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4 5 **Post-disturbance vegetation dynamics during the Late Pleistocene and the** 6 **Holocene: an example from NW Iberia**

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22 23 **Abstract**

24
25 There is a wealth of studies dealing with the reconstruction of past environmental changes and their
26 effects on vegetation composition in NW Iberia, but none of them have focussed specifically on the
27 post-disturbance dynamics (i.e. the type of response) of the vegetation at different space and time
28 scales. To fill this gap, we analysed the record of pollen and non-pollen palynomorphs (NPP) of a 235-
29 cm thick colluvial sequence spanning the last ~13,900 years. The aims were to detect the changes in
30 vegetation, identify the responsible drivers and determine the type of responses to disturbance. To
31 extract this information we applied multivariate statistical techniques (constrained cluster analysis and
32 principal components analysis on transposed matrices, PCA_{tr}) to the local (hydro-hygrophites and NPP)
33 and regional (land pollen) datasets separately. In both cases the cluster analysis resulted in eight local
34 and regional assemblage zones, while five (local types) and four (regional types) principal components
35 were obtained by PCA_{tr} to explain 94.1% and 96.6% of the total variance, respectively. The main drivers

36 identified were climate change, grazing pressure, fire events and cultivation. The vegetation showed
37 gradual, threshold and elastic responses to these drivers, at different space (local vs. regional) and time
38 scales, revealing a complex ecological history. Regional responses to perturbations were sometimes
39 delayed with respect to the local response. The results also showed a ecosystem resilience, such as the
40 persistence of open *Betula*-dominated vegetation community for ~1700 years after the onset of the
41 Holocene, and elastic responses, such as the oak woodland to the 8200 cal yr BP dry/cold event. Our
42 results support the notion that palaeoecological research is a valuable tool to investigate ecosystem
43 history, their responses to perturbations and their ability to buffer them. This knowledge is critical for
44 modelling the impact of future environmental change and to help to manage the landscape more
45 sustainably.

46

47 **Key-words:** palynology; vegetation composition; vegetation response; principal component analysis;
48 transposed matrix; Holocene; NW Iberia.

49

50 1. Introduction

51

52 Environmental and climatic changes were frequent during the Late Quaternary; some even
53 relatively abrupt ([Mayewski et al., 2004](#)). Many of them have been reliably recorded by
54 environmental archives in the form of long-term records, which contain key information that
55 offers a unique opportunity to study the patterns of ecological change ([Willis et al., 2010](#);
56 [Williams et al., 2011](#)). Among these records those related to vegetation dynamics are the most
57 investigated. As with any other natural system, vegetation has some resilience to withstand
58 environmental change. However, the capacity to buffer changes, either natural or
59 anthropogenic, varies at different spatial and time scales, and sometimes involves gradual or
60 abrupt modifications/reorganisations of the structure and functioning in response to
61 perturbations ([Holling, 1973](#); [Dearing, 2008](#)). Thus, there is an obvious need to understand the
62 post-disturbance responses of vegetation since disturbance is a key factor structuring its
63 composition. As [Ritchie \(1986: 72\)](#) proposed “*The central issue of palaeoecologists is to*
64 *measure accurately the response of vegetation to environmental change and to express*
65 *differing patterns of response in quantitative terms*”.

66 [Carrion et al. \(2010a\)](#) outlined the patterns of vegetation change for the Late
67 Quaternary in the Iberian Peninsula, emphasising the strong regional differences, mainly
68 related to the Eurosiberian and Mediterranean biogeographical regions. While in the
69 Mediterranean region a large heterogeneity in vegetation change has been pointed out, in the
70 Eurosiberian one, comprising the north and northwest, as well as in other areas with Atlantic

71 influence, a more homogeneous picture has emerged. Moreover, in the Eurosiberian area the
72 vegetation change generally follows the Central European floristic model, where a rapid spread
73 of mesophytic species occurred at the onset of the Holocene. Overall, the last ~14,000 years of
74 palaeoenvironmental and vegetation changes in NW Iberia have been investigated using a
75 variety of proxies, including pollen, non-pollen palynomorphs (NPP), charcoal, plant
76 macroremains, diatoms, geochemistry and molecular markers, in several types of archives
77 such as lacustrine deposits (Allen et al., 1996; Santos et al., 2000; Muñoz Sobrino et al., 2001,
78 2004; Leira and Santos, 2002; Jalut et al., 2010; Moreno et al., 2011; López-Merino et al.,
79 2011a), mires (Muñoz Sobrino et al., 1997; Martínez Cortizas et al., 1999, 2005; Mighall et al.,
80 2006; López-Merino et al., 2010a, 2011b; Morales-Molino et al., 2011; Schellekens et al.,
81 2011), colluvial soils (Kaal et al., 2008, 2011; Costa Casais et al., 2009; Carrión et al., 2010b),
82 coastal sediments (Santos and Sánchez-Goñi, 2003; García-Amorena et al., 2007), marine
83 sediments (Desprat et al., 2003; Muñoz Sobrino et al., 2007a), and archaeological deposits
84 (López-Sáez et al., 2003, 2009; López-Merino et al., 2010b). These studies were mainly
85 undertaken in mountain areas and showed complex histories where climate, fire, vegetation
86 change and human activities, e.g. animal husbandry, agriculture and mining, were ultimately
87 responsible for past and current landscape configuration (Ramil-Rego et al., 1998; Muñoz
88 Sobrino et al., 2005, 2007b; Martínez Cortizas et al., 2005, 2009). Briefly, from the onset of the
89 Holocene to ~2000 years ago forests expanded and were important in the landscape.
90 Indicators of human impact started to appear around ~7600 years ago, increasing at ~4500
91 years cal BP with widespread phases of deforestation since Roman times onwards (Jalut et al.,
92 2010). But despite the many studies focussing upon past vegetation, climate trends and impact
93 of human activities, investigations comparing vegetation composition and post-disturbance
94 dynamics are lacking. The same is true for other parts of the Iberian Peninsula, with notable
95 exceptions for the SE of Iberia. Firstly, the study of the pollen record of Siles Lake by Carrión
96 (2002), which covers the last ~20,300 years, showed gradual, rapid and threshold responses,
97 which involved complete changes in forest composition, as well as abrupt shifts at the local
98 scale, pointing towards hydroclimatic variations. Moreover, lags in vegetation development in
99 comparison with limnological stages were identified at the centennial scale. Secondly, in
100 another study carried out by Carrión et al. (2001) in the Villaverde Lake, timelags in vegetation
101 response to environmental change were detected, especially in response to climate
102 amelioration at the beginning of the Holocene, pointing towards the resilience of established
103 *Pinus* populations during ~2200 years, as well as decadal shifts in the pollen record since the
104 mid-Holocene. Finally, Gil-Romera et al. (2010a) defined ecosystem functioning and resilient

105 behaviour at long-term time scales at two sites. At Zoñar, it seems that disturbance promoted
106 changes in biodiversity and landscape structure, shifting from one state to another; while in
107 Gádor several stable phases linked to arid conditions and the spread of the grassland were
108 detected.

109 In other parts of Europe a similar picture emerges, as only a few long-term ecological
110 studies have focused upon vegetation response and most of them do not contextualise the type
111 of response to perturbation. Some exceptions include the research done by [Tinner et al. \(2000\)](#)
112 in the Alps, in which they identified several possible responses of plants to fire of medium and
113 high frequency; by [Hellberg et al. \(2003\)](#) in Sweden, where vegetation dynamics and
114 disturbance history has been detected in several deciduous forests; or by [Feurdean et al.](#)
115 [\(2010\)](#) in Romania, where they explored the potential driving factors for the vegetation change
116 in eight pollen datasets, but also the response of the vegetation at different spatial and time
117 scales in the sense of differentiation and homogenization, i.e. reduction or increase in similarity,
118 an increasingly important feature for modern-day conservation plans. However, in other parts of
119 the world this approach has been applied more often, i.e. the disturbance history of a *Tsuga*-
120 dominated forest in New England (Massachusetts, [Foster and Zebryk, 1993](#)), the threshold
121 responses and differential resilience behaviour of vegetation to environmental perturbation in
122 Madagascar ([Virah-Sawmy et al., 2008](#)), and the alternating open and encroaching phases in
123 the Ethiopian savannah that showed a non-linear response to environmental change ([Gil-](#)
124 [Romera et al., 2010b](#); also see [Willis et al., 2010](#); [Gil-Romera et al., 2010a](#) for more examples).
125 All the examples stress the importance of such knowledge for conservation and management
126 of ecosystems and to better assess the consequences of future changes.

127 In this paper we present a palynological study of a colluvial soil (PRD-4), spanning the
128 last ~13,900 years, sampled in Campo Lameiro (Pontevedra, NW Iberia). Campo Lameiro is
129 considered a suitable site because, apart from the fact that it is located in an archaeological
130 area with one of the most important collections of pre-historic rock art in Europe, several
131 studies developed there recently (e.g. [Kaal et al., 2008, 2011](#); [Costa Casais et al., 2009](#);
132 [Carrión et al., 2010b](#); [Kaal, 2011](#)) showed that colluvial soils are suitable archives for
133 palaeoenvironmental research. The objectives of this work were to i) detect changes in the
134 vegetation composition and their drivers, and ii) decipher the post-disturbance dynamics, at
135 regional and local scales. In addition, in order to get statistical information about vegetation
136 composition and response to environmental change, novel multivariate analyses were applied.

137

138 **2. Materials and methods**

139

140 2.1. Study area

141

142 The PRD-4 sequence is located in the Rock Art Park of Campo Lameiro (42°32'N 8°31'W,
143 Pontevedra, NW Spain, Fig. 1), in a local depression on the isolated hill Monte Paradela (260-
144 320 m a.s.l.). The area is located in the Atlantic/Eurosiberian climate region, with mild (mean
145 annual temperature of 15 °C) and humid (mean annual precipitation of 1200 mm) climatic
146 conditions (Martínez Cortizas and Pérez Alberti, 1990). Currently, *Pinus pinaster*, *Quercus*
147 *robur*, *Pteridium aquilinum* and heathlands with different species of *Erica* and *Calluna vulgaris*
148 are the main components of the vegetation, with remnants of *Eucalyptus globulus* plantations,
149 *Ulex* and *Cytisus*, which are periodically eliminated since 2003 with the setting up of the
150 archaeological park. In the valleys, the riparian vegetation is composed of *inter alia* *Alnus*
151 *glutinosa*, *Corylus avellana*, *Fraxinus excelsior*, *Ulmus glabra*, *Populus*, *Betula alba* and
152 *Crataegus monogyna*.

153

154 2.2. Sampling and palynological analysis

155

156 A soil monolith (PRD-4, 235 cm-thick, Fig. 2) was sampled from a trench and sliced into 5 cm
157 sections. Samples were treated following the classic chemical methodology (Moore et al.,
158 1991) to obtain pollen, spores and other NPP with concentration in heavy liquid (Goeyry and de
159 Beaulieu, 1979). Palynological counting was conducted at 400x under the light microscope,
160 and the average total land pollen sum (TLP) was 575 terrestrial pollen grains, excluding hydro-
161 hygrophytes and NPP (expressed as percentages of the TLP). The average sum of hydro-
162 hygrophytes and NPP was 170 palynomorphs. Palynomorphs were well preserved and no
163 taphonomic problems were detected. The identification was aided by the reference collection of
164 the Archaeobiology laboratory (CCHS, CSIC, Madrid), identification keys and atlases (Moore et
165 al., 1991; Reille, 1992). NPP classification follows the nomenclature proposed by the Hugo de
166 Vries (HdV) laboratory of the University of Amsterdam. Pollen diagrams were obtained using
167 TILIA (Grimm, 1992, 2004).

168

169 2.3. Radiocarbon dates and chronology

170

171 Six samples were selected for ¹⁴C dating using the AMS technique. The ¹⁴C dates (Table 1)
172 were calibrated using the IntCal09.14C calibration curve (Reimer et al., 2009). The age-depth

173 model was obtained using the Clam software developed by [Blaauw \(2010\)](#), using a smooth-
174 spline solution. According to this model, the 235 cm represents the last ~13,900 years (Fig. 3).

175

176 2.4. Separating local and regional taxa

177

178 In this study we consider the taxa included in the TLP as related to a regional signal, while
179 hydro-hygrophytes and NPP as components of the local signal. When we refer to regional
180 vegetation we mean close regional. Distinguishing local from regional vegetation in a soil
181 sequence, compared to sequences from wetlands such as mires and lakes, is challenging. In
182 the latter, the local vegetation communities can be identified, but in colluvial soils this approach
183 is not as straightforward. However, NPP can be safely considered as local indicators as their
184 dispersal is limited. The case of the hydro-hygrophyte taxa is more complex, as they could also
185 be part of the regional communities. The PRD-4 sequence is located in a small depression, so
186 variations in moisture and water availability could be responsible for differences in local
187 communities. For this reason, we have included the hydro-hygrophytes into the local signal as
188 they follow patterns related to those found for the NPP (Fig. 4), i.e. maximum development of
189 Cyperaceae, Filicales and Ranunculaceae are synchronous with *Spirogyra* and *Mougeotia*,
190 while maximum values of *Pteridium aquilinum* and *Polypodium vulgare* type are coeval with the
191 presence of *Coniochaeta cf. ligniaria*, *Coniochaeta xylariispora* and *Anthostomella cf. fuegiana*.
192 However, it is important to remind that this separation is just an approach, a model to try to
193 understand the changes at different scales. In fact, previous anthracological research ([Kaal et
194 al., 2011](#)) demonstrated that woody vegetation was abundant at the margins of the small basin,
195 and that ferns were components of the forest. With the proposed separation into regional and
196 local, we want to extract general trends taking into account the spatial limitations cited here. As
197 an example, in pollen research done in peatlands the general approach is to consider the
198 Ericaceae (*Erica* and *Calluna*) as a component of the regional vegetation, when some species
199 are frequent components of bog communities. The same problem applies to Poaceae, as it is
200 also considered as a regional indicator, or Cyperaceae, considered as local, when both could
201 be part of regional and local communities. But, although with limitations, we believed the
202 established categories enable to assess the main general trends and, therefore, the separation
203 of signals proposed could be a valid approach when combined with multivariate statistics.

204

205 2.5. Statistical analyses

206

207 When working with large datasets of environmental proxies, multivariate methods are helpful to
208 reduce the dimensionality or group/classify samples. With such techniques it is possible to
209 avoid extensive descriptions of results, making the interpretation and explanation of the
210 observed patterns easier in terms of underlying processes operating at relevant spatial and
211 time scales (Birks, 1985). Thus, to extract the information of the local and regional proxies we
212 applied multivariate statistical techniques. Stratigraphically constrained cluster analysis by the
213 method of total sum of squares (Grimm, 1987) was used to define local and regional
214 palynological zones, which are based on changes (in terms of Euclidian distance) in the pollen
215 assemblages between consecutive samples. These zones are usually interpreted as shifts in
216 vegetation composition. Two cluster analyses were performed: one for regional taxa, including
217 the types considered in the TLP; and another for local taxa, including hydro-hygrophytes and
218 NPP. As such, the data comprised 41 and 24 taxa, respectively. Percentage values were used
219 after the palynological data were re-summed to 100% for the taxa not included in the TLP (local
220 signal). Thus the purpose was to perform two independent zonations that enable the
221 comparison between the results of local and regional proxies.

222 In addition, principal component analysis (PCA) was used to describe the main
223 features of the palynological record and get insights into the representativeness of changes in
224 vegetation composition through time and the type of response to environmental change. Again,
225 separate analyses were performed for regional and local taxa, both on the transposed data
226 matrices (PCA_{tr}); that is, with samples in columns (variables) and taxa in rows (cases). This
227 approach is intuitive to interpret palynological data from an ecological point of view, and it
228 enables summarizing the palynological composition of the samples based on co-variation
229 patterns. Correlation matrices were used, and varimax rotation solutions were applied to
230 constrain the co-variation in the components. PCA analyses were done using SPSS 15.0.

231 Due to the fact that the number of palynomorphs in the local signal is lower than the
232 number of types in the regional signal, the reliability of the statistical results is of concern.
233 However, the average of the local sum is 170, and the average number of taxa per sample is
234 10.6, not too low if we consider that the number of counted NPP is often lower in most
235 palynological studies. Nonetheless, some samples have low local sums, mainly at the bottom
236 and the top of the sequence (24-49 palynomorphs), but the taxonomic diversity is not much
237 lower in these samples (6-12 different taxa), so that we believe that the results of the statistical
238 analysis are representative and significant.

239 The use of a transposed matrix demands a careful interpretation of some key concepts
240 associated to conventional PCA, typically applied to non-transposed datasets (i.e. samples as

241 rows and variables as columns). This is because, contrary to the usual focus of the PCA, i.e.
242 the co-variation of taxa, with PCA_{tr} we detect the co-variation of samples, i.e. the co-variation of
243 the palynological assemblages of the different soil sections/age periods. This allows for the
244 comparison of samples taking into account their palynological composition and the
245 characterization of assemblages of co-existing principal taxa, i.e. ecological groups composing
246 the palynological record, as well as their importance in each sample/age period. For each
247 principal component, the taxa showing large factor scores (i.e. larger abundances) are those
248 explaining most of the variation of the pollen and NPP signal in samples with large factor
249 loadings (Silva Sánchez, 2010). Thus, the PCA_{tr} approach allows the identification of
250 assemblages of palynomorphs with statistically significant contribution to the total variance, and
251 to express quantitatively for each sample the proportion of variance of its composition
252 explained by each principal component (i.e. significant assemblages of palynomorphs). These
253 two aspects are valuable for defining vegetation composition and for assessing the type of
254 response. Regarding the type of responses, we distinguished between gradual, threshold and
255 elastic ones on the basis of the PCA_{tr} results. i) Threshold when a complete change from one
256 sample to the next is detected, in terms of the main principal component (i.e. palynological
257 assemblage) explaining most of the variance of the palynological composition of the samples.
258 ii) Gradual, when the change detected in the composition of the vegetation implies the decline
259 of the importance of one principal component and the increase of another. This change could
260 involve a complete or partial replacement of the principal component (i.e. vegetation formation)
261 explaining the variance of the palynological composition of the samples. iii) Elastic, when a
262 complete recovery of the previous palynological composition occurs after a short-term
263 disturbance. Additionally, we have included the term of “sensitivity” for those cases where the
264 cluster analysis identified the boundary of a palynological zone but the PCA_{tr} did not suggest a
265 change in the vegetation composition.

266

267 **3. Results and interpretation**

268

269 3.1. Local signal

270

271 Eight Local Assemblage Zones (LAZ) were detected by cluster analysis (Fig. 4) while five
272 principal components explained 94.1% of the total variance in the dataset. The percentage of
273 the variance explained by each principal component can be seen in Table 2, and the
274 fractionation of communalities and the factor scores are represented in Figs. 5 and 6.

275 In **LAZ-1** (235-210 cm; ~13,900-12,370 cal yr BP) the fourth principal component
276 (PC4_L) explains most of the variance (65-96%) of the palynological composition of samples
277 (Fig. 5), with *Pleospora* commanding the largest positive factor score (Fig. 6). *Pleospora* is a
278 fungal ascospore and has been found in relatively dry sections of ombrotrophic peat (van Geel,
279 1978; Yeloff et al., 2007). PRD-4 is a black, organic-rich, colluvial soil, but the ascospores
280 could still be related to dry conditions.

281 **LAZ-2** (210-185 cm; ~12,370-10,670 cal yr BP) is characterised by the first principal
282 component (PC1_L), explaining most of the variance (63-95%) of this zone (Fig. 5). Cyperaceae
283 is the taxon with the largest positive factor score (Fig. 6). The expansion of sedges represented
284 a major change in the palynological composition at local scale (Fig. 5) and it is most likely
285 related to more humid (or wetter?) conditions.

286 **LAZ-3** (185-140 cm; ~10,670-7580 cal yr BP) is also characterised by the dominance
287 of PC1_L, reflecting the consolidation of Cyperaceae. It accounts for most of the variance (92-
288 96%), except at a depth of 160-155 cm (32%; Fig. 5). The emergence of *Spirogyra* and
289 *Mougeotia* (van Geel, 1978) and increased percentages of ferns (Fig. 4) seem reflect a shift
290 towards more humid conditions. At 160-155 cm (~8920-8620 cal yr BP), PC3_L and PC4_L also
291 explain a significant part of the variance (40 and 13%, respectively, Fig. 5). PC4_L indicates dry
292 conditions, while in PC3_L *Pteridium aquilinum* is the taxon with the largest positive factor score
293 and *Coniochaeta xylariispora* has a moderate negative factor score (Fig. 6). Thus, at this depth,
294 PC3_L reflects an abrupt short-term shift in this zone between sedges and bracken, but also
295 indicates an opposite pattern between *Pteridium aquilinum* and *Coniochaeta xylariispora*, which
296 may reflect woodland opening and accumulated dead wood, respectively. Moreover, the
297 punctual presence of *Glomus* in this sample could be related to erosion linked to drier
298 conditions.

299 In **LAZ-4** (140-100 cm, ~7580-4800 cal yr BP), PC1_L still explains most of the variance
300 (36-94%), but with increasing proportions accounted by PC3_L (3-56%; Fig. 5), indicating a more
301 or less gradual replacement of Cyperaceae by *Pteridium aquilinum*. The detection of
302 coprophilous fungi, such as *Sordaria*-type, *Sporormiella*-type, *Podospora*-type and *Cercophora*-
303 type (Fig. 4), suggests that this change could be related to grazing activities in the local
304 surroundings. Moreover, the abundance of macroscopic (>2 mm) charcoal particles (from
305 hereon charcoal, Fig. 2) increased simultaneously with the appearance of grazing indicators.

306 From 100 to 45 cm, corresponding to zones LAZ-5 to LAZ-7, charcoal concentration
307 increased (Fig. 2), most of which originated from deciduous *Quercus* (Kaal et al., 2011). **LAZ-5**
308 (100-70 cm; ~4800-3400 cal yr BP) is characterised by the second principal component (PC2_L),

309 which explains the vast majority of the variance in the pollen composition of this zone (71-94%;
310 Fig. 5). *Polypodium vulgare* type has a large positive score, while *Coniochaeta xylariispora* has
311 a moderate positive score (Fig. 6). The increase in charcoal fragments in this zone is not
312 associated to grazing activities, as they are not recorded in tandem with synanthropic pollen
313 and coprophilous fungal spores (Figs. 4 and 7), but could be climate-induced, although human
314 activities with purposes other than animal husbandry could have also been important.

315 In **LAZ-6** (70-55 cm; ~3400-2510 cal yr BP), PC2_L also explains most of the variance
316 (63-85%), although the fifth principal component (PC5_L) increases in importance throughout the
317 zone (8-26%; Fig. 5). For PC5_L, *Pseudoschizaea* and *Polypodium vulgare* type have large
318 positive factor scores, while *Coniochaeta xylariispora*, *Coniochaeta cf. ligniaria* and
319 *Anthostomella cf. fuegiana* have large negative factor scores (Fig. 6). *Polypodium vulgare* type
320 continues to be the main taxon in the local vegetation although soil erosion is inferred from the
321 presence of *Pseudoschizaea*. Soil erosion was probably exacerbated by grazing (renewed
322 appearance of coprophilous fungi) and the lack of arboreal tree cover (low arboreal pollen
323 percentages; Fig. 7).

324 In **LAZ-7** (55-45 cm; ~2510-1830 cal yr BP), PC2_L dominates the record (55-57%),
325 although PC3_L is also important (25-28%; Fig. 5). Thus, *Polypodium vulgare* type and *Pteridium*
326 *aquilinum* are the best represented local taxa. In this zone, the maximum concentration of
327 charcoal particles was detected (Fig. 2).

328 Finally, local zone **LAZ-8** (45 cm-top; ~1830 cal yr BP-present) is heterogeneous and
329 could reflect a phase of structural reorganization of the vegetation following long-term fire
330 perturbation, as charcoal concentrations declined. At the beginning of the zone, ~1830-1200
331 cal yr BP, PC2_L and PC5_L explain most of the variance (30-37% and 27-34%, respectively; Fig.
332 5), pointing towards an increase in soil erosion (*Pseudoschizaea*) and the persistence of
333 *Polypodium vulgare* type. After this short-term episode, PC3_L explains most of the variance (41-
334 69%), and PC2_L shows decreasing values (3-48%; Fig. 5), reflecting a decline in the
335 abundance in *Polypodium vulgare* type while *Pteridium aquilinum* increased. In the top sample
336 PC1_L (Cyperaceae) is important again, explaining 52% of the variance (Fig. 5).

337

338 3.2. Regional signal

339

340 Eight Regional Assemblage Zones (RAZ) were detected with the cluster analysis (Fig. 7) while
341 four principal components explained 96.6% of the total variance. The percentage of the

342 variance explained by each principal component can be seen in Table 3, and the fractionation
343 of the communality and the factor scores are given in Figs. 8 and 9, respectively.

344 In **RAZ-1** (235-210 cm, ~13,900-12,370 cal yr BP) the second principal component
345 (PC_{2R}) explains most of the variance (91-98%; Fig. 8). *Betula* has the largest positive factor
346 score, while Poaceae and *Cytisus/Ulex* type also have positive scores and deciduous *Quercus*
347 a moderate negative score (Fig. 9). Although these pollen types are the taxa that show the
348 largest statistical association to this zone, *Artemisia*, Chenopodiaceae and *Juniperus* are also
349 present (Fig. 7) and they are indicative of dry, cold conditions.

350 In **RAZ-2** (210-185 cm; ~12,370-10,670 cal yr BP) the PC_{2R} still explains most of the
351 variance (79-89%), indicating the persistence of the *Betula* open woodland, but with increasing
352 loadings of PC_{1R} (6-10%) and PC_{3R} (4.5-10.4%; Fig. 8). In PC_{1R} deciduous *Quercus* has a
353 large positive factor score, while other mesophytes such as *Corylus*, *Alnus* and *Betula* have
354 moderate ones, while Poaceae has a negative moderate score (Fig. 9). In PC_{3R}, Poaceae
355 shows the largest positive factor score; deciduous *Quercus* and *Cistus ladanifer* have moderate
356 scores, while *Betula*, *Corylus* and *Pinus* show moderate negative scores. Both PC_{1R} and PC_{3R}
357 would be indicative of a slight incipient spread of both closed (PC_{1R}) and open oak (PC_{3R})
358 forests.

359 In **RAZ-3** (185-155 cm; ~10,670-8620 cal yr BP), while PC_{2R} still explains part of the
360 variance (25-48%), PC_{1R} becomes more important (49-71% of the variance; Fig. 8). In
361 contrast, in the top sample of the zone (~8920-8620 cal yr BP) PC_{1R} only explains 13% while
362 the PC_{2R} 73% of the variance. In general, this zone shows a gradual replacement of *Betula* by
363 deciduous *Quercus* forest, but by the end of this zone open *Betula* woodland becomes more
364 important. As found for the local vegetation, the latter could be related to a short-term abrupt
365 shift in environmental conditions.

366 **RAZ-4** and -5 represent the consolidation of the deciduous oak forest. In **RAZ-4** (155-
367 130 cm; ~8620-6870 cal yr BP) PC_{1R} explains most of the variance (81-90%), with PC_{2R}
368 accounting for only a minor part (3-14%; Fig. 8). This implies that the deciduous *Quercus*
369 forests were extensive and only some remnants of the "cold vegetation", more abundant in
370 previous stages, still persisted. In **RAZ-5** (130-100 cm; ~6870-4800 cal yr BP), PC_{1R} continues
371 to explain most of the variance (86-93%; Fig. 8). It is noteworthy that, although in RAZ-5 the
372 oak forest is well developed, indicators of human pressure such as *Plantago lanceolata* type,
373 *Plantago major/media* type, *Urtica dioica* type and *Rumex acetosella* type were also detected
374 (Fig.7). Additionally, at a local scale, an increase in coprophilous fungi was also detected at
375 140 cm (~7580 cal yr BP).The local vegetation underwent some changes (see above), but

376 apparently these were minor at the regional scale as they did not affect the overall composition
377 of the regional forest and it seems that only a small reduction of the arboreal cover occurred
378 (Fig.7).

379 In **RAZ-6** (100-55 cm; ~4800-2510 cal yr BP), PC1_R loses significance gradually (18-
380 84% of the variance) while PC3_R shows increasing percentages (12-61%; Fig. 8). This may
381 imply a gradual response of the regional vegetation to the intensification in the fire regime, as
382 suggested by the increase in charcoal concentration (Fig. 2) and the substitution of the mature
383 oak forest by an open oak forest with an increasing expansion of grass- and shrubland.
384 Moreover, palynological indicators of grazing activities (coprophilous fungi, *Plantago lanceolata*
385 type, *Plantago major/media* type and *Urtica dioica* type) are detected from 70 cm depth (~3400
386 cal yr BP), suggesting there was a phase of fires without simultaneous grazing disturbance
387 beforehand (~4800-3400 cal yr BP).

388 In **RAZ-7** (55-35 cm; ~2510-1200 cal yr BP) the open oak forest is the dominant
389 vegetation community, as PC3_R explains most of the variance (53-70%) of the samples (Fig. 8).
390 A reduction in charcoal concentration was observed for the top 45 cm of the soil sequence
391 (from ~1830 cal yr BP; Fig. 2), although a change in the regional vegetation is not recorded
392 until ~1200 cal yr BP when grazing indicators lose their importance (Fig. 7). At that time a
393 complete change in the vegetation composition defines the onset of **RAZ-8** (35 cm-top; ~1200
394 cal yr BP-present). PC4_R explains most of the variance (29-87%) of the samples (Fig. 8). *Erica*
395 type has a large positive factor score, while *Pinus sylvestris* type, *Pinus pinaster* and *Calluna*
396 have moderate positive scores. Thus they reflect the spread of heathland and pine occurring
397 during the last few centuries. Additionally, *Eucalyptus* pollen has also been found in this zone
398 (Fig. 7).

399

400 **4. Vegetation composition and post-disturbance vegetation dynamics**

401

402 Several features from the results described above are worth of emphasising (Fig. 10). First,
403 complex ecological histories reflected by changes in the vegetation composition were detected
404 at both local and regional scales, because multiple drivers were operating across different
405 space and time scales. Second, gradual, threshold and elastic responses occurred during the
406 last millennia. And, third, the regional response to a perturbation was sometimes delayed with
407 respect to the local response.

408

409 4.1. Onset of the Holocene, non-equilibrium forests and the 8200 cal yr BP event

410

411 In the PRD-4 record, the shift towards warmer conditions during the onset of the Holocene was
412 dated at ~12,370 cal yr BP, which, taking into account the uncertainties of an extrapolated age
413 (no radiocarbon date for the bottom sample of the sequence), matches well with previous
414 studies in NW Iberia (i.e. [Allen et al., 1996](#); [Muñoz Sobrino et al., 2001, 2005, 2007b](#); [Carrión et](#)
415 [al., 2010a](#); [Moreno et al., 2011](#)). At the local scale a main change in the palynological
416 composition from the pre-Holocene dominance of *Pleospora* (PC4_L) to Cyperaceae (PC1_L) after
417 the onset of the Holocene is interpreted as a threshold response (Fig. 10). At the regional
418 scale, although the vegetation was sensitive to the change in environmental conditions (the
419 cluster analysis distinguishes a RAZ suggesting a change in the pollen record), an open
420 landscape with *Betula* (PC2_R) persisted, with only a minor, incipient, increase of the
421 mesophilous trees (PC1_R) (Fig. 10). The regional persistence of an open landscape with *Betula*
422 reflects the resilience of the established Late Pleistocene vegetation to the onset of the
423 Holocene, and indicates that such vegetation could persist in a state of non-equilibrium with
424 climate for ~1700 years.

425 At ~10,670 cal yr BP a shift towards more humid conditions can be inferred from the
426 presence of *Spirogyra* and *Mougeotia* and virtual disappearance of *Pleospora* (Fig. 4), which is
427 probably related to the onset of the Hypsithermal/Holocene Thermal Maximum. Although the
428 change was recorded, it seems that the increase in humidity did not cause a significant
429 variation in the local palynological assemblage, as PC1_L (Cyperaceae) was still the main
430 principal component. At the regional scale a gradual response is suggested by a shift from the
431 open landscape with *Betula* (PC2_R) to a denser oak-dominated forest (PC1_R; Fig. 10). The
432 change in vegetation composition points to a gradual spread of the oak forest; however
433 remnants of the Late Pleistocene vegetation were still present. It is likely that the regional
434 vegetation was near its ecological limit and more humid, and probably warmer, conditions
435 prompted a change in the forest.

436 An abrupt short-lived change in the structure of the vegetation has been detected at
437 ~8920-8620 cal yr BP. At a local scale *Pteridium aquilinum* spread as the main taxon (PC3_L),
438 while at regional scale the open landscape with *Betula* (PC2_R) became re-established (Fig. 10).
439 Both are considered to be short-term disturbances in which the vegetation showed an elastic
440 response, as its composition (both local and regional) completely recovered thereafter (Fig.
441 10). This short-term perturbation is likely to be related to the cold 8200 cal yr BP event.
442 Although the chronology in PRD-4 is somewhat older, the difference can be assumed within the
443 uncertainty of the age-model. In fact, in other pollen records of NW Iberia similar short-term

444 forest reductions have been detected and related with this cold event (i.e. [Muñoz Sobrino et al.,](#)
445 [2004, 2005, 2007b](#)). At the regional scale, the oak forest (PC1_R) had expanded after the short-
446 term perturbation and the remnants of the open-landscape with *Betula* (PC2_R) almost
447 disappeared.

448

449 4.2. Fire events, grazing pressure and the origin of the heathland

450

451 Indicators of cattle grazing and fires were detected from approximately ~7580 cal yr BP (Figs.
452 4, 7 and 10). At the local scale, these perturbations represented the initiation of a gradual
453 response where Cyperaceae (PC1_L) decreased in abundance while *Pteridium aquilinum* started
454 to spread (PC3_L). Bracken easily colonizes disturbed ground, including burnt areas ([Salvo,](#)
455 [1990](#)), and the charcoal record provides unequivocal evidence of fires (Fig. 10). However, at
456 the regional scale the well-established oak forest did not show any significant change until
457 ~6870 cal yr BP (Fig. 10), when a sensitive response was detected on the basis of the cluster
458 analysis. Although a decrease in the arboreal pollen (Fig. 7) and an increase in charcoal ([Kaal](#)
459 [et al., 2011](#)) occurred, this sensitivity did not invoke a major change in the composition of the
460 regionally dominant oak forests (PC1_R). This might reflect the upslope reduction in arboreal
461 vegetation but intact downslope vegetation communities ([Carrión et al., 2010b](#)). By ~4800 cal
462 yr BP evidence of decreased grazing pressure while the fire regime intensified (higher
463 concentration of charcoal particles, Fig.10) is detected. Humidity indicators such as *Spirogyra*
464 and *Mougeotia* almost disappeared, indicating local dry conditions, probably related to the end
465 of the Hypsithermal/Holocene Thermal Maximum. The new environmental conditions may have
466 been responsible for the inferred responses at both scales (Fig. 10). At the local scale a
467 threshold response is suggested by the shift to an almost complete dominance of *Polypodium*
468 *vulgare* type and *Coniochaeta xylariispora* (PC2_L). The fern is likely to grow on dead trunks (in
469 particular after forest fires) while the fungus has been related to the presence of charcoal
470 particles ([Blackford et al., 2006](#); [Yeloff et al., 2007](#)) (Fig. 2). At the regional scale the response
471 was gradual with closed oak woodland (PC1_R) evolving into an open forest, and the spread of
472 Poaceae and, since ~3400 cal BP, of *Cistus ladanifer* (PC3_R) (Fig. 10). These results for the
473 period between ~4800-3400 cal yr BP can be summarized as a regional reduction of forest
474 cover and expansion of ferns and herbaceous species caused by increased fire activity (yet
475 negligible grazing pressure). The shift to locally drier conditions might suggest that the cause of
476 these changes was climatic –this chronology broadly coincides with the Neoglaciation, as found
477 in other records from NW Iberia ([Martínez Cortizas et al., 1999](#); [López-Merino et al., 2010a](#)) –

478 but further research, taking into account the information of nearby environmental records and
479 archaeological findings, is necessary to confirm it. In the nearby PRD-2 soil sequence the
480 overall picture is slightly different, as coprophilous fungi are present in the record since ~5500
481 cal yr BP, indicating local grazing (Carrión et al., 2010b). But between ~4000 and 3500 cal yr
482 BP a change in the composition occurred, with increased abundance of *Sporormiella*-type,
483 while *Sordaria*-type was more frequently recorded before ~4000 and after 3500 cal BP. From
484 ~4000 to 3500 cal yr BP there was an intensification of the fire regime, probably indicating
485 changes in landscape management.

486 Multiple responses were identified at PRD-4 after ~3400 cal yr BP. At the regional
487 scale a more open oak forest was dominant between ~2510 cal yr BP and ~1200 cal yr BP
488 (PC3_R, Fig. 10), the period with the lowest percentages of arboreal pollen of the whole record
489 (Fig. 7), and for which the maximum concentration of charcoal was found (Fig. 10). In general,
490 a renewed increase in grazing (indicated by coprophilous fungi, *Plantago lanceolata* type,
491 *Plantago major/media* type and *Urtica dioica* type) occurred accompanied by increased soil
492 erosion (*Pseudoschizaea*, PC5_L). *Pteridium aquilinum* (PC3_L) expanded even though
493 *Polypodium vulgare* type (PC2_L) remained the dominant taxon, providing further evidence of
494 local grazing impact. Furthermore, by ~1830 cal yr BP the intensity of the fire regime strongly
495 diminished, although not disappearing, and at the local scale an internal, post-disturbance
496 restructuring of the vegetation took place in three stages: i) *Polypodium vulgare* type /
497 *Pseudoschizaea* (i.e. erosion), ii) *Pteridium aquilinum* / *Polypodium vulgare* type, iii)
498 Cyperaceae / *Pteridium aquilinum*. In the last stage (top sample), the palynological composition
499 is dominated by Cyperaceae (PC1_L) and *Pteridium aquilinum* (PC3_L), which were the main taxa
500 prior to the period characterised by an intense fire regime, indicating an elastic response of the
501 local vegetation. However, at the regional scale there was no such immediate shift in the
502 system, although by ~1200 cal yr BP a threshold response is characterised by the abrupt
503 spread of heathland (PC4_R) coeval with the decrease in grazing indicators and greater
504 importance of pine and, somewhat later (~800 cal yr BP), cereal crops (Figs. 4 and 7). This
505 delayed response at the regional scale could be explained by the fires being localised and/or
506 by the oak woodland showing resilience until other drivers amplified the effects of the changing
507 environmental conditions (e.g. lower grazing pressure and perhaps the start of crop cultivation).
508 Heathland is a common feature of the current landscape of NW Iberia, but there are significant
509 differences in the chronology and intensity of the replacement of deciduous woodlands by
510 heathlands. In PRD-2, fire and grazing induced forest regression and Ericaceae/Fabaceae
511 shrubland expansion was significant by around ~5500 cal yr BP, and the complete colonisation

512 of the area by heathland was detected in the pollen record at ~1880-1695 cal BP (Carrión et
513 al., 2010b). In other palynological studies in nearby areas the spread of heathlands was found
514 since the initial stages of the Iron Age (~2800 cal yr BP; van Mourik, 1986), while in PRD-4 it
515 was detected during the Medieval Period (~1200 cal yr BP).

516

517 **5. Conclusions**

518

519 The palynological study of the PRD-4 sequence allowed us to infer the different environmental
520 factors that have affected the composition of the vegetation, and to understand the variations at
521 local and regional scales. Our results suggest that the vegetation of the studied area showed
522 multiple responses to Late Pleistocene/Holocene palaeoenvironmental changes. One was the
523 resilience of the *Betula* forest in an open landscape for approximately ~1700 years at the
524 beginning of the Holocene, but also other threshold, gradual and elastic responses occurred
525 with centennial delays to the initiation of the perturbations at a regional scale. This variability
526 reflects the complexity of the biotic response to environmental change and the stochastic
527 behaviour that natural systems often show across different spatial and time scales, as well as
528 their resilience and the way systems switch from one state to another.

529 With regard to the current observed and projected climate change, human-induced
530 perturbations and related vegetation dynamics, we believe that the PRD-4 record offers a good
531 example (Fig. 10) of the complexity and variability of vegetation responses (threshold, gradual,
532 elastic and resilience) to environmental perturbations since the late Pleistocene. The main
533 concern today is the impact of human-induced perturbations, not only on the landscape but
534 also on climate. Therefore a more profound knowledge of the buffering ability of ecosystems is
535 needed to predict to what extent human activities can promote drastic and unforeseen
536 changes, and to help to manage the landscape in a more sustainable way. We have to be
537 aware that the consequences of the increasing human-induced perturbations might be yet to
538 come. In this sense, long-term ecological research is a necessary tool to reconstruct the history
539 of ecosystems and its complexities.

540 The application of principal component analysis on the transposed data matrices
541 (PCA_{tr}) of palynological data seems to be appropriate to obtain information on the structure of
542 the variance of the palynological composition of the samples, resulting in lower
543 dimensions/groupings than the constrained cluster analysis. PCA_{tr} proved to be a valuable tool
544 to identify the type of responses of the vegetation to environmental change. Nonetheless, a
545 systematic comparison with other techniques is necessary to fully understand the advantages

546 and drawbacks of this approach. Moreover, in the studied record the responses usually
547 coincided with the boundaries of the palynological zones, although some of the boundaries did
548 not reflect a real change or reorganization in the composition of the vegetation.

549

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740 **Tables and table captions**

741

742 **Table 1.** Results of ^{14}C dating, showing calibrated age ranges (2σ) in cal yr BP.

743

Table 1

Sample	Depth (cm)	Lab code	^{14}C age BP	Age cal yr BP	Probability (%)
PRD-4-02	5-10	Ua-34719	104.3 \pm 0.4 pM	modern	~
PRD-4-06	25-30	Beta-297739	850 \pm 30	690 – 797	89.4
				820 – 820	0.1
				871 – 897	5.4
PRD-4-14	65-70	Beta-299229	3080 \pm 30	3219 – 3231	2.9
				3238 – 3368	92
PRD-4-20	95-100	Beta-299230	4090 \pm 30	4448 – 4466	3.4
				4518 – 4651	65.6
				4670 – 4701	6.7
				4759 – 4808	19.2
PRD-4-25	120-125	Beta-297740	5540 \pm 40	6286 – 6403	100
PRD-4-39	190-195	Beta-240963	9760 \pm 50	10910 – 10911	0.1
				11096 – 11258	94.9

744

745

746 **Table 2.** Eigenvalues and variance explained by the principal components obtained by PCA analysis of
747 the transposed data matrix of local taxa (hydro-hygrophytes and NPP).

748

Table 2

PCA Local taxa						
Component	Initial Eigenvalues			Rotation Sums of Squared Loadings		
	Total	% Variance	Cumulative %	Total	% Variance	Cumulative %
PC1_L	25.4	54.0	54.0	19.9	42.3	42.3
PC2_L	9.8	20.9	74.9	11.0	23.4	65.7
PC3_L	4.6	9.8	84.7	6.7	14.3	80.0
PC4_L	3.1	6.6	91.3	5.1	10.9	91.0
PC5_L	1.3	2.8	94.1	1.5	3.1	94.1

Extraction method: Principal Component Analysis with Varimax rotation.

749

750

751 **Table 3.** Eigenvalues and variance explained by the principal components obtained by PCA analysis of
752 the transposed data matrix of regional pollen indicators.

753

Table 3

PCA Regional taxa						
Component	Initial Eigenvalues			Rotation Sums of Squared Loadings		
	Total	% Variance	Cumulative %	Total	% Variance	Cumulative %
PC1_R	30.3	64.5	64.5	19.9	42.4	42.4
PC2_R	7.3	15.5	80.0	12.9	27.5	69.9
PC3_R	5.1	10.9	90.9	7.0	14.8	84.7
PC4_R	2.7	5.7	96.6	5.6	11.9	96.6

Extraction method: Principal Component Analysis with Varimax rotation.

754

755 **Figure captions**

756

757 **Figure 1.** Location of the study area in NW Spain.

758

759 **Figure 2.** PRD-4 soil stratigraphy (courtesy of Manuela Costa Casais) and charcoal concentration (Kaal
760 [et al., 2011](#)).

761

762 **Figure 3.** Age-depth model of the PRD-4 sequence, fitted with a smooth-spline function using Clam
763 ([Blaauw, 2010](#)). Red blocks show 95% the highest posterior density ranges

764

765 **Figure 4.** Local (hydro-hygrophites and NPP) palynological diagram. The filled silhouettes show the
766 percentage curves of the taxa, while the open silhouettes show the 5x exaggeration curves. CONISS
767 cluster analysis together with the Local Assemblage Zones (LAZ), and the estimated chronology are
768 plotted as well. Values of hydro-hygrophites and NPP are expressed as percentages of the total land
769 pollen sum (trees, shrubs and herbs).

770

771 **Figure 5.** Squared factor loadings of the five principal components (transposed matrix) explaining the
772 variation of the local signal of PRD-4 soil sequence.

773

774 **Figure 6.** Factor scores of the five local principal components (transposed matrix) obtained for the local
775 signal of PRD-4 soil sequence.

776

777 **Figure 7.** Regional (total land pollen sum) palynological diagram. The filled silhouettes show the
778 percentage curves of the taxa, while the open silhouettes show the 5x exaggeration curves. CONISS
779 cluster analysis together with the Regional Assemblage Zones (RAZ), and the estimated chronology are
780 plotted as well. Values of trees, shrubs and herbs are expressed as percentages of the total land pollen
781 sum, meaning the sum of these three groups.

782

783 **Figure 8.** Squared factor loadings of the four principal components (transposed matrix) explaining the
784 variation of the regional signal of PRD-4 soil sequence.

785

786 **Figure 9.** Factor scores of the four regional principal components (transposed matrix) obtained for the
787 regional signal of PRD-4 soil sequence.

788

789 **Figure 10.** Synthesis of the palaeoenvironmental history as inferred from the PRD-4 palynological data.
790 The graphs to the left show the proportion of variance of each sample that can be explained by the five
791 extracted local principal components and four regional principal components (communalities) obtained
792 by PCA_{tr}. From left to right, the remaining columns present the RAZ and LAZ, the description of local
793 and regional vegetation composition, the type of responses, charcoal concentration and the drivers of
794 environmental change (see text for details).

795

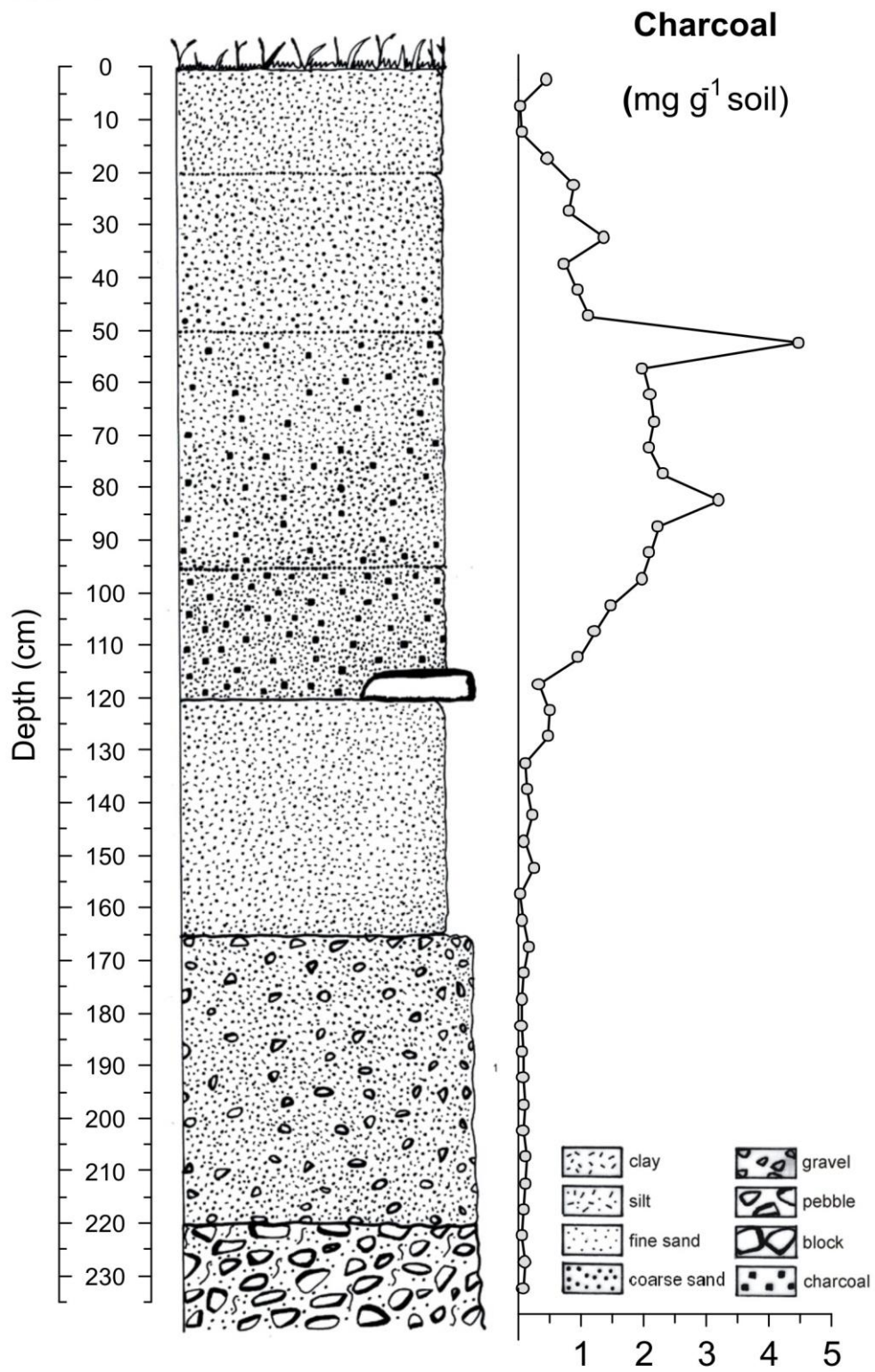
796 Figure 1

Iberian Peninsula



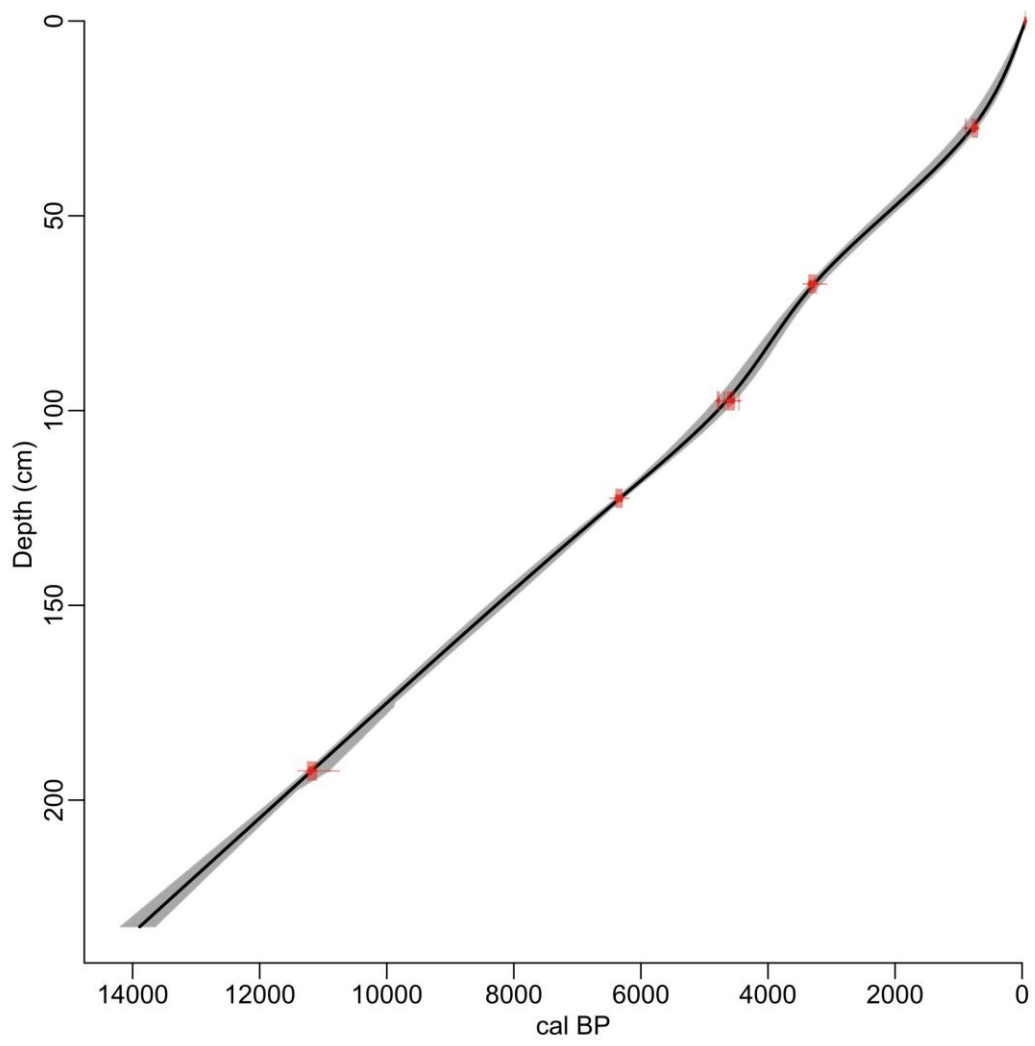
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799 Figure 2

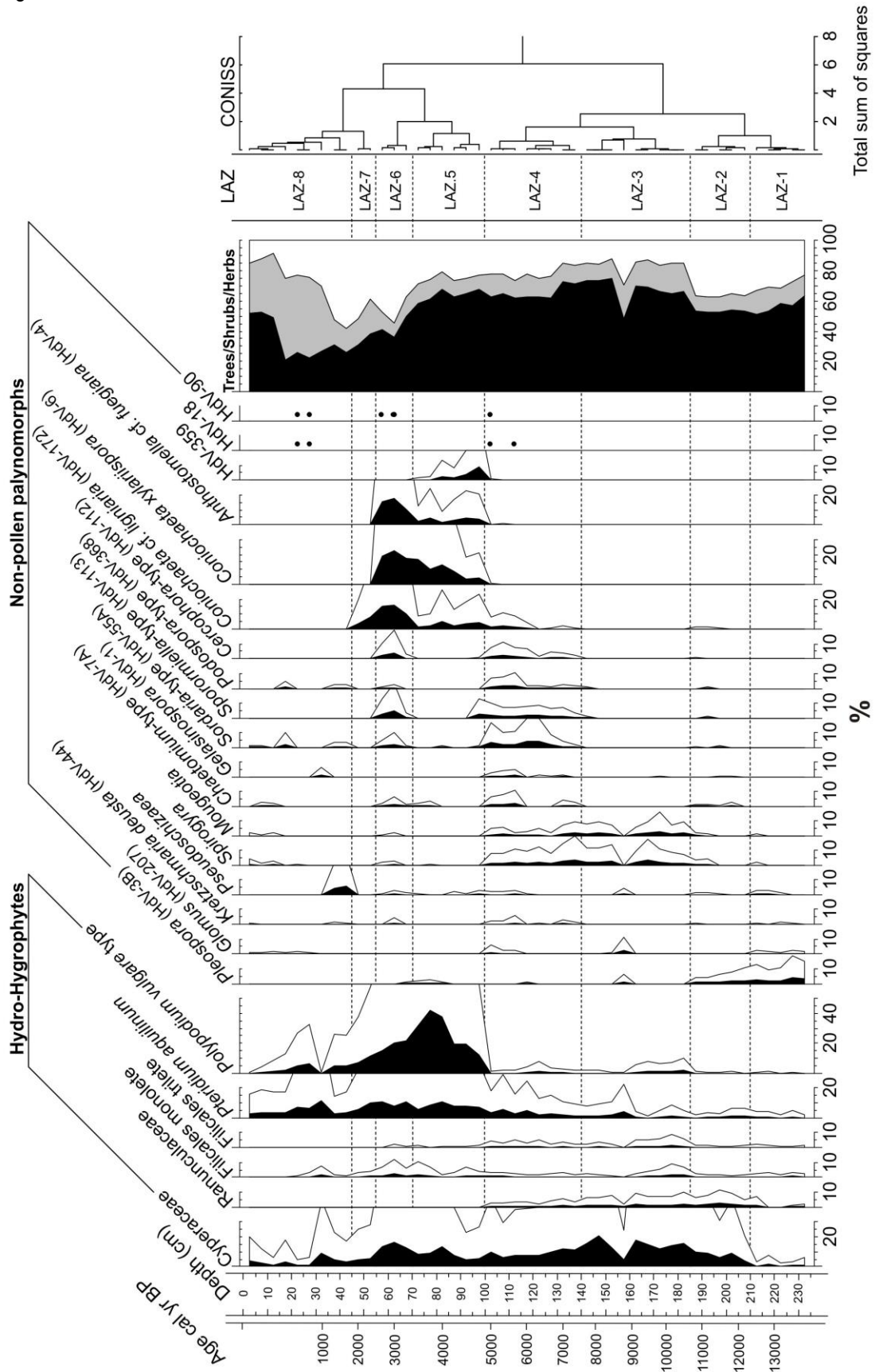


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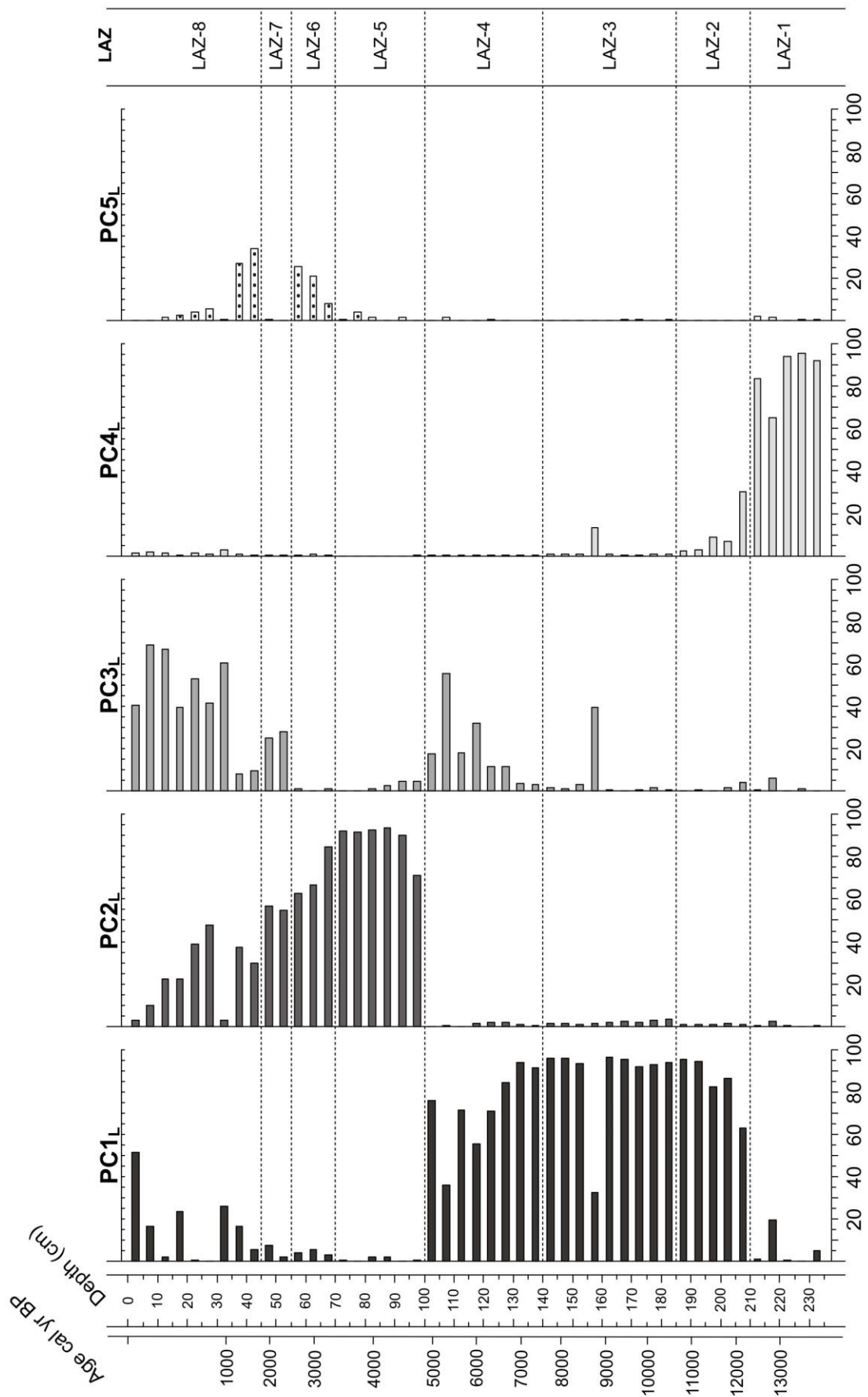
802 Figure 3



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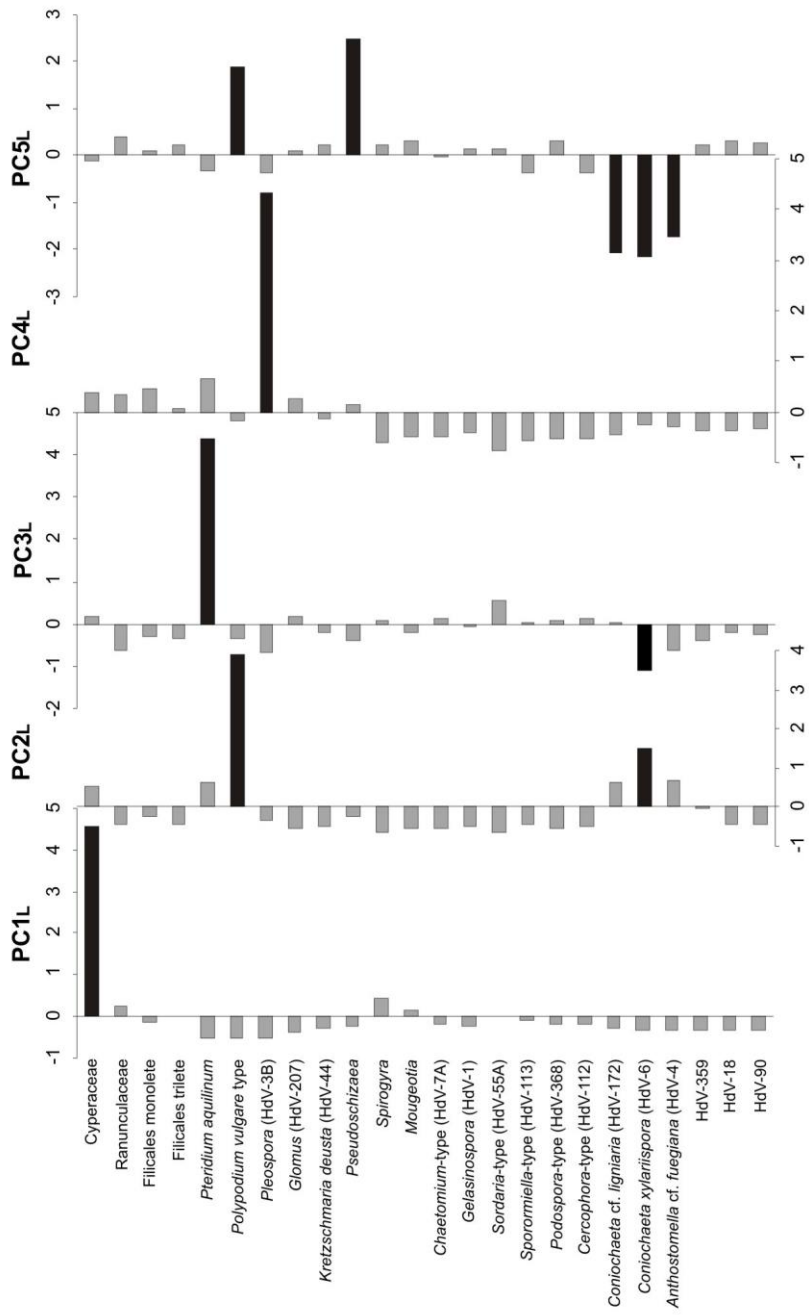


807 Figure 5

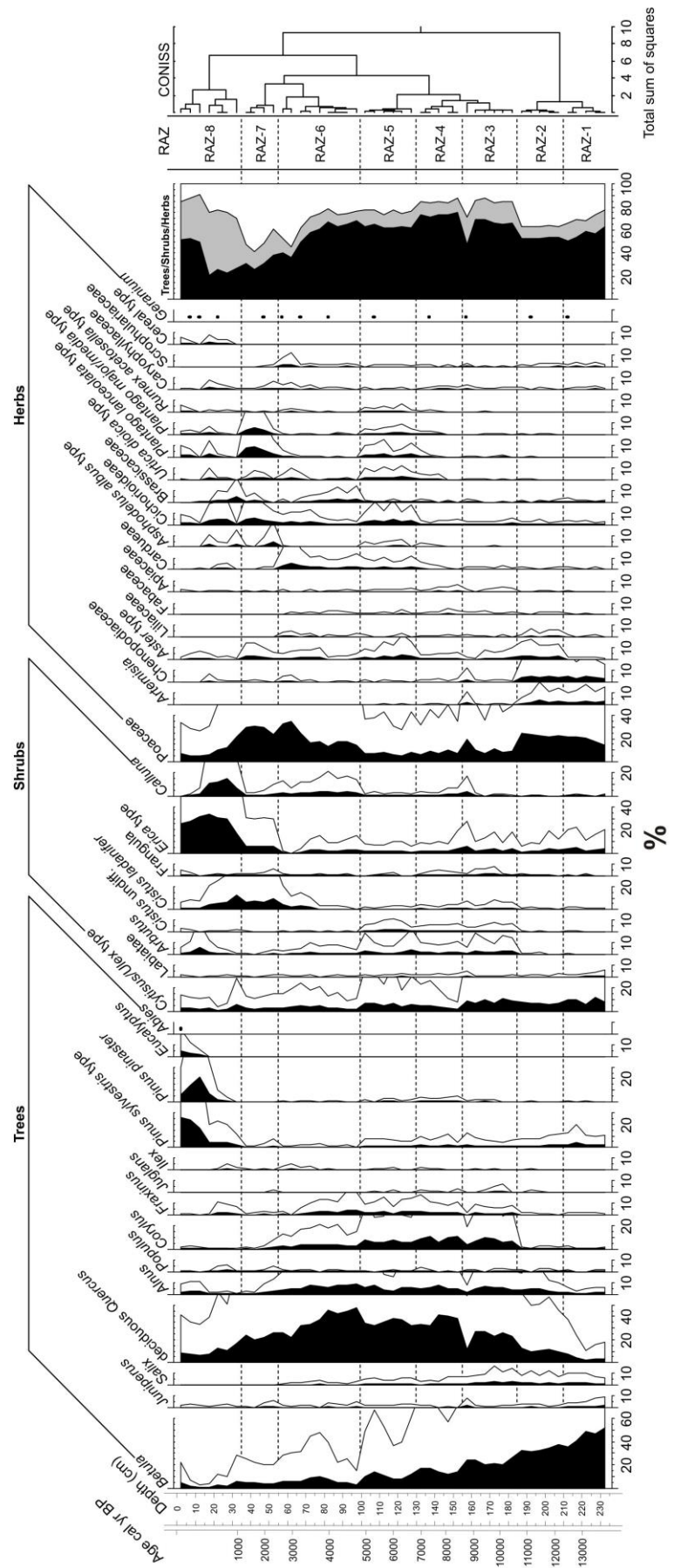


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810 Figure 6

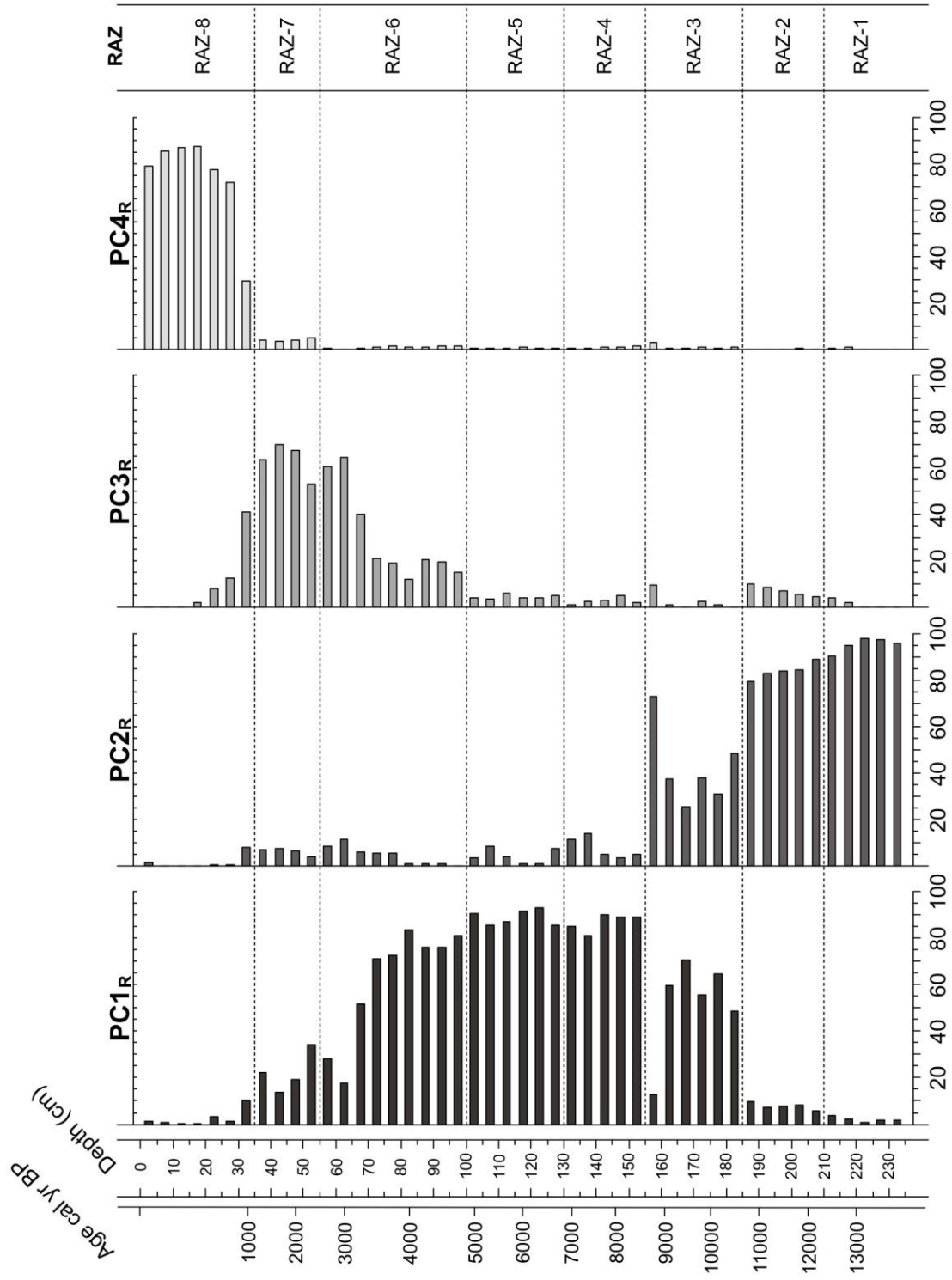


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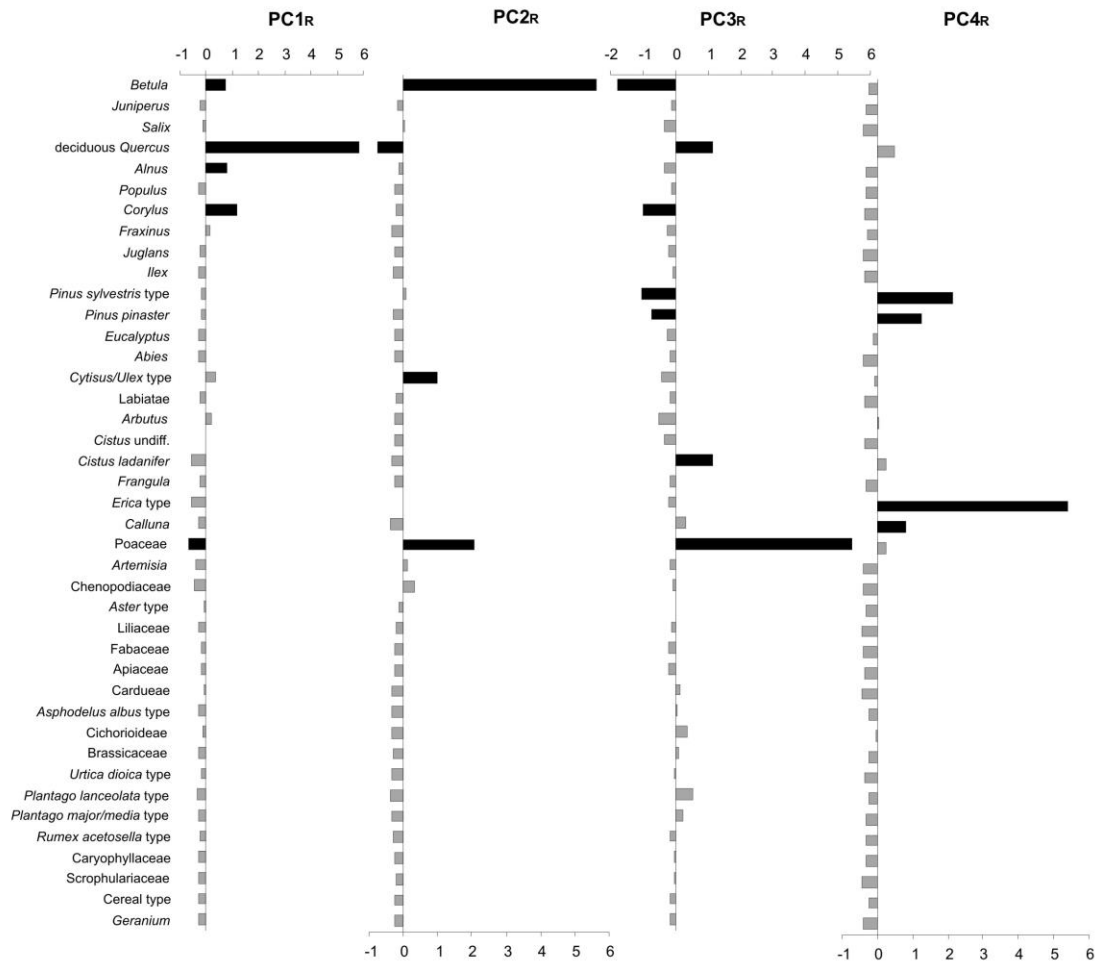
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816 Figure 8



817
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819 Figure 9



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