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Clara Plancher, Didier Galop, Thomas Houet, Emilie Lerigoleur, Laurent Marquer, et al.. Spatial and temporal patterns of upland vegetation over the last 200 years in the northern pyrenees: Example from the Bassiès valley, Ariège, France. *Quaternary Science Reviews*, 2022, 294, 10.1016/j.quascirev.2022.107753 . hal-03779057

**HAL Id: hal-03779057**

**<https://hal.science/hal-03779057>**

Submitted on 19 Sep 2022

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## Title

Spatial and temporal patterns of upland vegetation over the last 200 years in the northern Pyrenees : example from the Bassiès valley, Ariège, France

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## **Abstract**

Quantitative estimates of past vegetation with a clearly defined spatial scale are a critical step to better understand the patterns and processes of changes in vegetation and land-cover over time and space. However, such estimates are difficult to obtain from pollen data due to their lack of spatial dimension and the inter-taxonomic differences in pollen production, dispersal, and deposition mechanisms. This study assesses the potential of the Landscape Reconstruction Algorithm (LRA) to reconstruct the spatial and temporal patterns of upland vegetation over the last 200 years in the Bassiès Valley, northern Pyrenees. We used well-dated pollen records from eight bogs and ponds and vegetation and land-cover data within a 1-km radius from each site to evaluate the LRA-based reconstruction of local land-cover. The LRA approach was then used to reconstruct the 200-year history of local land-use dynamics at 10 to 20-year intervals around each site in relation to land-abandonment. Our study shows that LRA-based estimates, in addition to allowing long-term reconstruction, (1) are more sensitive to vegetation composition changes over time and space compared to historical land-cover maps and pollen percentages, (2) improve the reconstruction of local vegetation compared to pollen percentages alone and (3) reveal site-specific land-cover trajectories. These trajectories distinguish four types of sites within the Bassiès valley despite the small-sized study area. Some sites have undergone strong variations in their land-cover composition over time (ESC and EM), and others have remained more stable but differing in their land-cover composition, either dominated exclusively by heathland (LEG and W1652) or by grassland (OT), or characterised by a dominance of heathland with intermediate proportions of grassland (FOUZ and SIG). These results highlight the variability of relationships between pastoral practices and land-cover in such a complex environment as a high altitude mountain cirque. The quantification of past vegetation dynamics provides opportunities for bridging the gap between researchers, policy makers and practitioners, and should be taken into account to further investigate the effect of long-term grazing activities on the past and modern plant and landscape diversity.

## Key words

Vegetation dynamics, Historical land-cover maps, pollen data, Landscape Reconstruction Algorithm, grazing activities, shrub encroachment, Western Europe, Pyrenees

## 1. Introduction

1       **1. Introduction**

2       The well-functioning of mountain ecosystems is closely linked to their biodiversity (Cardinale et al.,

3       2012; Loreau et al., 2001; Naeem et al., 1994) and provides ecosystem services essential to over 50%

4       of the world's population (Ariza et al., 2013; Egan and Price, 2017; Viviroli and Weingartner, 2004). In

5       European mountains, biodiversity and ecosystem services are particularly impacted by ongoing land-

6       cover changes (Engler et al., 2011; Körner, 2019; Körner and Spehn, 2002; Olsson et al., 2000; Payne

7       et al., 2017; Szczypta et al., 2013). After millennia of human activities, socio-economic changes since

8       the 1950s have led to a sharp decline in mountain agro-pastoral activities (MacDonald et al., 2000;

9       Price et al., 2022), particularly in the Pyrenees (Chevalier, 1954; Galop et al., 2011; Gragson et al.,

10      2015; Mottet, 2005). The abandonment of traditional pastoral practices has favoured the expansion

11      of dwarf shrub species, gradually leading to shrub encroachment and/or reforestation of sub-alpine

12      summer pastures (Carré, 2010; Kuemmerle et al., 2016; Pereira and Navarro, 2015). These recent

13      changes raise questions about the conservation and management of their biodiversity, closely linked

14      to the landscape configuration (i.e. spatial characteristics; Gardner and Engelhardt, 2008; Harlio et

15      al., 2019; Herrault et al., 2015) and composition (Freléchoux et al., 2007). Therefore, understanding

16      past land-cover dynamics is a research priority for the sustainable management of mountain

17      landscapes, ecosystems and resources (Bruley et al., 2021; Davies and Bunting, 2010; Gleeson et al.,

18      2016; Price et al., 2022; Willis et al., 2007).

19      Although long-term palaeoecological data, and pollen data in particular, are valuable for addressing

20      conservation biology issues (Froyd and Willis, 2008; Rull, 2010; Willis and Birks, 2006), they are still

21 underused in this field due to several methodological challenges (Willis and Bhagwat, 2010). While  
22 various approaches exist to transform pollen data into land-cover, most of them are not adaptable to  
23 the reconstruction of quantitative and local land-cover at a defined spatial scale (Fyfe et al., 2010,  
24 2015; Mazier et al., 2006; Pirzamanbein et al., 2014; Prentice et al., 1996). The Landscape  
25 Reconstitution Algorithm (LRA; Sugita, 2007a, 2007b) is currently the most appropriate approach to  
26 infer past quantitative vegetation cover composition within a defined area, namely the relevant  
27 source area of pollen (RSAP; Sugita, 1994), based on pollen data from lakes and bogs. Using a 2-step  
28 process that corrects for inter-taxonomic differences in pollen production, dispersal, and deposition  
29 mechanisms, the LRA approach estimates and distinguishes the relative abundances of plant taxa at a  
30 regional scale (REVEALS; Sugita, 2007a) from those around targeted sedimentary sites at a known  
31 local scale (LOVE; Sugita, 2007b). Ideally in mountain areas, applying the LRA would require pollen  
32 counts from large and small sites randomly distributed in both mountains and lowland areas in the  
33 region of interest to distinguish the regional from the local pollen signal using the REVEALS and LOVE  
34 models respectively (Marquer et al., 2020a). However, it is hard to achieve this scenario in reality, as  
35 suitable pollen sites in mountains are mainly small and located in sub-alpine or alpine zones  
36 (Simonneau et al., 2013). Based on simulated and empirical data, Marquer et al. (2020a)  
37 showed that, as long as multiple pollen sites are available, the application of LRA appears to provide  
38 reasonable estimates of regional and local vegetation even if the sites are systematically selected in  
39 the high-elevation patches, making the LRA approach a promising method for the reconstruction of  
40 mountain vegetation dynamics. They used a simulation experiment to clarify the biases affecting LRA  
41 estimates in the Bassiès valley (Auzat, French Pyrenees) and successfully tested its robustness, on  
42 three recent time windows, by comparing vegetation and land-cover data both within a 50-km radius  
43 around the Bassiès valley and within a 2-km radius from each site for evaluation of the REVEALS- and  
44 LOVE-based reconstruction of the regional and local plant cover.

45 This study is a step forward from that of Marquer et al. (2020a) in evaluating the potential of LOVE to  
46 reconstruct past local vegetation changes in mountainous areas. Based on a series of vegetation

47 maps available between 1942 and 2008 for the Bassiès valley, local-cover data were compared to  
48 those estimated by pollen percentages and LOVE-based reconstruction of vegetation around each  
49 site. The LRA approach was then applied at a fine spatial scale with a 10-20 year time resolution over  
50 the past 200 years to study the impact of land-abandonment on local vegetation composition, as this  
51 period illustrates significant socioeconomic upheavals in the Auzat area, ranging from  
52 overexploitation to agro-pastoral abandonment of summer pastures, reforestation, hydroelectric  
53 construction, migration from rural to urban areas, socio-economic transformation and the  
54 introduction of recreational activities (Carré, 2010; Houet et al., 2012; Vacquié et al., 2016). A  
55 previous study compared palaeoecological data (pollen, soil erosion and fire data) to documentary  
56 sources (demographic and pastoral data) to investigate the role of land-abandonment, linked to the  
57 decline of the sheep stock from ca 20,000 in the early 1800s to less than 1,000 in 2005, on vegetation  
58 dynamics and plant diversity on the Bassiès summer pastures (Galop et al., 2011). Pollen data  
59 revealed that a sharp increase in shrub species (*Calluna vulgaris* and *Juniperus*) and trees (*Pinus* and  
60 *Betula*) correlated with a loss of floristic diversity around a small peatbog (Galop et al., 2011).  
61 However, it is very unlikely that the vegetation dynamics at this specific site are uniform on the  
62 whole Bassiès valley scale, given the heterogeneous pressure of extensive pastoral activity on the  
63 vegetation (Deleglise, 2011; Gartzia et al., 2014; Mottet, 2005) and the ecological constraints linked  
64 to mountain topography (Anzini et al., 2013; Gartzia et al., 2014; Kampmann et al., 2008; Sanjuán et  
65 al., 2018).

66 Thus, understanding local-scale vegetation composition and patterning of the Bassiès summer  
67 pastures requires a multi-site approach to study the links between grazing activities and their impact  
68 on the landscape. Along with insights into the applicability and reliability of the LRA approach in a  
69 mountain context, this paper explores the reconstruction of the local land-cover composition and  
70 trajectories around multiple small sites over the last 200 years and discusses these trajectories in  
71 relation to the evolution of local pastoral practices.

72        **2. Material and methods**

73        **2.1 Study area**

74        The Bassiès valley is located within the Hercynian axial zone of the Pyrenees in the Auzat municipality  
75        of the High Vicdessos area. Its granitic base is punctuated by flat areas and concave depressions,  
76        remnants of the last glacial period. This topography has favoured the post-glacial appearance of small  
77        lakes and peatbogs. This upland area is characterised by an Atlantic mountain climate, with abundant  
78        rainfall (1640 mm per year), 30% of which falls as snow from November-December to April-May, and  
79        an average annual temperature of 6.6°C (Quintana-Seguí et al., 2008; Simonneau et al., 2013). The  
80        dominant winds are west and north-west, with speeds varying between 0 and 4 m.s<sup>-1</sup> (Szczypta et al.,  
81        2015).

82        The current dominant vegetation types in the Bassiès valley are heathlands followed by multiple-  
83        sized grassland patches mainly distributed on the slopes above the current tree-line at around 1600  
84        m. Heathlands are dominated by *Calluna vulgaris* or *Rhododendron ferrugineum*, associated with  
85        *Vaccinium myrtillus*, *Nardus stricta* and *Scirpus cespitosum*. Grasslands are dominated by patches of  
86        *Festuca eskia*, an endemic community characterised by poor forage quality, and patches of *Nardus*

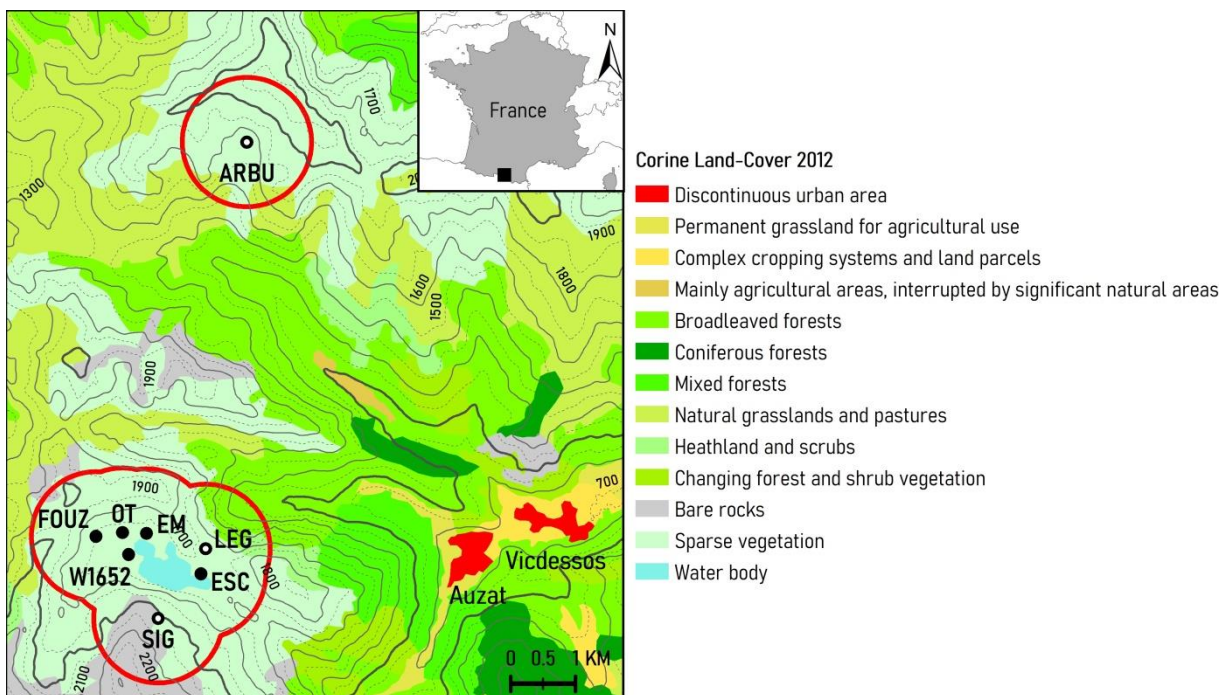


Figure 1: Location of the study area and sedimentary sites. Black dots: peat bogs; White dots: lakes; Red lines: Relevant Source Areas of Pollen.

87 *stricta* growing on wetter and more productive grasslands (Komac et al., 2014; Saule, 2018). Forest  
88 patches are concentrated on northern slopes, beech forests and clumps of mountain pine (*Pinus*  
89 *uncinata*) with understory layers of *R. ferrugineum* and *V. myrtillus*, are respectively located below  
90 and above 1600m.

## 91 **2.2 Datasets**

### 92 **2.2.1 Pollen records**

93 We used pollen records from eight small sedimentary sites (radius varying from 6 to 113m, [Table 1](#)):  
94 two lakes and five peat bogs in the Bassiès valley, and one lake (ARBU) in a neighbouring watershed 6  
95 km to the north ([Fig. 1](#)). All sites are above the current tree-line distributed between 1600 and 2000  
96 m a.s.l. ([Table 1](#)). The minimum and maximum distances between the Bassiès sites are 350m (W1652  
97 and OT) and 1730m (ESC and FOUZ) respectively. Raw radiocarbon dates, dated material, type of age-  
98 depth model at each individual site were previously published ([Table. 1](#)) and reviewed by Marquer et  
99 al. (2020a). Age-depth models of sediments were constructed by using both the  $^{210}\text{Pb}$  CRS  
100 (Constant Rate of Supply) model (Appleby, 2001) and the CLAM radiocarbon age depth model  
101 (Blaauw, 2010). To integrate chronological uncertainties, the pollen counts were pooled together for  
102 each 10-year time window between 1940-2013 cal AD and each 20-year time window from 1800 to  
103 1940 cal AD. Hereafter the time windows (TW) are referred to by their centre (e.g. TW1810 for 1800  
104 to 1820). Among the 14 TWs, the number of sites per TW varied from two (TW1850) to eight  
105 (TW1930, TW1955 and after TW1965) and the total sum of pollen counts varied from 2477 (TW1850)  
106 to 25509 (TW2005).

### 107 **2.2.2 Observed land-cover maps**

108 Local land-cover maps of the Bassiès valley for 1942, 1953, 1962, 1976, 1983, 1993 and 2008  
109 (Haunold, 2015; Houet et al., 2012) were suitable for the data-model comparison for the 7 most  
110 recent time windows (TW1945 to TW2005; [Fig.2](#)). The land-cover classifications were performed on  
111 panchromatic (1942-1983) or colour (1993 and 2008) aerial images with a geographic object-based



112 image analysis combining visual interpretation and automatic classification (Houet et al., 2012;  
113 Sheeren et al., 2012). Due to the different types of aerial images, the pre- and post-1993 land-cover  
114 maps differ in their land-cover types, except for broadleaved and mixed forests. For the pre-1993  
115 land-cover maps, the land-cover types include grasslands dominated by *Calluna*, grasslands  
116 dominated by other Ericaceae, Shrubs and low trees (Houet et al., 2012; Marquer et al., 2020a). The  
117 post-1993 land-cover types include Pine forest, *Calluna* heathland, Mixed heathland, *Rhododendron*  
118 heathland, Peatbogs, *Festuca* grassland and other grasslands.

119

## 120 **2.3 Methods**

### 121 **2.3.1 Reconstruction of vegetation composition over 200 years**

122 In the absence of large lakes, several studies have demonstrated that it is possible to use a network  
123 of small-sized sites to calculate the regional vegetation abundance with REVEALS, although error  
124 estimates are likely to be larger (Trondman et al., 2016). Hjelle et al. (2015) have argued that the  
125 larger the number of small sites used, the better the REVEALS estimates. Preliminary analysis showed  
126 that incorporating all available pollen sites from public (EPD) or private databases (PaleoPyr;  
127 Lerigoleur et al., 2015) within a 50-km radius around our study area did not significantly improve the  
128 REVEALS results. Therefore well-dated and high-resolution pollen data from eight sites within the  
129 High Vicdessos area (Fig.1) were used as input to the LRA, although not all sites cover the same time  
130 duration (Table 1).

131 We used the Leave-One-Out strategy (Efron and Tibshirani, 1998; Mazier et al., 2015; Sugita et al.,  
132 2010) to reconstruct local plant abundance around each target site. Pollen data from the 'target' site  
133 of each run were used as input to the LOVE model, but excluded from the REVEALS regional  
134 vegetation estimates. The resulting values are distance-weighted plant abundances (DWPA,  
135 expressed as percentage of total cover) within the Relevant Source Area of Pollen (RSAP) defined as  
136 the distance from which, for each site, the results for all taxa fall between 0 and 100%.

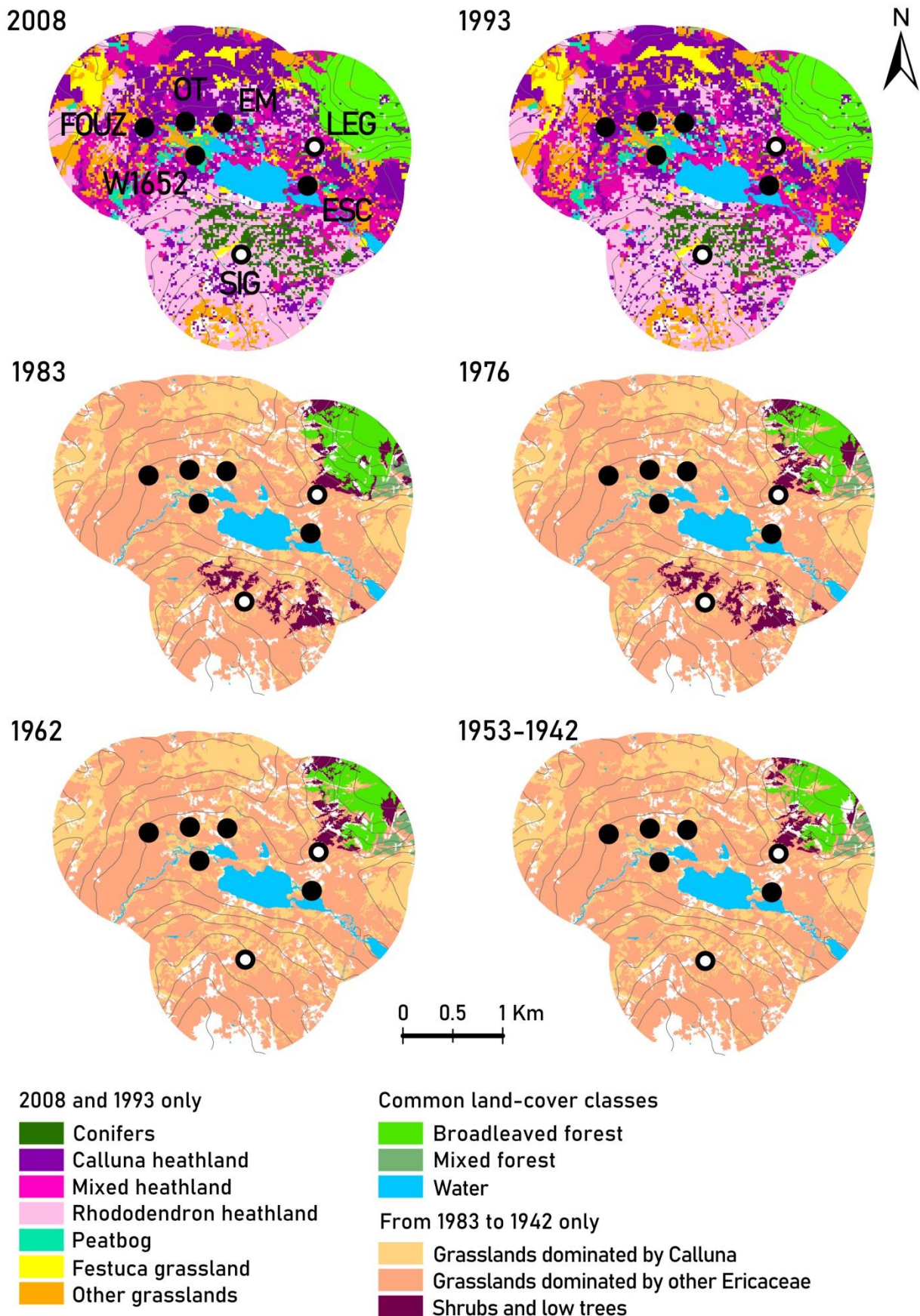


Figure 2: Land-cover maps used for comparison with pollen-based estimates (Pollen percentage or LOVE estimates) of vegetation composition from TW1945 to TW2005. Black dots: peat bogs; White dots: lakes.

Adapted from Marquer et al. (2020a).

137 The LOVE estimates are based on 18 taxa previously identified as dominant and characteristic taxa in  
138 this area (Marquer et al., 2020a). The Relative Pollen Productivity (RPP) and fall speed of pollen (FSP)  
139 are those established by Mazier et al. (2012, [Table 2](#)). In this study, Zmax, the maximum spatial  
140 extent of the regional vegetation from the centre of the study sites was set to 25 km, while it was set  
141 to 50 km by Marquer et al. (2020a), to better fulfil the LRA assumption of similarity between regional  
142 and local vegetation composition in our area (Sugita, 2007a) by excluding the cultivated areas in the  
143 most distant plains. All other conditions and parameters specific to the LRA are the same as those in  
144 Marquer et al. (2020a): airborne pollen transport was approximated by the Gaussian Plume model  
145 (Prentice, 1985; Sugita, 2007a, 2007b, 1994, 1993) for lakes (Sugita, 1993) and for peatbogs  
146 (Prentice, 1988, 1985), assuming a neutral atmospheric condition and a wind speed of 3 msec<sup>-1</sup>. The  
147 REVEALS.v6.2.4.exe and LOVE.6.4.4.exe computer programmes (Sugita, unpublished) were used for  
148 the LRA application.

149

## 150 [2.3.2 Numerical analysis](#)

### 151 [2.3.2.1 Map-based DWPAs](#)

152 For the comparison with the LOVE estimates and pollen percentages, the plant composition  
153 extracted from each land-cover map needs to be distance-weighted (Mazier et al. 2015). The  
154 proportions of the area (m<sup>2</sup>) occupied by individual land-cover type were estimated in successive  
155 concentric rings at each 5m-increment out to 1km from the centre of each site (ARBU excluded as no  
156 maps were available). The radius was chosen based on the results of the estimation of the RSAPs of  
157 the sedimentary sites (see section 3.1). Plant composition in each land-cover type ([Table 3](#)) was  
158 adapted from Marquer et al. (2020a) including recent botanical surveys for beech and mixed forest  
159 categories. Cumulative estimates of plant composition within a 1-km radius were calculated using a  
160 distance weighting method based on the Gaussian Plume Model and the FSP ([Table 2](#)), hereafter

161 referred to as DWPAs. For all calculations, we used ArcGIS 10.4, an R script (Binet, unpublished) and  
162 the “DWPACalculator.v7.3” (Sugita, unpublished).

#### 163 2.3.2.2 Dissimilarity indices

164 The reliability of reconstructions based on pollen proportions (PPs) or LOVE estimates (LOVEs) was  
165 evaluated according to their dissimilarity from the DWPAs, and the variability of land-cover  
166 trajectories was assessed through past-present dissimilarity. For this purpose, two dissimilarity  
167 indices based on squared chord distance were used:

- 168 - The Dissimilarity index between PPs and DWPAs (PPs-DWPAs) and between LOVEs and  
169 DWPAs (LOVEs-DWPAs) from TW1945 to TW2005, the period covered by the observed  
170 vegetation maps.
- 171 - The Dissimilarity index between Past and Present vegetation (PPD, Marquer et al., 2017,  
172 2014), calculated between the modern time window (TW2005) and each other time window,  
173 up to TW1945 for DWPAs (DWPAs-PPD) and up to TW1810 for both PPs (PPs-PPD) and LOVEs  
174 (LOVEs-PPD).

175 A Spearman rank correlation test between the number of pollen sites available at each time window  
176 and the interquartile ranges of PPs-PPDs and LOVE-PPDs was performed to test the influence of  
177 missing data on their variability.

#### 178 2.3.2.3 Land-cover reconstructions

179 The comparison between PPs, LOVEs and DWPAs was performed on four land-cover categories  
180 grouping all land-cover types of the observed maps (Table 3): Broadleaved forests (including  
181 broadleaved and mixed forests), Pine forest, Heathlands (including *Calluna* heathland, Mixed  
182 heathland, *Rhododendron* heathland, Shrubs and Low Tree and *Rhododendron* grassland), and  
183 Grasslands (including *Festuca* Grassland, Other Grasslands, *Calluna* grassland and Peatbogs). Each of  
184 the 18 taxa was assigned to one of the land-cover categories based on their dominance in each land-  
185 cover type (Table 3). The integration of floristic data from local forest inventories (Mazier et al., 2022)

186 explains the modification of the pollen taxon groupings compared to those of Marquer et al. (2020)  
187 which was based on expert judgement, especially the integration of *Abies* and *Picea* in the  
188 broadleaved forest instead of the conifers category (Table 3). The mean and standard errors of each  
189 category were obtained following the delta method (Stuart et al., 1994).

190 Exploration and testing of the LOVEs patterns across all pollen sites over the last 200 years was  
191 performed by direct gradient analysis. Preliminary Detrended Correspondence Analysis showed that  
192 the categorized LOVE dataset has a short gradient length (<2.2), therefore a linear-based method  
193 analysis was found suitable in this case (Ter Braak and Prentice, 1988). Principal components analysis  
194 (PCA) was run on log-transformed, standardised and categorised LOVEs and implemented by the R  
195 package VEGAN (Oksanen et al., 2013).

## 196 **3. Results**

### 197 **3.1 Relevant Source Area of pollen (RSAP)**

198 The RSAP represents the smallest scale for which local vegetation composition can be estimated  
199 (Sugita, 2007b). In our study, the RSAP estimates for the 14 time windows varied from 250 to 900m.  
200 Hereafter we assume that the area within a 1-km radius from each site is appropriate and suitable for  
201 the local scale of reconstruction of vegetation in the area. This RSAP was used to compare LOVE  
202 estimates (LOVEs) and DWPAs and was considered as the spatial unit of vegetation reconstruction  
203 around the sites.

### 204 **3.2 Dissimilarity between pollen-based estimates of vegetation composition (PPs or 205 LOVE estimates) and DWPAs**

206 Considering the 18 taxa and over the 7 time windows used for the comparison, the median  
207 dissimilarity index between LOVEs and DWPAs (LOVEs-DWPAs), ranging from 0.42 at TW1955 to 0.80

208 at TW2005, is always lower than the median PPs-DWPAs, ranging from 0.87 at TW2005 to 1.01 at  
 209 TW1945 (Fig. 3a). The interquartile ranges of LOVEs-DWPAs are also larger, except for TW1955.  
 210 The LOVEs are more accurate than pollen percentages, as evidenced by the lower LOVEs-DWPAs for  
 211 all TWs used for comparison (Fig. 3a), but accuracy varies between the four land-cover types (Fig. 3b).  
 212 Pine forest and broadleaved forest are the two categories with the smallest standard errors and  
 213 whose LOVEs are the most similar to the DWPAs (Fig. 3b). Heathland is always under-represented in  
 214 PPs whereas it is broadly similar between the LOVEs and DWPAs, though with high uncertainties. The  
 215 cover of grasslands is in general overestimated by LOVEs and underestimated by PPs relative to the  
 216 DWPAs. However, considering their uncertainties, LOVEs are more often equivalent to DWPAs than  
 217 PPs are.

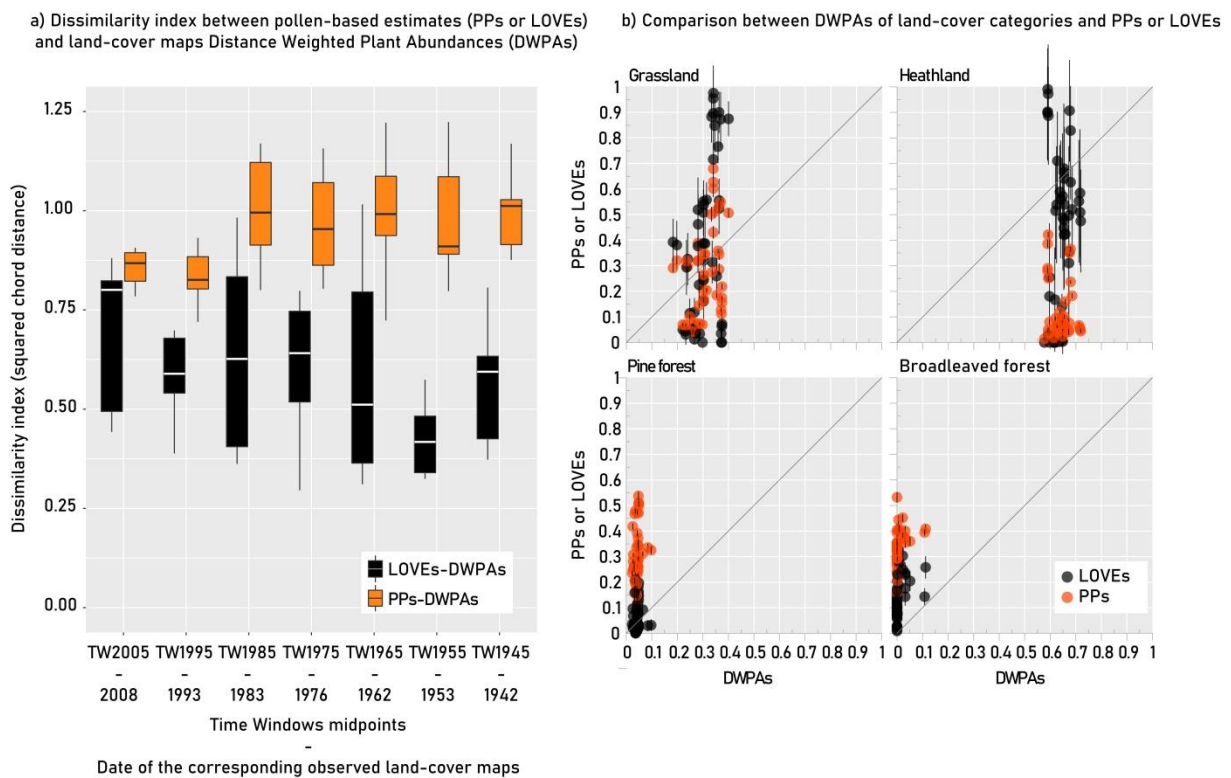


Figure 3: a) Evaluation of pollen-based estimates: Dissimilarity indexes between pollen-based estimates (PPs or LOVEs) with map-based DWPAs; b) Comparison of pollen-based estimates of land-cover categories with their map-based DWPAs. ARBU is excluded.

218 **3.3 Differences in dissimilarity between past and present vegetation (TW 2005) over**  
219 **time reflected by pollen proportions (PPs-PPD), LOVE estimates (LOVEs-PPD) and**  
220 **Distance-weighted plant abundance (DWPAs-PPD).**

221 The dissimilarity index between past and present vegetation (LOVEs-PPD, PPs-PPD or DWPAs-PPD)  
222 was calculated up to TW1945 for DWPAs-PPD and up to TW1810 for LOVEs and PPs-PPD (Fig. 4). No  
223 significant correlation was found between the number of available sites at each time window and the  
224 interquartile range of PPs-PPD ( $\rho=0.13$  and  $p\text{-value}=0.68$ ) or LOVEs-PPD ( $\rho=0.11$  and  $p\text{-}$   
225  $\text{value}=0.72$ ).

226 When available, DWPAs-PPD had a negligible median value (TW1995), intermediate between that of  
227 LOVEs-PPD and PPs-PPD, and the minimum between-site variability, indicated by minimum  
228 interquartile ranges. Over all time windows, LOVEs-PPDs had the largest and most variable median  
229 values (between 0.1 and 0.37, for TW1995 and TW1810) and interquartile ranges (at least 1.5 times  
230 larger than those of the PPs-PPDs, except TW1870 and TW1955). A first phase of high variability of  
231 LOVEs-PPDs can be distinguished at TW1810-TW1830, also corresponding to a first decrease in their  
232 median value. The PPD contraction observed at TW1850 is an artefact, as LEG was the only available  
233 site. A general trend of convergence towards their current composition (TW1870-TW1890) is then  
234 observed, with less than half the inter-site variability of the previous period. The LOVEs-PPD then  
235 become highly variable during the first half of the 20th century (TW1910-TW1945), with few  
236 markedly different sites (median off-centre towards the lower limit of the interquartile range, Fig.4;  
237 ESC, EM, Fig.5). Then the sites converge towards a higher median dissimilarity at TW1955, which  
238 drops drastically at TW1965 and then fluctuates slightly until TW1995 with a high inter-site variability  
239 that gradually decreases. LOVEs-PPD from sites ARBU, EM and ESC show greater variability over the  
240 last 200 years than LOVEs-PPD from other sites (Fig. 5). EM and ESC therefore have more influence  
241 on the variability of LOVEs-PPD than the other sites (ARBU being excluded from Fig.4). LOVEs-PPD for  
242 EM are particularly high for TW1910-TW1930, and remain stable and low after a sharp decrease at  
243 TW1945. The LOVEs-PPD at ESC first shows a decrease (TW1810-TW1870), then a phase of gradual

244 increase (TW1870-TW1965) and finally a rapid decrease until the present. Although all the other sites  
 245 show less variable LOVEs-PPD over time, a general increase in LOVEs-PPD can be seen around the  
 246 1950s (TW1945-TW1955).

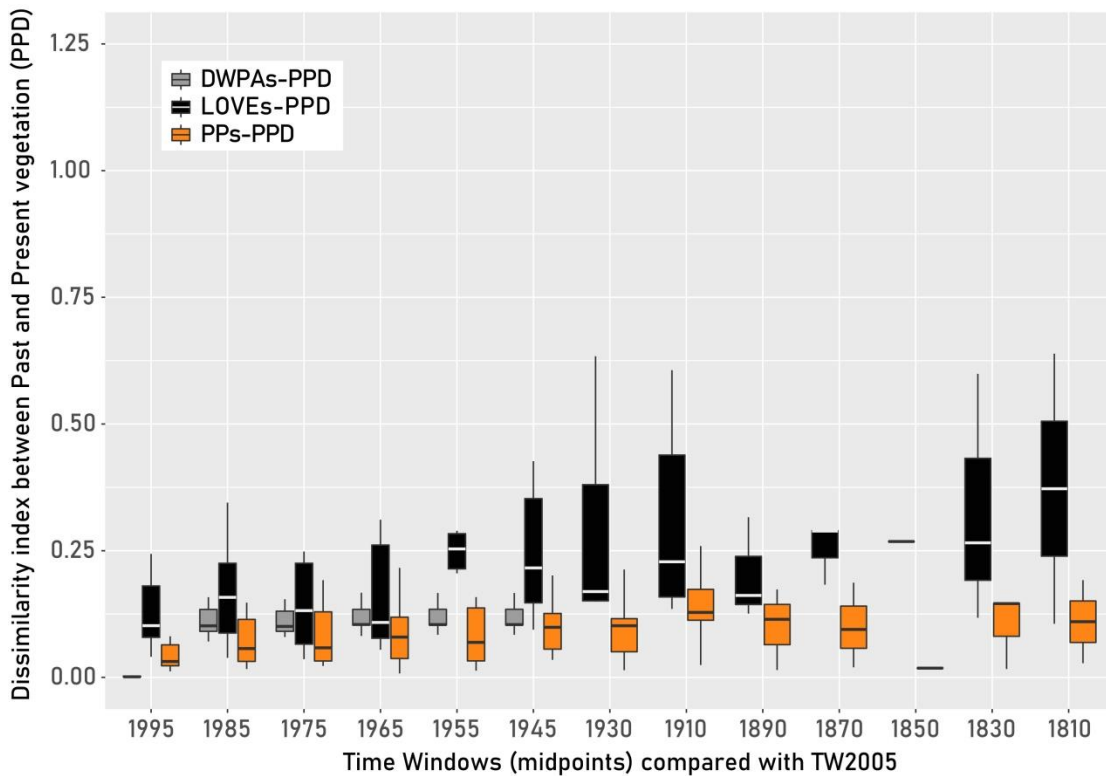


Figure 4: Land-cover dissimilarity with TW2005 composition revealed by Past-Present Dissimilarity indexes for DWPAs (DWPAs-PPD) or pollen-based estimates (PPs-PPD and LOVEs-PPD). ARBU is excluded.

247 **3. 4 LOVE-based reconstruction of land-cover composition and dynamics over 200**  
 248 **years**

249 Hereafter we will describe only the LOVE-based reconstructions of the four land-cover categories  
 250 (grassland, heathland, pine forest and broadleaved forest) over the last 200 years. LOVE estimates  
 251 revealed significant differences between and within sites, that can be classified into four types of  
 252 trajectories: highly variable sites (ARBU, ESC, EM, Fig. 5a), intermediate-grassland sites (FOUZ, SIG,  
 253 Fig. 5b), heathland-dominated sites (LEG, W1652 Fig. 5c) and one grassland-dominated site (OT, Fig.  
 254 5d).



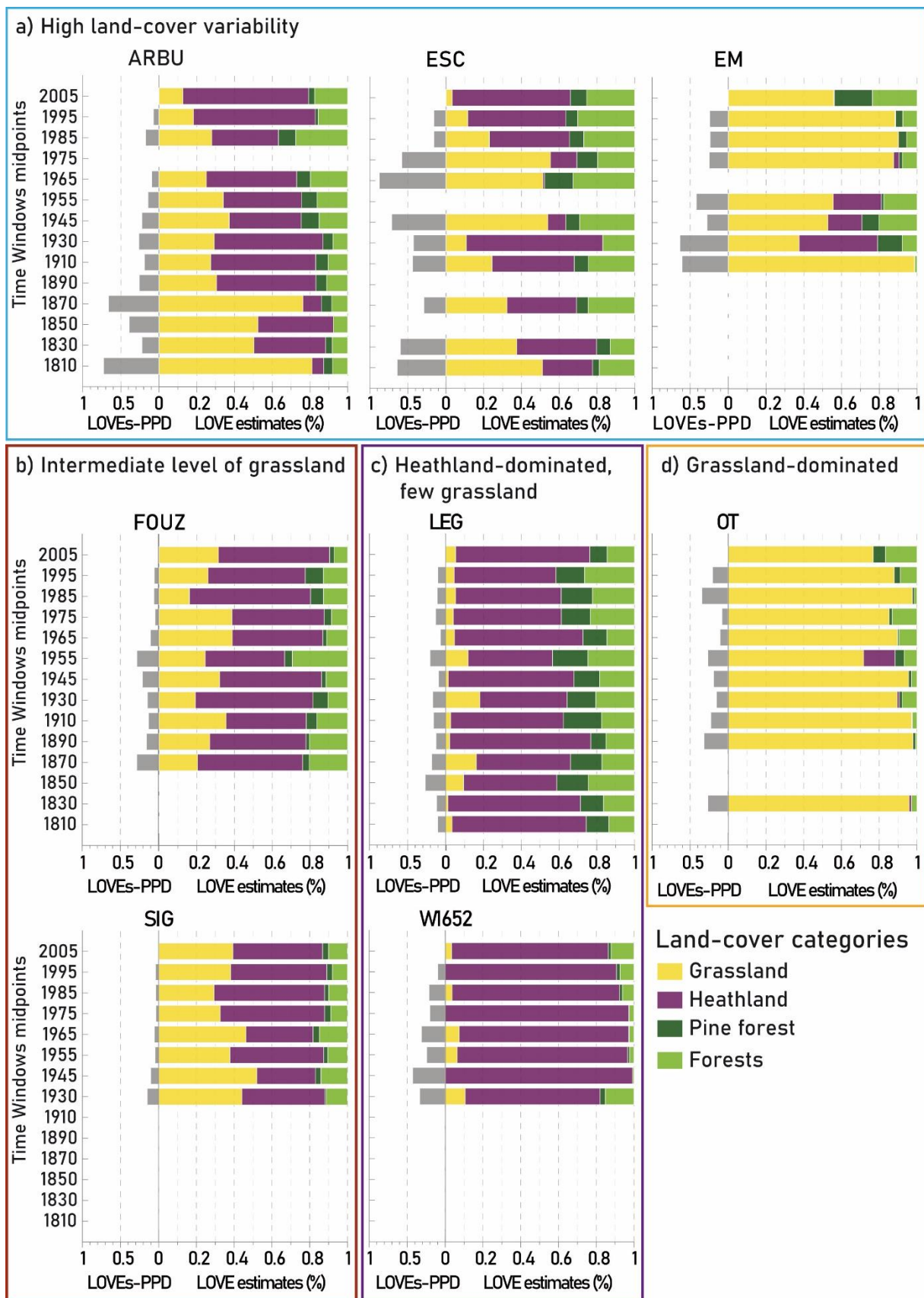


Figure 5: Site land-cover dissimilarity with TW2005 (LOVEs-PPD) and land-cover reconstruction over 200 years based on LOVE estimates.

255 Over the last 200 years, the landscape around ARBU, ESC and EM has changed from a predominance  
256 of grassland to a mosaic incorporating heathland and trees in greater proportions. At ARBU and ESC,  
257 the grassland cover has changed significantly since the early 1800s, with a decline in the 1800s,  
258 followed by an increase in the mid-1900s. This grassland increase was higher and lasted longer at ESC  
259 (+43% at TW1945, with 50-55% until TW1975) compared to ARBU (+9.8% between TW1910 and  
260 TW1945 with 37%). Grasslands then dropped to their lowest cover from 1985 to the present (12.7%  
261 and 3.2% at ARBU and ESC respectively). The heathland cover has gradually expanded since the  
262 1800s but declined in the mid-1900s and then increased until TW2005 (66.6% around ARBU and  
263 62.7% around ESC). Woodland cover slowly increased at both ARBU and ESC over the entire period.  
264 On the contrary, at EM, heathland, pine forest and broadleaved forest expanded sharply at TW1930  
265 (+41.5%, +12.9% and +6.6% respectively) while the percentage of grassland cover decreased  
266 drastically to 37.5%. It subsequently increased gradually while heathland decreased and eventually  
267 disappeared locally at TW1985. Wooded communities, although also declining until TW1985, reached  
268 their maximum cover at TW2005 (20.1% and 23.7% for pine forest and broadleaved forest).

269 The other sites exhibit fewer land-cover composition changes over the last 200 years. The landscape  
270 of LEG and W1652 was dominated by heathland (>45% at LEG and >71% at W1652) and almost no  
271 grassland (<2% at both sites), with a higher forest cover at LEG (>23% compared to a maximum of  
272 18% for W1652 at TW1930). Intermediate grassland sites, SIG and FOUZ, showed higher proportions  
273 and continuity of grassland, which has gradually increased since the minimum cover reached at  
274 TW1985 (29% at SIG and 16% at FOUZ). While the TW2005 land-cover composition at SIG is  
275 intermediate between the compositions experienced since TW1930, that of FOUZ is a special case  
276 characterised by a very low proportion of tree categories. Finally, OT is the only grassland-dominated  
277 site with no heathland during the whole period, except at TW1955. This peat bog also shows an  
278 irregular increase in the proportions of broadleaved forest and pine forest since TW1930, reaching  
279 their maximum proportions at TW2005.

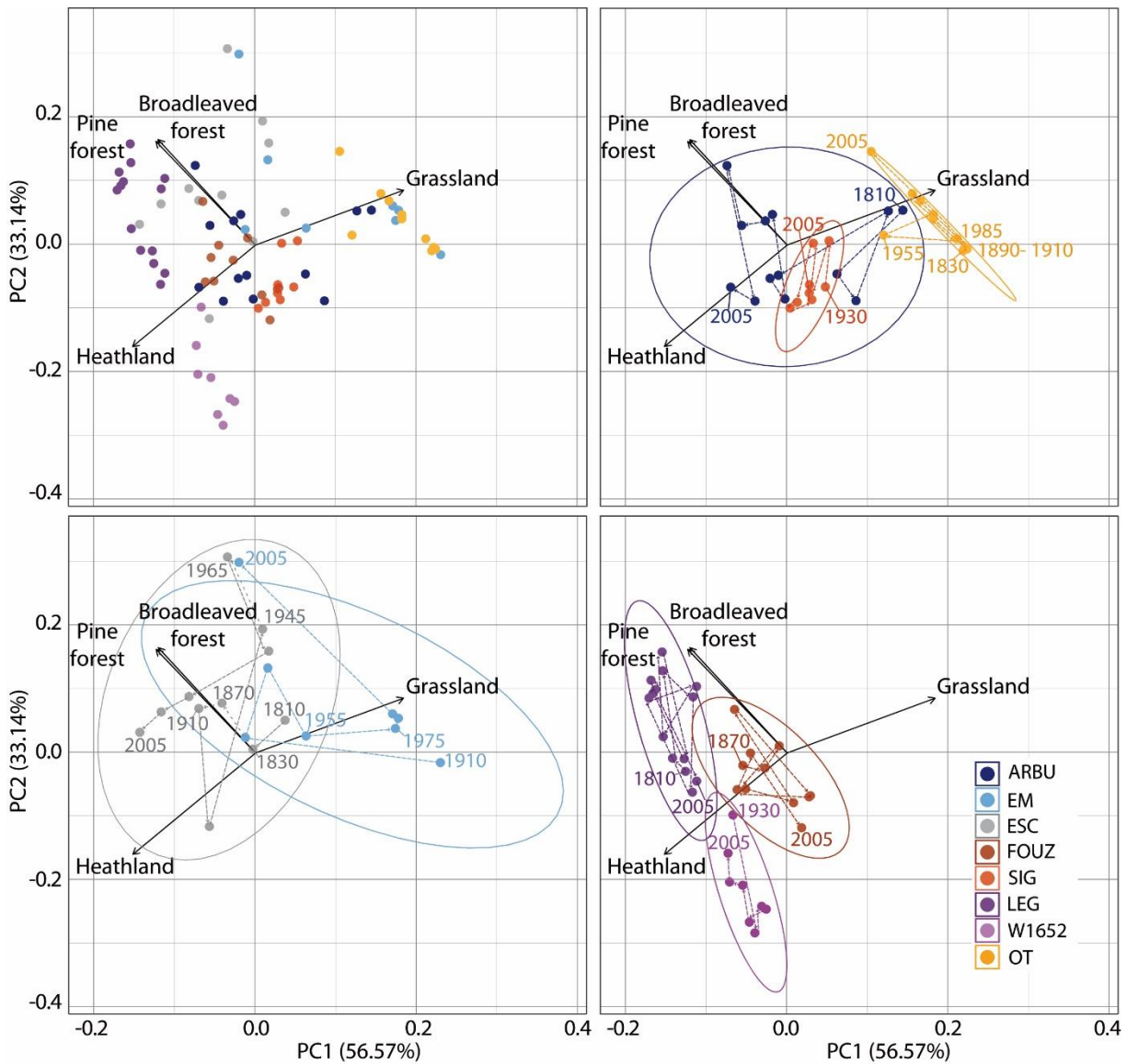


Figure 6: Site land-cover trajectories over time (TW midpoints) resulting from the PCA analysis of the LOVE-based land-cover composition. The top left-hand corner shows all the sites together, the others represent sites whose trajectories overlap as little as possible for a better visibility of the results.

280 PCA analysis was used to explore time trajectories of land-cover based on the LOVE estimates of  
 281 individual sites over the 14 TWs (Fig.6) and to show their spatial and temporal variability within and  
 282 between sites. The first two PCA axes capture 89.7% of the total variance of the data (i.e. 56.6% and  
 283 33.1% respectively) and explain significantly the variability of the dataset with an inertia rate of  
 284 90.09% (> 61.86% the 0.95 quantile of a normal random distribution). Axis 1 represents a gradient of

285 openness and contrasts wooded land-cover TWs with grassland TWs. It is highly correlated with LOVE  
286 estimates from site OT ( $r^2=0.97$ ). Axis 2 separates heathland from other land-cover types. Land-cover  
287 around the sites over the 14 TWs can be distinguished into heathland-dominated TWs (bottom left of  
288 the PCA axis), heathland-grassland-influenced TWs (bottom right), grassland-dominated TWs (top  
289 right) and wood-covered TWs (top left). With the exception of the land-cover trajectory of W1652  
290 which remains exclusively heathland-dominated, all site trajectories fluctuate between these land-  
291 cover influences, and no trajectory is similar to another, reflecting the high spatial and temporal  
292 variability of land-cover in the study area.

## 293 **4. Discussion**

### 294 **4.1 Advantages and disadvantages of pollen data and historical maps for past land-** 295 **cover reconstruction**

#### 296 **4.1.1 Map-based approach to estimate changes in vegetation composition**

297 Time series of spatially-explicit land-cover maps appear to be less sensitive than pollen percentages  
298 and LOVE estimates to record plant composition changes (Fig.4). The sources of errors in the map-  
299 based estimates of land-cover changes relate to the interpretation of original maps (derived from  
300 black and white or colour infra-red aerial images), to the accompanying descriptions in terms of land-  
301 cover types and plant composition, and to the harmonization of land-cover types between maps. The  
302 land-cover maps from Houet et al. (2012) were initially designed to evaluate the magnitude, the  
303 direction and the dynamics of land-cover changes from 1942 to 2008 over a larger area than Bassiès.  
304 Their results indicated a landscape enclosure process that began in the 1990s on the highest parts  
305 (Bassiès area included) with an increase in forest cover from 2 to 9%. However, aerial images might  
306 underestimate the increase in tree and shrub cover sensed by the LOVE-based estimates. Mapping  
307 historical mountain vegetation at a high spatial resolution is challenging as the classification of aerial  
308 images is often hindered by i) the lack of spectral discernibility between vegetation types, ii) the

309 difficulty of delineating the boundaries of different vegetation types in a heterogeneous landscape  
310 mosaic, iii) the fact that a given vegetation formation may have a different phenology due to  
311 seasonal or composite classes of vegetation; iv) the shadow effect from nearby trees or cliffs (Cots-  
312 Folch et al., 2007; Dirnböck et al., 2003; Dobrowski et al., 2008; Li and Shao, 2014; Zhang et al.,  
313 2020). The overall accuracy of the 2008 classified map was assessed at 82.5% when comparing the  
314 classified land-cover types with their corresponding ground truth data (Haunold, 2015). As field data  
315 from older maps are not available, it is assumed that a similar accuracy was achieved for 1993 using  
316 the same method. Accuracy for the land-cover maps pre-1993 cannot be assessed and therefore can  
317 partly explain the difficulty of evaluating the shrub encroachment (increase in Ericaceae plants)  
318 before 1993.

319 Plant composition in each land-cover type was approximated by a local botanical expert for land-  
320 cover maps pre-1993 and by a botanical survey on the valley of Bassiès for the two recent maps. The  
321 vegetation surveys were based on 116 spermatophyte species that were further grouped into pollen  
322 morphological types. Taxonomic harmonization and the application of the distance-weighted method  
323 to land-cover maps are necessary for a comparison of the LOVE- and map-based vegetation  
324 estimates (see section 2.3.2.1). For this study we worked with 18 pollen taxa representing 80% to  
325 98% of the total plant cover. Since most of the 18 taxa are present in several land-cover types ([Table](#)  
326 [3](#)), the transition from one land-cover type to another between two maps does not necessarily imply  
327 a large change in 18 taxa-based composition, also explaining the minimal change in composition  
328 estimated from the maps in this study. Given this limitation, the tree land-cover types are the best  
329 point of comparison between the LOVE-based and map-based vegetation composition estimates,  
330 since (1) they are the only types dominated by trees ([Table 3](#)), meaning that a change from a non-  
331 tree to a tree cover type (or vice versa) is detectable based on the 18 taxa, and (2) their  
332 nomenclature is the same for all maps from 1942 to 2008.

333 The relative overestimation of grassland cover in LOVE estimates compared to land-cover maps is  
334 similar to that described in several studies (Cui et al., 2014; Mazier et al., 2015; Nielsen and Odgaard,

335 2010). To a lesser extent heathland cover is also overestimated in our study. The best explanation is  
336 directly and irreversibly linked to our assumptions of assigning each taxon to a unique land-cover  
337 category, while the taxa which dominate heathlands are ubiquitous taxa present in most other land-  
338 cover types. In spite of the sources of error and drawbacks discussed above, land-cover maps have  
339 been widely used in other studies (Cui et al., 2014; Hjelle et al., 2015; Marquer et al., 2020a; Nielsen  
340 and Odgaard, 2010, 2004; Overballe-Petersen et al., 2013; Poska et al., 2014) as they constitute a  
341 unique opportunity to evaluate LOVE estimates against independent data.

342

#### 343 **4.1.2 Potential and limitation of the LRA approach for land-cover reconstruction in mountain areas**

##### 344 **4.1.2.1 Site selection, pollen productivity and dispersal in mountains**

345 The importance of the site-selection strategy when applying the LRA approach for reconstruction of  
346 vegetation and land cover has been widely acknowledged (Abraham et al., 2017; Hjelle et al., 2015;  
347 Marquer et al., 2020a; Trondman et al., 2016). In mountain areas, the complex topography imposes  
348 sampling small sites above the tree line (Simonneau et al., 2013), influencing the evaluation of long  
349 distance pollen transport from lower altitudes (Fall, 1992; Leunda et al., 2017; Li et al., 2017;  
350 Markgraf, 1980; Ortu et al., 2006) - an important step for an objective reconstruction of local  
351 vegetation (Sugita, 2007b, 2007a). This constraint is responsible for an underestimation of regional  
352 tree taxon proportions by REVEALS, and thus for their overestimation in the local vegetation by LOVE  
353 (Marquer et al., 2020a). In the present study, this overestimation is the highest for sites closer to tree  
354 stands (LEG, ESC, EM, results not shown). Both LOVE and DWPA reconstructions are based on the  
355 Gaussian Plume Model for pollen dispersal that gives greater importance to pollen arriving from  
356 shorter distances (Prentice, 1985; Sugita, 2007a, 2007b, 1994, 1993), especially for pollen types with  
357 a high fall speed such as *Abies* and *Fagus*. Thus the overestimation caused by the mountain site  
358 sampling bias is amplified when sites locally record high proportions of arboreal pollen due to their  
359 geographical proximity to tree stands. The use of a Lagrangian Stochastic Model (LSM) as pollen

360 dispersal scheme (Kuparinen et al., n.d.; Theuerkauf et al., 2016, 2013) instead of a GPM could help  
361 pollen-based mountain vegetation reconstructions, but more work needs to be done before the LSM  
362 scheme can be adopted (Marquer et al., 2020b). Overall, the LRA approach is a significant  
363 improvement in pollen-based mountain vegetation reconstruction at the local- and landscape-scales  
364 over pollen percentages alone as it reduces the overestimation of broadleaved and pine forests.  
365 Therefore the LOVE results provide an accurate estimate of heathland and grasslands (Fig.3), the  
366 dominant land-cover types in Bassiès (i.e. covering 86% of the surveyed area on the 2008 land-cover  
367 map).

368 Most LRA reconstructions assume that pollen production is constant over space and time.  
369 Differences in abiotic (e.g. geology, soil types, and climate), biotic (e.g. genetics, species' range limits,  
370 demography, spatial structure of vegetation, and succession stages), and anthropogenic (e.g. land-  
371 use, grazing pressure, etc.) factors might – and in some cases were shown to – influence pollen  
372 productivity estimates (Broström et al., 2008, 2004; Gaillard et al., 2008; Matthias et al., 2012;  
373 Sjogren et al., 2006; Sugita et al., 2010a; van der Knaap et al., 2010; Waller et al., 2012).

374 For example, while dendrochronological analyses show the presence of some mature pine trunks  
375 with a 706-year chronology (1305-2010, Coughlan, 2012) within a 1-km radius of SIG, the LOVE-based  
376 conifer cover estimated here is very low and underestimated over recent time windows (data not  
377 shown). This underestimation may be caused partially by young trees that do not produce pollen in  
378 great quantities, i.e. *Pinus* reaches its flowering age at 20 years (Matthias et al., 2012). Moreover, SIG  
379 is located 260m above other sites, at 2000m. Under harsh climatic conditions, the flowering age of  
380 *Pinus* may be even later, and at this altitude the period of pollinisation may be reduced to a couple of  
381 days and be climate-dependent as has been shown along a latitudinal gradient (Hicks et al., 2001;  
382 Mazier et al., 2012), although the evidence to support this is limited.

383 Concerning herb species, they are likely to have a lower pollen productivity in pastures than in hay  
384 meadows, especially if grazing pressure is high, leading to an underestimation of grassland cover  
385 (Baker, 2012; Vera, 2000). Therefore changes in LOVE-based grassland cover might be related to

386 changes in grazing pressure through time. In the context of land abandonment in our study area,  
387 grazing pressure has decreased gradually over the last 200 years (Galop et al., 2011, Fig. 7), and has  
388 never exceeded 0.3 GLU/ha (Galop, unpublished), a value considered as low to medium compared to  
389 extensive alpine farms (Dobremez and Borg, 2015). Therefore LOVE-based grassland changes more  
390 likely reflect changes in grassland area rather than changes in grazing intensity around sedimentary  
391 sites. Further empirical studies on the effect of land-use management, and grazing pressure in  
392 particular, on pollen productivity would help understand pollen-vegetation relationships within  
393 complex managed landscapes (Bunting et al., 2016). Coprophilous fungi can also be used as  
394 independent indicators of grazing intensity (Cugny et al., 2010) and are currently being analysed in  
395 the Bassiès sediment cores (Galop unpubl.) They will further help elucidate grassland vegetation-  
396 grazer interactions and assess the spatio-temporal variability of pastoral activity between our pollen  
397 sites.

398 Another important issue is the availability of estimates of relative pollen productivity (RPP) for the  
399 constituent taxa. This study used a set of RPP-means per taxon from Mazier et al. (2012) created by  
400 calculating the mean of all RPP values compiled from previous studies in NW Europe excluding  
401 outliers (Mazier et al., 2012). An alternative set of RPP-means recently published by Githumbi et al.  
402 (2022) with more taxa, Mediterranean taxa in particular, was tested but did not produce better  
403 results. Whilst the RPP dataset from Mazier et al. 2012 would probably differ from RPP values  
404 derived from modern pollen and vegetation data in the Pyrenees, it is the best one at hand for now.

405

#### 406 [4.1.2.2 Impact of departures from assumptions on LOVE-based estimates](#)

407 This section discusses the main departures from the basic assumptions and necessary conditions for  
408 the LRA approach in landscapes with complex topography and wind field in mountain regions.

409 The LRA approach assumes that no source plants for pollen grow on the sedimentary basin (Sugita,  
410 2007a). Therefore, applying the LRA approach for reconstruction using pollen records from peat bogs  
411 could be problematic as some herb taxa (Poaceae, Cyperaceae, Ericaceae and *Calluna vulgaris*)



412 frequently grow on peatbog surfaces and produce pollen but can also originate from other  
413 vegetation types (Andersen and Berglund, 1994; Cui et al., 2014, 2013; Nielsen et al., 2012;  
414 Trondman et al., 2016). In our case, the sites associated with the highest overestimates of grasslands  
415 are indeed those where Cyperaceae dominates the herbaceous pollen assemblage (OT and EM, data  
416 not shown), while the site concerned by the overestimation of heathlands has high proportions of  
417 *Calluna vulgaris* (W1652, data not shown). As plant species are grouped into pollen morphological  
418 type and one taxon may belong to distinct land-cover categories, it is not possible to distinguish  
419 pollen coming from on-site peat bog vegetation from surrounding and distant vegetation. The sedge  
420 family (Cyperaceae) is abundant in several vegetation types such as peat bogs and mixed heathlands  
421 and *Calluna vulgaris* - dominant in the heathland communities - is also found in various land-cover  
422 types (Table 3). Within the sedge family, *Scirpus cespitosum* is the dominant plant species. Although  
423 its presence is assumed to be characteristic of marshy peat bogs (Saule, 2018), in our study area it is  
424 favoured by the local microtopography and the granitic rocks controlling water retention and is  
425 therefore widespread across several land-cover types (Table 3). Those two taxa have higher LOVE  
426 estimates around peat bog sites compared to lake sites. Several studies have excluded both or one of  
427 them from the pollen records in recognition of their likely strong local signal (Fyfe et al., 2018;  
428 Nielsen et al., 2012), however *Calluna* and Cyperaceae are widespread across our study area and are  
429 not restricted to peat bogs. Therefore, they have been included as important components of the  
430 upland vegetation.

431 Another issue is the inclusion of insect-pollinated taxa; it would violate one the LRA assumptions that  
432 pollen transport is predominantly airborne. Mazier et al. (2012) excluded entomophilous taxa from  
433 the REVEALS reconstructions to produce European land-cover reconstruction. However, plant  
434 communities above the tree line, and particularly the widespread heathland types, are dominated by  
435 insect-pollinated taxa such as Ericaceae (e.g. *Rhododendron* spp. and *Vaccinium* spp.) and *Calluna*  
436 *vulgaris* (Table 3) (Marquer et al., 2020a). Moreover, the development of these dwarf shrub taxa in  
437 mountain regions following pastoral abandonment represents a scientific challenge as its drivers and

438 impacts on biodiversity and ecosystem functionality are still not well understood (Eldridge et al.,  
439 2011; Galop et al., 2011; García-Ruiz et al., 1996; Gartzia et al., 2016; Koch et al., 2015; Pasche et al.,  
440 2004). As suggested by former studies (Mariani et al., 2017; Marquer et al., 2020a), however, this  
441 study also demonstrates that the LRA approach is efficient for reconstructing vegetation and local  
442 land-cover, in particular heathland cover, when entomophilous taxa are included.

443

## 444 **4.2 LOVE-based reconstruction of spatial heterogeneity in past vegetation**

445 Previous studies have already demonstrated vegetation patterning and composition differences using  
446 pollen percentages only (Davies and Tipping, 2004; Fyfe, 2012; Fyfe and Woodbridge, 2012; Poska et  
447 al., 2008a) or LRA-based estimates (Cui et al., 2014, 2013; Fyfe et al., 2018; Hultberg et al., 2014;  
448 Mehl et al., 2015; Mehl and Hjelle, 2016; Poska et al., 2018; Prøsch-Danielsen et al., 2020). Few  
449 studies have focused on the last centuries, with a temporal and spatial resolution high enough to  
450 capture the short-term land-use changes that occurred during certain critical time intervals such as  
451 the last two hundred years (Allen et al., 2020; Marquer et al., 2020a; Mazier et al., 2015). This period  
452 witnessed an unprecedented turnover from “traditional” to postmodern landscapes characterized by  
453 significant differences in the dynamics, speed and scale of mountainous landscape change (Cevasco  
454 and Moreno, 2013). To our knowledge, our study is the first one to explore the LRA approach to  
455 reconstruct small-scale land-cover reconstruction based on several nearby small-sized sites with a  
456 temporal resolution of 10 to 20 years over the last 200 years.

457 A considerable advantage of the application of LRA is the estimation of the RSAP, which delimits the  
458 area of local vegetation reconstruction. For Bassiès sites, RSAPs vary from 250m to 900m across the  
459 14 time windows. Fluctuating RSAPs over time may have been caused by variations in landscape  
460 configuration at regional or local scales (Sugita, 1994). However, it is common to set a constant RSAP  
461 for the LRA application, allowing a direct comparison of reconstructions between sites and between  
462 time windows (Fredh et al., 2019; Mazier et al., 2015). We therefore set this RSAP at 1km, which is in  
463 line with the RSAPs obtained by Marquer et al. (2020a) using the Gaussian plume dispersion model

464 (663-1038 m), but smaller. The estimation of generally smaller RSAPs here is consistent with the  
465 exclusion from the regional reconstruction area used for REVEALS of lowland cereal crops present  
466 between 25 km and 50 km around Bassiès (see section 2.3.2). Indeed, the inclusion rare taxa can lead  
467 to the estimation of larger RSAPs (Bunting et al., 2004; Hellman et al., 2009).

468 The RSAPs obtained here are rather low given that they mainly fluctuate between 1000-2000m in  
469 most studies carried out on small to medium sites on plains or plateaus in Europe and China (Cui,  
470 2013; Hellman et al., 2009; Hjelle and Sugita, 2012; Poska et al., 2008b). It is likely that the small-scale  
471 heterogeneity of the vegetation at Bassiès as well as the preponderance of herbaceous taxa explain  
472 this result, as RSAPs are generally smaller in open grass-dominated landscapes or with a mosaic of  
473 fine-grained vegetation (Broström et al., 2005; Bunting et al., 2004; Hellman et al., 2009; Li et al.,  
474 2017; Matthias et al., 2012; Poska et al., 2011). The complex topography of the environment could  
475 also have an influence on the RSAPs of the study sites, but other applications of LRA in a mountain  
476 context would be necessary to better understand this influence.

477 Because of the small distance between sites (<1730m), the RSAPs overlap and create a contiguous  
478 study area of less than 9km<sup>2</sup>, particularly suited to the small-scale study of the Bassiès landscape.

479 LOVE-based land-cover reconstructions pointed out site land-cover specificities, not easily recognized  
480 by the pollen percentages or the land-cover maps (Fig.4), and reflect part of the heterogeneity of the  
481 Bassiès vegetation despite the close proximity and the overlapping of the site RSAPs. The dissimilarity  
482 index between past and present LOVE-based estimates over the last 200 years highlighted the time  
483 trajectory of vegetation composition and its variability over time within the study area (Fig.4) or at  
484 each individual site (Fig.5). The PCA results showed convergences or divergences in land-cover  
485 composition changes between or within sites (Fig 6). Our results indicate that variability in land-cover  
486 composition over time is heterogeneously spread across the studied landscape, some sites showing  
487 much more variable land-cover trajectories (ARBU, EM, ESC, Fig.5, Fig.6). Considering their respective  
488 land-cover histories, the current vegetation composition around these sites is a peculiar case,  
489 characterised either by the lowest recorded grassland cover dominated by heathland (ARBU, ESC), or

490 by a grassland dominated cover with heathland disappearance and maximum tree cover (EM).  
491 Assessing the current land-cover situation of the sites with a greater time perspective than is possible  
492 with photo-interpretation is particularly important for better management of these areas (Bruley et  
493 al., 2021). Although the other sites are less variable over time, their composition differs, reflecting  
494 the local variability of land cover in the Bassiès valley: some are dominated by heathland (LEG and  
495 W1652), others have similar proportions of heathland and grassland (SIG and FOUZ), while one site is  
496 dominated exclusively by grassland (OT). The more or less intense and sustained increase in grassland  
497 cover recorded at most sites during the first half of the 20th century indicated that LOVE-based  
498 reconstructions could also distinguish common land-cover trends, which may result from common  
499 drivers of land-cover changes within the valley.

500 While not all sites show high variability in land-cover composition, it is very likely that the land-cover  
501 configuration has fluctuated under the influence of land-use changes over the last 200 years,  
502 particularly the abandonment of pastoralism (Mimet et al., 2016). Although the site-specific spatial  
503 structure of vegetation within the RSAP is still impossible to assess quantitatively using the LRA  
504 approach alone, further studies will couple these results with new modelling approaches to  
505 reconstruct the spatial and temporal distribution of plant taxa within the Bassiès area (Plancher et al.  
506 in prep.)

507

### 508 **4.3 Impact of pastoral abandonment on shrub encroachment dynamics over 200** 509 **years**

510 Local land-cover variability in mountains is controlled by a range of variables including biotic and  
511 environmental constraints (e.g. climate, soils, slope, aspect...), and disturbance regimes (i.e. human  
512 impact). At the local scale of Bassiès, assuming that neighbouring sites experience similar climatic  
513 conditions, climate change can be considered to have had little control over the spatial variability of  
514 land-cover. Microtopography and anthropogenic controls are most likely the significant determinants

515 of vegetation variability between the Bassiès sites, in particular grazing management. Over the last  
516 200 years, the sheep stock has sharply decreased in the whole area of Auzat (Fig. 7). Uplands of  
517 Bassiès were the first to be abandoned due to their low profitability compared to more accessible  
518 and productive grasslands in the surrounding summer pastures (local herders, personal  
519 communication). The cessation of this extensive activity favours the overgrowth of woody plants by  
520 removing the selection pressure it exerted against the woody plants (Corona Lozada, 2018; Deleglise,  
521 2011; Gartzia et al., 2016). Following this cessation, the most significant factor favouring grassland  
522 encroachment by woody plants is their proximity to established heathlands and forests (Dorée et al.,  
523 2001; Gartzia et al., 2014). However, of the three sites closest to the current tree-line (LEG and ESC)  
524 or pine stands (SIG), only ESC shows a clear decrease in grassland cover following Auzat pastoral  
525 decline (Fig.7), in favor of heathland mainly, and deciduous and pine forest to a lesser extent (Fig.6).  
526 Variability of the time trajectory of land cover between the Bassiès sites may be related to  
527 microtopography, and to the spatial and temporal pattern of local pastoral activities.

528 There is evidence that pastoral activities are spatially heterogeneous and not congruent at landscape  
529 scale (Kohler, 2004; Rook et al., 2004b), although pastoral data of Auzat do not allow this local  
530 variability to be taken into account. The selection of grazing areas and the type of livestock that can  
531 be shepherded depend mainly on the natural and artificial barriers, herbage density and quality,  
532 water availability, proximity of a herder's cabin and rotational grazing systems (Anderson and  
533 Kothmann, 1980; Rice et al., 1983; Rook et al., 2004a; Vacquié et al., 2016). Traditional management  
534 of Bassiès uplands was grazing by cows on the most accessible, flatter areas with better forage  
535 quality, and mainly by sheep on remote, steeper and poorer areas, from spring to autumn (Vacquié  
536 et al., 2016). Extensive grazing cessation in such a complex area may have led to contrasting effects  
537 on the landscape, depending on the type of livestock and the productivity of the formerly grazed  
538 grasslands (Corona Lozada, 2018; Deleglise, 2011; Gartzia et al., 2016; Wehn et al., 2011), leading to  
539 different land-cover trajectories around the sites (Fig. 5, Fig.6, Fig.7).

540 Our results demonstrate that the local vegetation composition around LEG has always been  
541 dominated by heathland and forests over the last 200 years. Whilst there are no precise historical  
542 maps available in the 1800s, forests were in fact present in 1850 on the sloping area north of LEG  
543 according to the first ordnance survey map (French National Mapping Agency, IGN). Pastoral activity  
544 around LEG is attested by the presence of several herders' cabins near the lake but was abandoned  
545 in the early 19<sup>th</sup> century (Galop, unpublished). Therefore its influence on the vegetation composition  
546 within a 1-km radius around LEG was likely too low in the 1800s to perceive the effect of its  
547 abandonment from a pollen point of view. Grasslands around SIG and FOUZ were grazed until 2002  
548 (local herders, personal communication), confirming the LOVE-based grassland cover results. In  
549 addition, the high elevation of SIG makes it less vulnerable to encroachment following abandonment  
550 (Gartzia et al., 2016, 2014; Montané et al., 2010).

551 Moreover, uplands have been maintained by fire for centuries to restore their pastoral value when  
552 grazing pressure is too low (Galop et al., 2011), especially encouraged by the European Common  
553 Agricultural Policy created in 1962. In the 1970s, fire was punctually used to clear abandoned land  
554 colonised by shrubby vegetation (*Calluna vulgaris*) on southern slopes in the north of our study area  
555 (Galop et al., 2011). Higher grassland cover recorded at OT and EM could thus be explained by both  
556 surrounding grazing activities and the regular use of fire and clearings to limit the development of  
557 heathland on sunny slopes. It is therefore likely that the increase in forest cover recorded at both  
558 sites, which are today further from the tree stands than LEG, ESC and SIG, reflects the development  
559 of tree formations in the margins of their RSAPs.

560 Although it is widely acknowledged that pastoral abandonment since the 1950s has led to scrubland  
561 and forest expansion in European mountains (Améztegui et al., 2010; Chauchard et al., 2007;  
562 MacDonald et al., 2000; Pereira and Navarro, 2015), this study shows that the vegetation  
563 composition dynamics are far more complicated at the upland scale where traditional practices are  
564 partly constrained by a complex topography (Sebastià et al., 2008). Our results underline the  
565 importance and potential of the LRA approach to improve the spatial resolution of pollen-based

566 reconstructions of past land-cover changes, for a better understanding of their drivers and their  
 567 potential legacy to the biodiversity of these endangered environments.

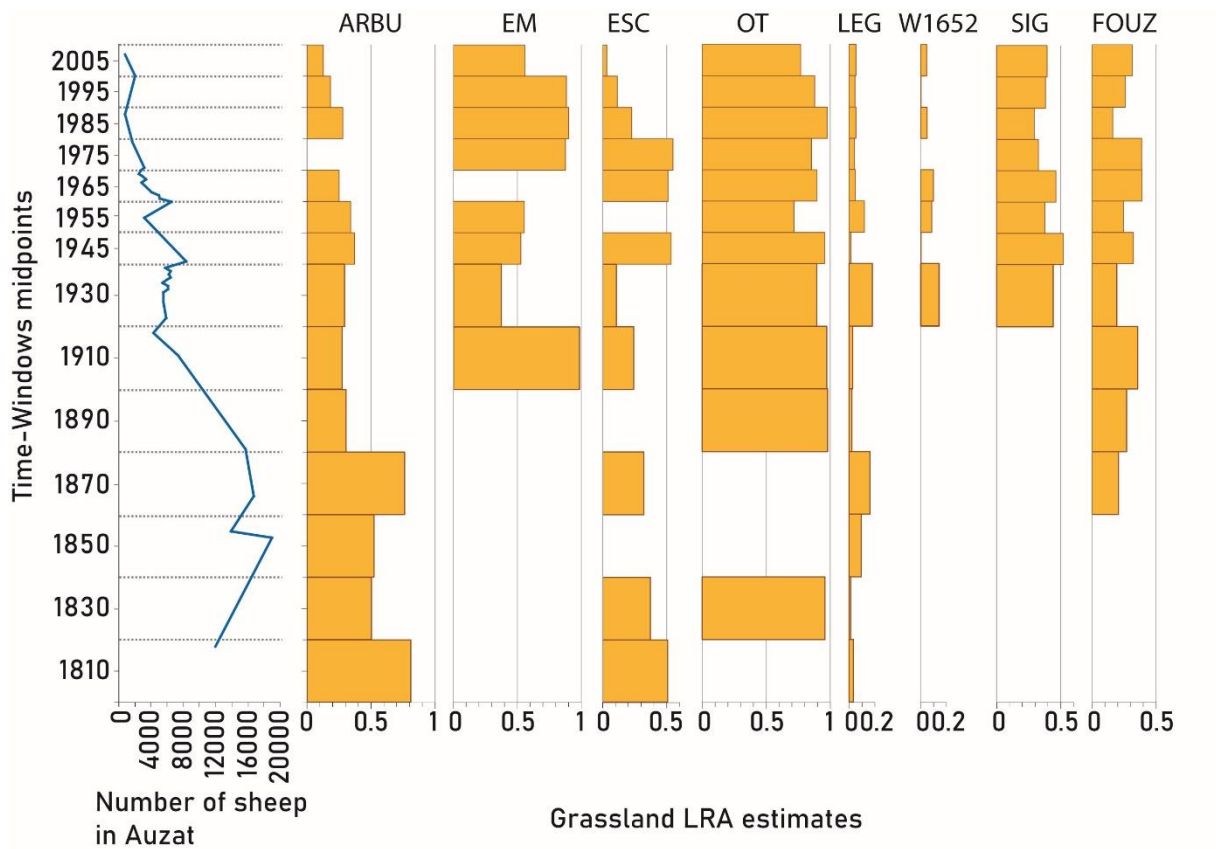


Figure 7: Auzat pastoral load (Galop et al., 2011) and LOVE estimates of grassland proportion

568 **5. Conclusion**

569 Spatially explicit reconstructions of past land-cover in mountain areas are currently needed but  
 570 remain limited due to the high heterogeneity of mountain vegetation, which is difficult to infer from  
 571 pollen data. This study highlights several advantages of applying the LRA approach for reconstruction  
 572 of local vegetation and land-cover in the past: (i) LOVE-based estimates, in addition to allowing long-  
 573 term reconstruction, are more sensitive to vegetation composition changes over time and space  
 574 compared to historical land-cover data and pollen percentages, and (ii) LOVE-based estimates  
 575 improve the reconstruction of local vegetation compared to pollen percentages alone and reveal site-

576 specific land-cover trajectories. This study provides opportunities for bridging the gap between  
577 researchers, policy makers and practitioners by initiating a dialogue between them and raising their  
578 awareness of the applied potential of palaeoecology, the LRA approach in particular, to advance  
579 mountain conservation. An understanding of local- to landscape-scale changes over time and space is  
580 essential to further investigate the effect of long-term pastoral practices on past and modern plant  
581 and landscape diversity. Further studies will develop modelling approaches to generate LOVE-based  
582 land-cover maps to reconstruct both the composition and the configuration of past local vegetation.  
583 Combined with precise pastoral data now available on the study area, this will provide insights into  
584 how geophysical and socio-demographical drivers can shape the long-term land-cover changes and  
585 how the strength of these drivers may vary geographically according to site-specific conditions  
586 (Odgaard et al., 2018)

#### 587 **Acknowledgements**

588 This paper forms part of C. Plancher doctoral thesis co-supervised by F. Mazier and D. Galop and  
589 funded by the University Toulouse 2 Jean Jaurès. The data were funded and provided by the ANR  
590 JCJC TRAM (ANR-15-CE01-0008) (Trace metal legacy on mountains aquatic ecogeochemistry) and  
591 ANR-10-JCJC-1804 MODE-RESPYR (Modeling Past and future land cover changes in the Pyrenees)  
592 projects coordinated respectively by G. Le Roux and T. Houet, the PEPS CNRS BIOPAST and POPEYE  
593 projects coordinated respectively by D.Galop and F. Mazier. This work was carried out within the  
594 framework of the Observatoire Homme-Milieu Pyrénées Haut Vicdessos (headed by D. Galop) and  
595 (co)funded by the ANR under the LabEx DRIIHM ANR-11-LABX0010 as part of the DYVAH, GEOSPAT  
596 and PASTSERV projects. S. Sugita was partially supported by grants from the Estonia Research Council  
597 (IUT18-9; PRG1471). Special thanks are due to Elizabeth Rowley-Jolivet for proofreading the article.



## Tables:

Table 1: Sites characteristics and age/depth models references. Lat.:Latitude ; Long.:Longitude

Bassin type	Names	Acronym	Lat. (D.D)	Long. (D.D)	Elevation (m)	Radius (m)	Time windows without pollen data	Age/depth model
Lakes	Arbu	ARBU	42.821	1.437	1740	113	TW1975	<a href="#">Marquer et al. (2020)</a>
	Legunabens	LEG	42.764	1.431	1680	58	-	<a href="#">Marquer et al. (2020)</a>
	Sigriou	SIG	72.754	1.422	2000	66	TW1810-TW1910	<a href="#">Simonneau et al. (2013)</a>
Bogs	Escale	ESC	42.761	1.43	1630	40	TW1850 ; TW890 ; TW1955	<a href="#">Hansson et al. (2017)</a>
	Etang mort	EM	42.766	1.419	1670	36	TW1810-TW1890 ; TW1965	<a href="#">Hansson et al. (2017)</a>
	Fouzes	FOUZ	42.766	1.41	1720	13	TW1810-TW1850	<a href="#">Marquer et al. (2020)</a>
	Orry de Théo	OT	42.766	1.415	1680	31	TW1810 ; TW1850	<a href="#">Galop et al. (2011)</a>
	W1652a	W1652	42.763	1.416	1660	6	TW1810-TW1910	<a href="#">Hansson et al. (2017)</a>

Table 2: LRA parameters for targeted taxa (from Mazier et al., 2012)

Land-cover type	Pollen taxa	RPP and standard errors	Fall speeds of pollen (m/s)
Broadleaved forest	<i>Abies</i>	6.88 ± 1.44	0.12
	<i>Betula</i>	3.09 ± 0.27	0.024
	<i>Corylus</i>	1.99 ± 0.19	0.025
	<i>Fagus</i>	2.35 ± 0.11	0.057
	<i>Fraxinus</i>	1.03 ± 0.11	0.022
	<i>Picea</i>	2.62 ± 0.12	0.056
	<i>Quercus</i>	5.83 ± 0.15	0.035
	<i>Tilia</i>	0.8 ± 0.03	0.032
Pine forest	<i>Juniperus</i>	2.07 ± 0.04	0.016
	<i>Pinus</i>	6.38 ± 0.45	0.031
Heathland	<i>Calluna vulgaris</i>	0.82 ± 0.02	0.038
	Ericaceae	0.07 ± 0.04	0.038
Grassland	Comp. SF. Cich.	0.16 ± 0.02	0.051
	Cyperaceae	0.87 ± 0.06	0.035
	<i>Plantago lanc.</i>	1.04 ± 0.09	0.029
	Poaceae	1 ± 0	0.035
	<i>Potentilla-t</i>	1.19 ± 0.13	0.018
	<i>Salix</i>	1.22 ± 0.11	0.022

Table 3: Harmonisation of land-cover types into land-cover categories used for LRA-based reconstruction and their associated 18 taxa-based composition. Coloured backgrounds highlight the maximum proportion of each taxon, justifying their assignment to the land-cover category of the same background colour. \*this type is botanically assimilated to the 2008-1993 mixed heathland type. \*\*: <0.005%; Broad.: Broadleaved; Mix.: Mixed; Rhodo.: Rhododendron; Dom.: Dominated by; Vulg.: *vulgaris*; Comp. SF. Cich.: Compositae SubFamily Cichorioideae; lanc.: *lanceolata*; -t:-type.

Land-cover categories used in this study		Broad. forest		Pine forest	Heathland			Grassland					
Land-cover types from maps		Broad.	Mix.	Pine forest	<i>Calluna</i>	Mix. / <i>Shrubs and low trees*</i>	Rhodo.	Dom. <i>Calluna</i>	Dom. other Ericaceae	Pasture land	Festuca	Other	Peat bogs
Corresponding maps		all maps		2008-1993 / 1983-1942			1983 to 1942			2008-1993			
18 taxa- based composi tion (%)	<i>Abies</i>	4.7	22.2	-	-	**	-	-	-	-	-	-	-
	<i>Betula</i>	4.3	1.2	**	0.01	-	-	-	-	-	-	-	-
	<i>Corylus</i>	12.4	-	-	-	-	-	-	-	6.1	-	-	-
	<i>Fagus</i>	49.5	55.0	-	-	-	-	-	-	-	-	-	-
	<i>Fraxinus</i>	4.5	-	-	-	-	-	-	-	-	-	-	-
	<i>Picea</i>	0.2	-	-	-	-	-	-	-	-	-	-	-
	<i>Quercus</i>	0.1	-	-	-	-	-	-	-	-	-	-	-
	<i>Tilia</i>	3.3	-	-	-	-	-	-	-	-	-	-	-
	<i>Juniperus</i>	0.02	-	6.3	4.1	0.7	0.8	1.1	5.0	-	0.9	-	-
	<i>Pinus</i>	-	-	32.4	0.2	2.0	**	-	-	-	-	-	-
	<i>Calluna vulg.</i>	**	**	15.3	53.3	22.6	10.7	16.8	10.0	-	6.1	4.3	5.4
	Ericaceae	9.0	16.5	43.9	16.0	14.0	72.5	5.6	67.0	6.1	4.9	7.2	5.4
	Comp. SF. Cich.	0.01	0.3	0.03	0.6	0.03	0.02	5.6	2.0	6.1	2.3	0.01	3.2
	Cyperaceae	1.6	2.7	0.06	4.4	42.2	2.0	11.2	5.0	12.2	2.7	26.8	43.0
	<i>Plantago lanc.</i>	-	-	-	**	-	-	1.1	-	3.7	-	**	-
	Poaceae	8.8	2.0	1.9	19.1	17.2	12.1	56.2	10.0	61.0	79.7	60.6	37.6
	<i>Potentilla-t</i>	1.7	-	0.01	2.2	1.3	1.8	2.2	1.0	3.7	3.4	1.1	5.4
	<i>Salix</i>	-	-	-	**	-	-	-	-	1.2	-	-	-

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