing activities around LM

408   during this period coincided with higher extreme rainfall events in the area (Fig. 2;

409   Corella et al., 2014) that resulted in higher erosion rates in the lake watershed (Fig.

410   5). This pattern has also been documented in other Mediterranean catchments

411   where the coupled effect of deforestation and grazing with higher frequency of

412   extreme run-off events resulted in higher sediment yield during the late 19th century

413   (Rodriguez-Lloveras et al. 2017).

414   Periods of high pasturage in nearby sequences inferred from coprophilous fungi have been

415   dated at 160-820 CE and 1770-1990 CE in Lake Estanya (Riera et al. 2006); 1550-1650 CE and

416   1800-1900 CE in Pradell fen (although there is a peak of *Sordaria*-type, not considered

417   coprophilous by the original authors, between 900 and 1080 CE) (Ejarque et al. 2009); 890-1190

418   CE and 1850-1900 CE in Lake Arreo (Corella et al. 2013); and 1300-1500 CE and 1900-1990 CE in

419   Sourzay peat bog (Mazier et al. 2009). Considering all these records, the maximum abundances

420   of grazing occurred in the Pyrenees at 1770-1990 CE (Lake Estanya), 1530-1795 CE (LM), 1550-

421   1650 CE (Pradell fen), and 1300-1500 CE (Sourzay peat bog). In spite of chronological

422   uncertainties based on the different age models applied in the studied sequences, it is

423   noticeable that these records span almost the last millennium without much overlapping (Fig.

424 5). The temporal asynchrony could be mainly related to: (i) regional differences of land use

425 history related to local demographic and political causes, and (ii) the variable landscape impact

426 of the wide range of human activities associated with husbandry: meat consumption, farming,

427 clothing, or transport among others.

428 Some studies have reconstructed grazing history based just on the pollen record. However, given

429 the different source and dispersion of the pollen taxa, interpretations can be speculative or

430 inaccurate (for an accurate methodology, see Mazier et al. 2009). This could be especially severe

431 in landscapes with great land use heterogeneity (Graf and Chmura 2006). Based on the

432 palynological record of LM, Rull et al. (2011) and Rull and Vegas-Vilarrúbia (2015) inferred past

433 grazing from meadows/pastures and weed pollen taxa indicators. The pollen and coprophilous

434 curves from LM mimic the general trends *sensu lato*, suggesting that the selected pollen taxa in

435 LM provide mostly local information despite some regional influence (e.g. *Pinus*). However, it

436 should be noticed that fungal spores define better the intervals with higher grazing, matching

437 more accurately with the available historical documents. Another handicaps for pollen as the

438 only proxy for grazing activities are due to: (i) The lack of agreement of the taxa that should be

439 included; and (ii) The generalist nature of some of the pollen taxa used (not specific or exclusive

440 of pastures), which may cause some overlapping with other weeds or ruderal taxa not used by

441 the livestock. This lack of homogeneity in the indicator value also prevents further comparison

442 between different records across regions. Therefore, the use of NPP in addition to pollen studies

443 is encouraged to obtain an accurate and independent proxy for grazing reconstructions.

444

445 **6. Conclusions**

446 A differentiation between local and regional fires and other human activities has been possible

447 through the use of specific fungal spores' morphotypes. The high resolution provided by the

448 varve chronology has allowed comparison between NPP trends and historical documents. The

449 coprophilous fungi record has shown four main periods of high grazing pressure in LM watershed

450 (830-865 CE, 1120-1290 CE, 1530-1795 CE and 1865-1880 CE), similar to other reconstructions

451 based on pollen and geochemical/sedimentological proxies, but narrowing down the intervals

452 and providing a more coherent evolution with the available historical documents. The large local

453 scale variability of past human activities in the Pyrenees during the last millennium

454 demonstrated by the limited NPP records available highlights the strength of this analysis in

455 reconstructing local anthropogenic impact, and therefore, its use is encouraged in routine pollen

456 based studies. Moreover, grazing history provided by NPP help to constrain the origin and

457 dynamics of erosional processes identified from sedimentological or geochemical proxies. In this

458 sense, multi proxy studies including historical documents are crucial to independently test the

459 suitability of the tools used and accurately frame the spatial scale of the different events

460 occurred in a particular area.

461

472

473 **8. References**

474   Anderson, R.S., Homola, R.L., Davis, R.B., Jacobson, G.L. 1984. Fossil remains of the mycorrhizal

475   fungal *Glomus fasciculatum* complex in postglacial lake sediments from Maine. Canadian Journal

476   of Botany, 62: 2325-2328.

477   Argant, J., López-Sáez, J.A., Bintz, P. 2006. Exploring the ancient occupation of a high altitude

478   site (Lake Lauzon, France): Comparison between pollen and non-pollen palynomorphs. Review

479   of Palaeobotany and Palynology, 141: 151-163.

480   Baker, A.G., Bhagwat, S.A., Willis, J.K. 2013. Do fungal spores make a good proxy for past

481   distribution of large herbivores? Quaternary Science Reviews, 62: 21-31.

482   Bakker, M., van Smeerdijk, D.G. 1982. A palaeoecological study of a late Holocene section from

483   "Het Ilperveld", Western Netherlands. Review of Palaeobotany and Palynology, 36: 95–163.

484   Bell, A. 2005. An illustrated guide to the coprophilous Ascomycetes of Australia. CBS Biodiversity

485   series, n°3.

486   Bennett, K.D. 1996. Determination of the number of zones in a biostratigraphical sequence. New

487   Phytologist, 132:155-170.

488   Bennett, K.D., Willis, K.J. 2001. Pollen. In: Smol, J.P., Birks, H.J.B., Last, W.M. (eds) Tracking

489   environmental change using lake sediments. Vol 3: terrestrial, algal, and siliceous indicators.

490   Kluwer, Dordrecht, pp 5-32.

491   Bringué, J.M. 2005. L'edat moderna. In: Marugan, C.M., Rapalino, V, (eds) Història del Pallars.

492   Dels orígens als nostre dies. Pagès Editors, Lleida, pp 87-120.

493   Camps, J., Gonzalvo, I., Güell, J., López, P., Tejero, A., Toldrà, X., Vallespinos, F., Vicens, M. 1976.

494   El lago de Montcortès, descripción de un ciclo anual. Oecologia Aquatica, 2: 99-110.

495 Cañellas-Boltà, N., Rull, V., Vigo, J., Mercadé, A. 2009. Modern pollen–vegetation relationships

496 along an altitudinal transect in the central Pyrenees (southwestern Europe). Holocene, 19: 1185-

497 1200.

498 Corella, J.P., Moreno, A., Morellón, M., Rull, V., Giralt, S., Rico, M.T., Pérez-Sanz, A., Valero-

499 Garcés, B.L. 2011. Climate and human impact on a meromictic lake during the last 6,000 years

500 (Montcortès Lake, Central Pyrenees, Spain). Journal of Paleolimnology, 46: 351-367.

501 Corella, J.P., Brauer, A., Mangili, C., Rull, V., Vegas-Vilarrúbia, T., Morellón, M., Valero-Garcés,

502 B.L. 2012. The 1.5-ka varved record of Lake Montcortès (southern Pyrenees, NE Spain).

503 Quaternary Research, 78: 323-332.

504 Corella, J.P., Stefanova, V., El Anjoumi, A., Rico, E., Giralt, S., Moreno, A., Plata-Montero, A.,

505 Valero-Garcés, B.L. 2013. A 2500-year multi-proxy reconstruction of climate change and human

506 activities in northern Spain: The Lake Arreo record. Palaeogeography Palaeoclimatology

507 Palaeoecology, 386: 555-568.

508 Corella, J.P., Benito, G., Rodrigez-Lloveras, X., Brauer, A., Valero-Garcés, B.L. 2014. Annually-

509 resolved lake record of extreme hydro-meteorological events since AD 1347 in NE Iberian

510 Peninsula. Quaternary Science Reviews, 93: 77-90.

511 Corella, J.P., Valero-Garcés, B. L., Gerard, J. 2015. Deciphering turbidite triggers by core facies

512 analyses. Implications for geohazards and reservoir characterization. 77th EAGE Conference and

513 Exhibition 2015: Earth Science for Energy and Environment, pags 1110-1114.

514 Corella, J.P., Valero-Garcés, B., Vicente-Serrano, S.M., Brauer, A., Benito, G. 2016. Three

515 millennia of heavy rainfalls in Western Mediterranean: frequency, seasonality and atmospheric

516 drivers. Scientific Reports. 6: 38206.

517 Corella, J.P., Valero-Garcés, B., Wang, F., Martínez-Cortizas, A., Cuevas, C., Saiz-Lopez, A. 2017.

518 700 years reconstruction of mercury and lead atmospheric deposition in the Pyrenees (NE

519 Spain). Atmospheric Environment, 155: 97-107.

520 Charman, D.J., Hendon, J., Woodland, W.A. 2000. The identification of Testate Amoebae

521 (Protozoa: Rhizopoda) in peats. QRA Technical guide, No. 9. Quaternary Research Association,

522 London.

523 Christopher, R.A. 1976. Morphology and taxonomic status of *Pseudoschizaea* Thiergart and

524 Frantz ex R. Potonié emend. Micropaleontology 22, 145–150.

525 Cugny, C., Mazier, F., Galop, D. 2010. Modern and fossil non-pollen palynomorphs from the

526 Basque mountains (western Pyrenees, France): the use of coprophilous fungi to reconstruct

527 pastoral activity. Vegetation History and Archaeobotany, 19: 391-408.

528 Ejarque, A., Julià, R., Riera, S., Palet, J.M., Orengo, H.A., Miras, Y., Gascón, C. 2009. Tracing the

529 history of highland human management in the eastern Pre-Pyrenees: an interdisciplinary

530 palaeoenvironmental study at the Pradell fen, Spain. The Holocene, 19: 1241-1255.

531 Ejarque, A., Miras, Y., Riera, S., Palet, J.M., Orengo, H.A. 2010. Testing micro-regional variability

532 in the Holocene shaping of high mountain cultural landscapes: a palaeoenvironmental case-

533 study in the eastern Pyrenees. Journal of Archaeological Science, 37: 1468-1479.

534 Ejarque, A., Miras, Y., Riera, S. 2011. Pollen and non-pollen palynomorph indicators of vegetation

535 and highland grazing activities obtained from modern surface and dung datasets in the eastern

536 Pyrenees. Review of Palaeobotany and Palynology, 167: 123-139.

537 Ellis, M.B. 1971. Dematiaceous Hyphomycetes. The Eastern Press Ltd., London.

538 Ellis, M.B. 1976. More Dematiaceous Hyphomycetes. The Cambrian News Ltd., Aberystwyth.

539   Farràs, F. 2005. El Pallars contemporani. In: Marugan CM, Rapalino V (eds) Història del Pallars.

540   Dels orígens als nostre dies. Pagès Editors, Lleida, pp 121-144.

541   Folch, R. 1981. La vegetacio dels Països Catalans. Ketres, Barcelona.

542   Gelorini, V., Verbeken, A., van Geel, B., Cocquyt, C., Verschuren, D. 2011. Modern non-pollen

543   palynomorphs from East African lake sediments. Review of Palaeobotany and Palynology, 164:

544   143-173.

545   González-Sampériz, P., Aranbarri, J., Pérez-Sanz, A., Gil-Romera, G., Moreno, A., Leunda, M.,

546   Sevilla-Callejo, M., Corella, J.P., Morellón, M., Oliva, B., Valero-Garcés, B. 2017. Environmental

547   and climate change in the southern Central Pyrenees since the Last Glacial Maximum: A view

548   from the lake records. Catena, 149: 668-688.

549   Graf, M.T., Chmura, G.L. 2006. Development of modern analogues for natural, mowed and

550   grazed grasslands using pollen assemblages and coprophilous fungi. Review of Palaeobotany and

551   Palynology, 141: 139-149.

552   Gutiérrez, F., Linares, R., Roqué, C., Zarroca, M., Rosell, J., Galve, J.P., Carbonel, D. 2012.

553   Investigating gravitational grabens related to lateral spreading and evaporite dissolution

554   subsidence by means of detailed mapping, trenching, and electrical resistivity tomography

555   (Spanish Pyrenees). Lithosphere, 4: 331-353.

556   Hooghiemstra, H., van Geel, B. 1998. World list of Quaternary pollen and spore atlases. Review

557   of Palaeobotany and Palynology, 104: 157-182.

558   IPCC, 2013: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I

559   to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F.,

560   D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley

561   (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

562   Juggins, S. 2017. rioja: Analysis of Quaternary Science Data, R Package Version (0.9-15). Available

563   at: http://cran.r-project.org/package=rioja

564   López-Vila, J., Montoya, E., Cañellas-Boltà, N., Rull, V. 2014. Modern non-pollen palynomorphs

565   sedimentation along an elevational gradient in the south-central Pyrenees (southwestern

566   Europe) as a tool for Holocene paleoecological reconstruction. The Holocene, 24: 325-343.

567   Loughlin, N.J.D., Gosling, W.D., Montoya, E. 2018. Identifying environmental drivers of fungal

568   non-pollen palynomorphs in the montane forest of the eastern Andean flank. Quaternary

569   Research, 89: 119-133.

570   Macphail, M., Stevenson, J. 2004. Fungal spores in archaeological contexts. Centre for

571   Archaeological Research (CAR). Australian National University, Camberra. ACT 0200.

572   Marugan, C.M., Oliver, J. 2005. El Pallars medieval. In: Marugan, C.M., Rapalino, V. (eds) Història

573   del Pallars. Dels orígens als nostre dies. Pagès Editors, Lleida, pp 45-86.

574   Mazier, F., Galop, D., Gaillard, M.J., Rendu, C., Cugny, C., Legaz, A., Peyron, O., Buttler, A. 2009.

575   Multidisciplinary approach to reconstructing local pastoral activities: an example from the

576   Pyrenean Mountains (Pays Basque). The Holocene, 19: 171-188.

577   Mercadé, A., Vigo, J., Rull, V., Vegas-Vilarrúbia, T., Garcés, S., Lara, A., Cañellas-Boltà, N. 2013.

578   Vegetation and landscape around Lake Montcortès (Catalan pre-Pyrenees) as a tool for

579   palaeoecological studies of lake sediments. Collectanea Botanica, 32: 87-101.

580   Menozzi, B.I., Zotti, M., Montanari, C. 2010. A non-pollen palynomorphs contribution to the local

581   environmental history in the Ligurian Apennines: a preliminary study. Vegetation History and

582   Archaeobotany, 19: 503-512.

583   Miras, Y., Ejarque, A., Riera, S., Palet, J.M., Orengo, H.A., Euba, I. 2007. Dynamique holocène de

584   la végétation et occupation des Pyrénées andorranes depuis le Néolithique ancien, d'après

585   l'analyse pollinique de la tourbière de Bosc dels Estanyons (2180 m, Vall del Madriu, Andorre).

586   Comptes Rendus Palevol, 6: 291-300.

587   Miras, Y., Ejarque, A., Orengo, H., Mora, S.R., Palet, J.M., Poiraud, A. 2010. Prehistoric impact on

588   landscape and vegetation at high altitudes: An integrated palaeoecological and archaeological

589   approach in the Eastern Pyrenees (Perafita valley, Andorra). Plant Biosystems, 144: 924-939.

590   Modamio, X., Pérez, V., Samarra, F. 1988. Limnología del lago de Montcortès (ciclo 1978-79).

591   Oecologia Aquatica, 9: 9-17.

592   Montoya, E., Rull, V., van Geel, B. 2010. Non-pollen palynomorphs from surface sediments along

593   an altitudinal transect of the Venezuelan Andes. Palaeogeography Palaeoclimatology

594   Palaeoecology, 297: 169-183.

595   Montoya, E., Rull, V., Vegas-Vilarrúbia, T. 2012. Non-pollen palynomorph studies in the

596   Neotropics: The case of Venezuela. Review of Palaeobotany and Palynology, 186: 102-130.

597   Parker, N.E., Williams, J.W. 2011. Influences of climate, cattle density, and lake morphology on

598   *Sporormiella* abundances in modern lake sediments in the US Great Plains. The Holocene, 22:

599   475-483.

600   Pérez-Sanz, A., González-Sampériz, P., Moreno, A., Valero-Garcés, B., Gil-Romera, G.,

601   Rieradevall, M., Tarrats, P., Lasheras-Álvarez, L., Morellón, M., Belmonte, A., Sancho, C., Sevilla-

602   Callejo, M., Navas, A. 2013. Holocene climate variability, vegetation dynamics and fire regime in

603   the central Pyrenees: the Basa de la Mora sequence (NE Spain). Quaternary Science Reviews,

604   73: 149-169.

605   Raper, D., Bush, M. 2009. A test of *Sporormiella* representation as a predictor of megaherbivore

606   presence and abundance. Quaternary Research, 71: 490-496.

607   Revelles, J., van Geel, B. 2016. Human impact and ecological changes in lakeshore environments.

608   The contribution of non-pollen palynomorphs in Lake Banyoles (NE Iberia). Review of

609   Palaeobotany and Palynology, 232: 81-97.

610   Riera, S., López-Sáez, J.A., Julià, R. 2006. Lake responses to historical land use changes in

611   northern Spain: The contribution of non-pollen palynomorphs in a multiproxy study. Review of

612   Palaeobotany and Palynology, 141: 127-137.

613   Rodriguez-Lloveras, X., Corella, J. P., Benito, G. 2017. Modelling the hydro-sedimentary dynamics

614   of a Mediterranean semiarid ungauged watershed beyond the instrumental period. Land

615   Degradation & Development, 28: 1506-1518.

616   Rosell, J. 1994. Mapa Geológico de España y Memoria. Escala 1:50.000, Hoja de Tremp (252).

617   Rull, V. 2012. Community ecology: diversity and dynamics over time. Community Ecology 13:

618   102-116.

619   Rull, V., Vegas-Vilarrúbia, T. 2014. Preliminary report on a mid-19th century *Cannabis* pollen

620   peak in NE Spain: historical context and potential chronological significance. The Holocene, 24:

621   1378-1383.

622   Rull, V., Vegas-Vilarrúbia, T. 2015. Crops and weeds from the Estany de Montcortès catchment,

623   central Pyrenees, during the last millennium: a comparison of palynological and historical

624   records. Vegetation History and Archaeobotany, 24: 699-710.

625   Rull, V., González-Sampériz, P., Corella, J.P., Morellón, M., Giralt, S. 2011. Vegetation changes in

626   the southern Pyrenean flank during the last millennium in relation to climate and human

627   activities: the Montcortès lacustrine record. Journal of Paleolimnology, 46: 387-404.

628   Rull, V., Trapote, M.C., Safont, E., Cañellas-Boltà, N., Pérez-Zanón, N., Sigró, J., Buchaca, T, Vegas-

629   Vilarrúbia, T. 2017. Seasonal patterns of pollen sedimentation in Lake Montcortès (Central

630   Pyrenees) and potential applications to high-resolution paleoecology: a 2-year pilot study

631   Journal of Paleolimnology, 57: 95-108.

632   Scussolini, P., Vegas-Vilarrúbia, T., Rull, V., Corella, J.P., Valero-Garcés, B., Gomà, J. 2011. Middle

633   and late Holocene climate change and human impact inferred from diatoms, algae and aquatic

634   macrophyte pollen in sediments from Lake Montcortès (NE Iblerian Peninsula). Journal of

635   Paleolimnology, 46: 369-385.

636   Trapote, M.C, Vegas-Vilarrúbia, T., López, P., Puche, E., Gomà, J., Buchaca, T., Cañellas-Boltà, N.,

637   Safont, E., Corella, J.P., Rull, V. 2018 Modern sedimentary analogues and integrated monitoring

638   to understand varve formation in the Mediterranean Lake Montcortès (Central Pyrenees, Spain).

639   Palaeogeography, Palaeoclimatology, Palaeoecology, 496: 292-304.

640   van Smeerdijk, D.G. 1989. A palaeoecological and chemical study of a peat profile from the

641   Assendelver polder (The Netherlands). Review of Palaeobotany and Palynology, 58: 231-288.

642   van Geel, B. 1976. Fossil spores of Zygnemataceae in ditches of a prehistoric settlement in

643   Hoogkarspel (The Netherlands). Review of Palaeobotany and Palynology, 22: 337–374.

644   van Geel, B. 1978. A palaeoecological study of Holocene peat bog sections in Germany and The

645   Netherlands, based on the analysis of pollen, spores and macro- and microremains of fungi,

646   algae, cormophytes and animals. Review of Palaeobotany and Palynology, 25: 1–120.

647   van Geel, B. 2001. Non-pollen palynomorphs. In: Smol, J.P., Birks, H.J.B., Last, W.M. (eds)

648   Tracking environmental change using lake sediments. Vol 3: terrestrial, algal, and siliceous

649   indicators. Kluwer, Dordrecht, pp 99-119.

650   van Geel, B., Aptroot, A. 2006. Fossil ascomycetes in Quaternary deposits. Nova Hedwigia, 82:

651   313-329.

652   van Geel, B., Bohncke, S.J.P., Dee, H. 1981. A paleoecological study of an upper Late Glacial and

653   Holocene sequence from "De Borchert", The Netherlands. Review of Palaeobotany and

654   Palynology, 31: 367–448.

655   van Geel, B., Hallewas, D.P., Pals, J.P. 1983. A late Holocene deposit under the Westfriese

656   Zeedidijk near Enkhuizen (Prov. of N-Holland, The Netherlands): palaeoecological and

657   archaeological aspects. Review of Palaeobotany and Palynology, 31: 367-448.

658   van Geel, B., Klink, A.G., Pals, J.P., Wiegers, J. 1986. An Upper Eemian lake deposit from Twente,

659   eastern Netherlands. Review of Palaeobotany and Palynology, 47: 31–61.

660   van Geel, B., Coope, G.R., van der Hammen, T. 1989. Palaeoecology and stratigraphy of the

661   Lateglacial type section at Usselo (The Netherlands). Review of Palaeobotany and Palynology,

662   60: 25-129.

663   van Geel, B., Buurman, J., Brinkkemper, O., Schelvis, J., Aptroot, A., van Reenen, G., Hakbijl, T.

664   2003. Environmental reconstruction of a Roman Period settlement site in Uitgeest (The

665   Netherlands), with especial reference to coprophilous fungi. Journal of Archaeological Sciences,

666   30: 873-883.

667   Vegas-Vilarrúbia, T., Rull, V., Montoya, E., Safont, E. 2011. Quaternary palaeoecology and nature

668   conservation: a general review with examples from the neotropics. Quaternary Science Reviews,

669   30: 2361-2388.

670   Vegas-Vilarrúbia, T., Corella, J.P., Pérez-Zanón, N., Buchaca, T., Trapote, M.C., López, P., Sigró, J.,

671   Rull, V. 2018. Historical shifts in oxygenation regime as recorded in the laminated sediments of

672   lake Montcortès (Central Pyrenees) support hypoxia as a continental-scale phenomenon.

673   Science of the Total Environment, 612: 1577-1592.

674   Vigo, J. 2008. L'alta muntanya catalana: Flora i Vegetacio. Institut d'Estudis Catalans-C Excurs

675   Catalunya, Barcelona.

676 Whitlock, C., Larsen, C. 2001. Charcoal as a fire proxy. In: Smol, J.P., Birks, H.J.B., Last, W.M. (eds)

677 Tracking environmental change using lake sediments. Vol 3: terrestrial, algal, and siliceous

678 indicators. Kluwer, Dordrecht, pp 75-98.

679 Willis, K.J., Araújo, M.B., Bennett, K.D., Figueroa-Rangel, B., Froyd, C.A., Myers, N. 2007. How

680 can knowledge of the past help to conserve the future? Biodiversity conservation and the

681 relevance of longterm ecological studies. Philosophical Transactions of the Royal Society of

682 London. Series B, Biological Sciences, 362: 175-186.

683 Zhou, M., Sharik, T.L., Jurgensen, M.F., Ritcher, D.L. 1997. Ectomycorrhizal colonization of

684 *Quercus rubra* seedlings in response to vegetation removals in oak and pine stands. Forest

685 Ecology and Management, 93: 91-99.

686

687

688

689

690

691

692

693

694

695

696

697   **Table 1.** Lake Montcortès cores and proxies analysed so far. All data used in this paper belong

698   to the core MON04-1A-1K.

Core	Sampling date	Sediment length	Proxies analyzed	References
MON12-3A-1G	2004	6.2 m	Sedimentology Geochemistry	Corella et al. (2014,2015, 2016, 2017)
MON04-3A-1K	2004	6.2 m	Sedimentology Varve Counting	Corella et al. (2011) Corella et al. (2012)
MON04-4A-1K	2004	5.3 m	Sedimentology Geochemistry Diatoms Varve counting Pollen	Corella et al. (2011, 2016) Scussolini et al. (2011) Rull et al. (2011) ; Rull and Vegas-Vilarrúbia (2014, 2015)
MON07-1A-1G	2007	0.31 m	Sedimentology Geochemistry	Corella et al. (2011)
Physico-chemical parameters Modern analog traps	2012-2015	NA	Varve formation Limnological cycle Modern pollen sedimentation	Trapote et al. (2018) Rull et al. (2017)

699

700

701

702

703

704

705

706

707

708 **Table 2.** Non-pollen palynomorphs (NPP) included in Figures 3 and 4. The table shows identified

709 and unidentified forms with references to the original publications, and includes the code (NPP

710 type) for those morphotypes that were previously assigned to described types following

711 conventions of the NPP community. HdV: Hugo de Vries-Laboratory (University of Amsterdam);

712 UG: University of Ghent; IBB: Botanic Institute of Barcelona; TM: University of Toulouse-le Mirail.

ID	NPP Type	Nature	References
Arnium	HdV-261	Fungal spore	van Geel et al. (2003)
Arthrinium muelleri-type		Fungal spore	Ellis (1971)
Bispora-type		Fungal spore	Ellis (1971)
Cercophora-type	HdV-112	Fungal spore	van Geel (1978)
Chaetomium	HdV-7A	Fungal spore	van Geel (1978)
Coniochaeta cf. *ligniaria*	HdV-172	Fungal spore	van Geel et al. (1983)
Delitschia Type I	IBB-22, UG-1066	Fungal spore	Montoya et al. (2010), Gelorini et al. (2011)
Delitschia Type II (*D. nephrospora-*t)		Fungal spore	Cugny et al. (2010), Macphail and Stevenson (2004)
Diporotheca	HdV-143	Fungal spore	van Geel et al. (1986)
Entorrhiza	HdV-527	Fungal spore	van Geel et al. (1983)
Herpotrichiella-type	HdV-22	Fungal spore	van Geel (1976)
Gelasinospora	HdV-1	Fungal spore	van Geel (1978)
Glomus	HdV-207	Fungal spore	van Geel et al. (1989)
Kretzschmaria deusta	HdV-44	Fungal spore	van Geel (1978)
Neurospora crassa	HdV-55C	Fungal spore	van Geel (1978)
Podospora-type	HdV-368	Fungal spore	van Geel et al. (1981)
Sordaria-type	HdV-55A	Fungal spore	van Geel et al. (1981)
Sordariales		Fungal spore	Bell (2005)
Sporormiella	HdV-113	Fungal spore	van Geel et al. (2003)
Valsaria	HdV-140	Fungal spore	van Geel et al. (1983)
IBB-3	IBB-3	Fungal spore	Montoya et al. (2010)
IBB-29	IBB-29	Fungal spore	Montoya et al. (2010)
IBB-31	IBB-31	Fungal spore	Montoya et al. (2010)
HdV-495	HdV-495	Fungal spore	van Smeerdijk (1989)
IBB-6	IBB-6	Fungal spore	Montoya et al. (2010)
IBB-23	IBB-23	Fungal spore	Montoya et al. (2010)
TM-O	TM-O	Fungal spore	Cugny et al. (2010)
IBB-9	IBB-9	Fungal spore	Montoya et al. (2010)
UG-1118	UG-1118	Fungal spore	Gelorini et al. (2011)
IBB-18	IBB-18	Fungal spore	Montoya et al. (2010)
Botryococcus	HdV-766	Algal remain	Bakker and van Smeerdijk (1982), Jankovská and Komárek (2000)
Concentricystis		Algal remain	Christopher (1976)
Cosmarium	HdV-332	Algal remain	van Geel et al. (1989)

Debarya	HdV-214	Algal remain	van Geel et al. (1989)
Pediastrum	HdV-760	Algal remain	Bakker and van Smeerdijk (1982), Jankovská and Komárek (2000), Komárek and Jankovská (2001)
Spirogyra	HdV-130	Algal remain	Pals et al. (1980), van der Wiel (1983), van Geel et al. (1983)
Tetraedron	HdV-371	Algal remain	Bakker and van Smeerdijk (1982)
Zygnema	HdV-213, HdV-314	Algal remain	van Geel et al. (1981, 1989)
Acari	HdV-36	Zoological remain	van Geel (1976)
Centropyxis-type		Zoological remain	Charman et al. (2000)
Chironomidae	HdV-219, HdV-907	Zoological remain	van Geel et al. (1989)
Cladocera	HdV-72	Zoological remain	van Geel (1976), van Geel et al. (1983)
Plumatella	HdV-390, HdV-737	Zoological remain	Bakker and van Smeerdijk (1982), van Geel et al. (1981)
HdV-221	HdV-221	Zoological remain	Van Geel et al. (1989)

713

714

715

716

717

718

719

720

721

722

723   **Figure 1.** Study area. A. General map of the Iberian Peninsula (source: NASA/Caltech). Pyrenees

724   are highlighted by a yellow rectangle. B. Google Earth image of Pyrenees. Montcortès is marked

725   by a star. Other locations mentioned in the text are shown by numbers: 1) Lake Estanya. 2)

726   Pradell fen, 3) Madriu valley, 4) Lake Arreo, and 5) Sourzay peat bog. C. Aerial view of the lake

727   and surroundings (source: gencat.cat).

728   **Figure 2.** Summary framework of the main climatic and historical events occurred in the region

729   of LM during the last millennium (HHR and LHR are high and low heavy rainfall events

730   respectively). Main human activities based on pollen data include forest clearance (C), burning

731   (B) and agricultural (A) phases, whereas R refers to recovery of the forest or low anthropogenic

732   activities' periods. Figures and information extracted and modified from Rull and Vegas-

733   Vilarrúbia (2015) and literature therein. The chronology included here follows the original

734   publications.

735   **Figure 3.** Percentage diagram of fungal spores. Percentages are based on the pollen sum (see

736   Methods). Significant zones are based on the pollen record (Rull et al. 2011). Coprophilous fungi

737   sum is expressed as both percentage and concentration values. Asterisk marks the non-scaled

738   value of the upper sample, which has been reduced (/10) for more clarity. Calibrated ages (CE)

739   shown are extracted from varve counting analysis (Corella et al., 2012, 2014).

740   **Figure 4.** Percentage diagram of charcoal particles and non-fungal NPP. Percentages are based

741   on the pollen sum (see Methods). Significant zones are based on the pollen record (Rull et al.

742   2011). Charcoal concentration and pollen sum are plotted for comparison and were extracted

743   from Rull et al. (2011). *Tetraedron* and *Botryococcus* curves are shown in a reduced scale for

744   more clarity. A: Semi-aquatic plant taxa; Z: Zoological remains. Calibrated ages (CE) shown are

745   extracted from varve counting analysis (Corella et al., 2012, 2014).

746   **Figure 5.** Lake Montcortès landscape dynamics during the last millennium including vegetation

747   trends extracted from Rull et al. (2011) and land management based on Rull and Vegas-

748   Vilarrúbia (2015) and this work. Agricultural phases (A1 and A2) show the main cultivars based

749   on Rull and Vegas-Vilarrúbia (2015); Ti values are based on Corella et al. (2011); Forest clearings

750   (C1 and C2) and burnings (BI and BII) events are based on Rull and Vegas-Vilarrúbia (2015);

751   Charcoal influx is shown in logarithmic scale, and purple bars show the intervals with occurrence

752   of *Neurospora crassa*; Grazing periods correspond to LM (blue shades, this study) and to regional

753   peaks of coprophilous fungi of other lake records: Lake Arreo (LA; Corella et al. 2013), Sourzay

754   peatbog (SP; Mazier et al. 2009), Pradell fen (PF; Ejarque et al. 2009), and Lake Estanya (LE; Riera

755   et al. 2006).

756

757

758

759

760

761

762

763

764

765

766

767

768

769

770   **APPENDIX A**

771   Description of the new morphotypes recorded in this study. Illustrations of non-identified NPP

772   (IBB types) and Plumatella statoblasts are attached.

773   IBB-40: Ascospores fusiform, slightly concave (crescent-shaped), 17 x 3.8-5.2 µm, with apical

774   pores. Present as isolated spores or in tetrads (uncommon).

775   IBB-44: Ascospores one-septate, 10.2-12.6 x 17.4-23.7 µm, slightly constricted at the septum

776   and with paler wall around the apices. It has been tentatively related in this study to *Cordana*

777   (*C. pauciseptata* type) spores (Ellis 1971). *C. pauciseptata* is found on bark and wood of

778   deciduous trees and conifer forests in Europe and North America (Ellis 1971).

779   IBB-45: Ascospores one-septate, 16-40.3 x 32.7-86 µm, strongly constricted at the septum and

780   marked reticulum. Apical cell ends were found sometimes protruding.

781   IBB-46: Unknown microfossil fragments including abundant spine protuberances, although they

782   have been always observed broken or uncompleted. Partial remains observed are 12.9 x 17.1

783   µm in diameter.

784   IBB-47: Ascospores fusiform 7.3-11.3 x 13.8-20 µm, with apical pores. Morphology highly similar

785   to the previously described NPP coded as UAB-3 (Revelles and van Geel 2016), which occurred

786   in a soil erosion phase.

787   *Plumatella* sp. statoblasts: Asexual structure produced by some bryozoans, 346.3-367.6 x 237.6-

788   276.3 µm, with polygonal cells between 6.8-15.7 µm in diameter. In the NPP literature has

789   previously been named HdV-390A (van Geel et al. 1981)

790

791   **References**

792   Ellis, M.B. 1971. Dematiaceous Hyphomycetes. The eastern Press Ltd., London.

793   Revelles, J., Burjachs, F.van Geel, B. 2016. Pollen and non-pollen palynomorphs from the early

794   Neolithic settlement of La Draga (Girona, Spain). Review of Palaoebotany and Palynology, 225:
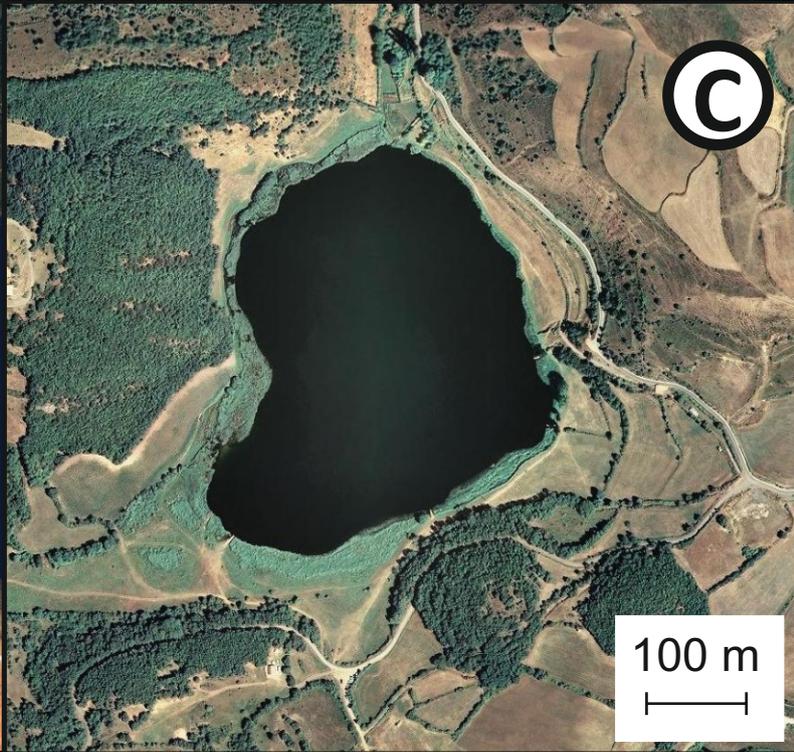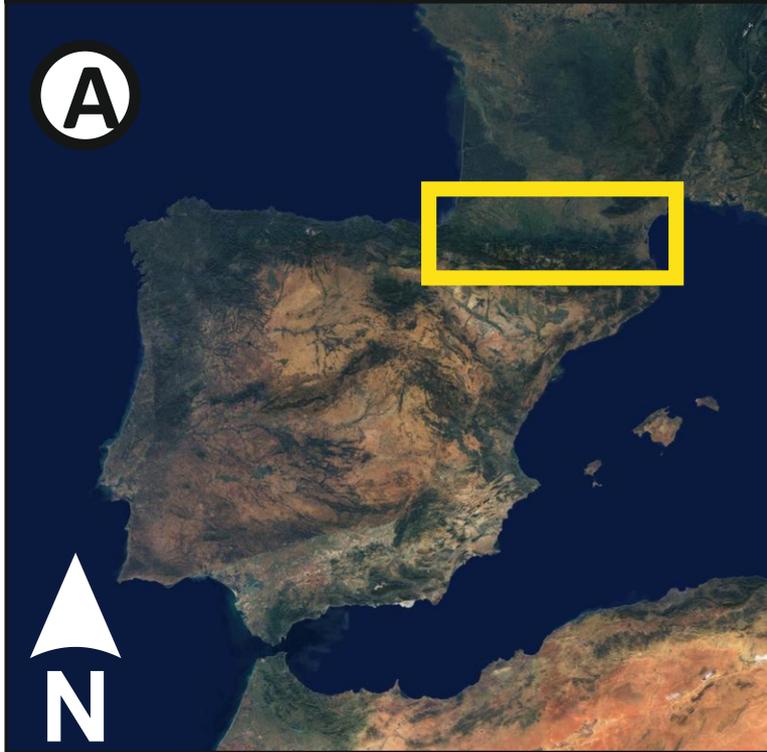
795   1-20.

796   van Geel, B., Bohncke, S.J.P., Dee, H. 1981. A palaeoecological study of an upper Late Glacial and

797   Holocene sequence from "De Borchert", The Netherlands. Review of Palaoebotany and
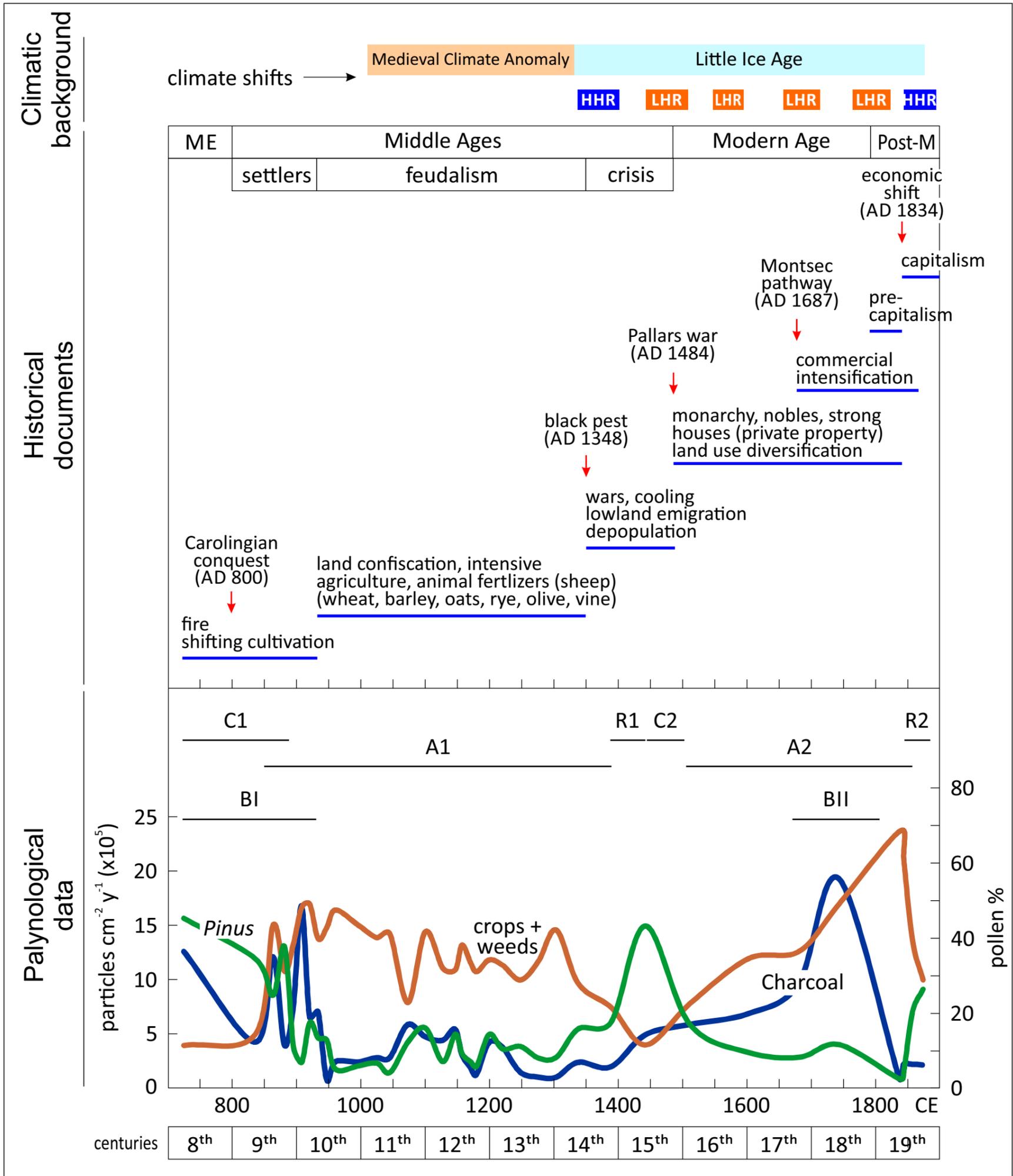
798   Palynology, 31: 367-448.

799

800

801

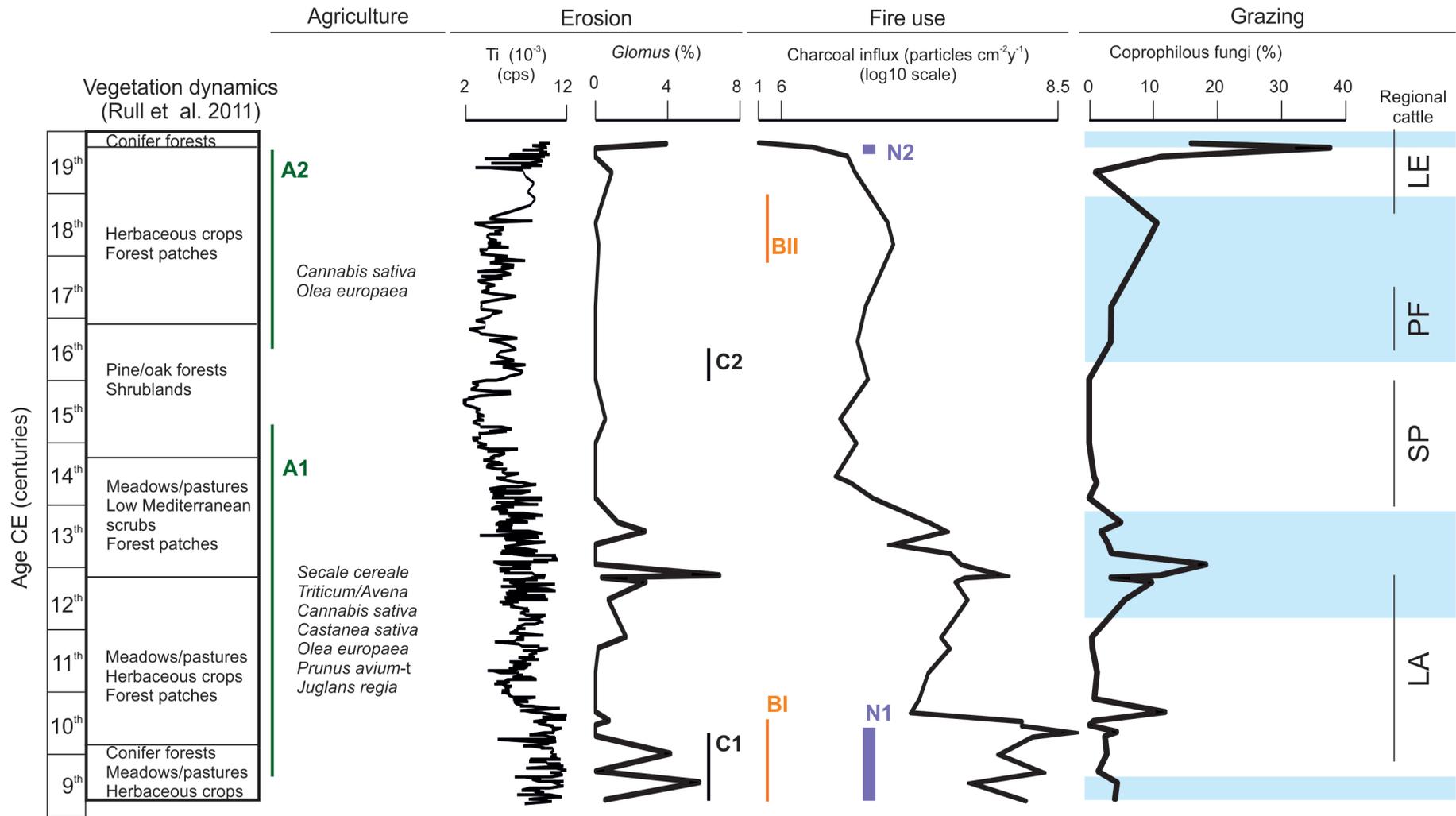- Non-pollen palynomoprhs (NPP) were analyzed in the Pyrenean Lake Montcortès
- NPP provided specific information about human practices for the last millennium
- Coprophilous fungi bracketed four important historical periods of grazing
- Fungal spores related to fire constrained the origin source of fires spatially
- *Glomus* mimicked the Ti values proving its indicative value for erosional processes

Climatic background

climate shifts →

Medieval Climate Anomaly | Little Ice Age

HHR LHR LHR LHR LHR HHR

| ME | Middle Ages | Modern Age | Post-M |

settlers | feudalism | crisis

economic shift (AD 1834)

Historical documents

capitalism

Montsec pathway (AD 1687)

pre-capitalism

Pallars war (AD 1484)

commercial intensification

black pest (AD 1348)

monarchy, nobles, strong houses (private property) land use diversification

wars, cooling lowland emigration depopulation

Carolingian conquest (AD 800)

land confiscation, intensive agriculture, animal fertlizers (sheep) (wheat, barley, oats, rye, olive, vine)

fire shifting cultivation

Palynological data

C1   R1 C2   R2

A1   A2

BI   BII

particles cm⁻² y⁻¹ (x10⁵)

25

20

15 *Pinus*

10

5

0

pollen %

80

60

40

20

0

crops + weeds

Charcoal

800   1000   1200   1400   1600   1800   CE

centuries | 8th | 9th | 10th | 11th | 12th | 13th | 14th | 15th | 16th | 17th | 18th | 19th

LAKE MONTCORTÈS (Core MON04-1A-1K)

LAKE MONTCORTÈS (Core MON04-1A-1K)

New morphotypes described

20 μm

IBB-40

IBB-44

IBB-46

IBB-47
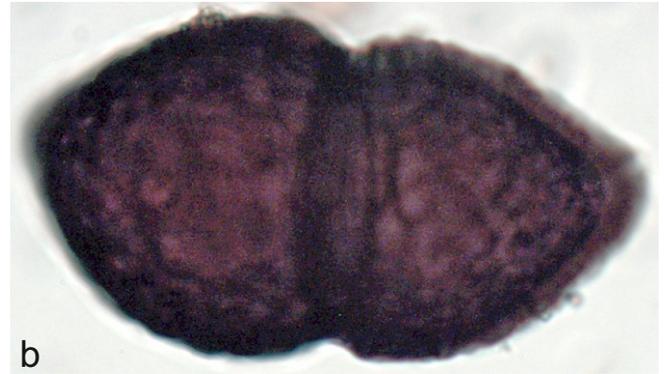
IBB-45

Plumatella sp. statoblasts

100 μm