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

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Abstract

There is a wealth of studies dealing with the reconstruction of past environmental changes and their effects on vegetation composition in NW Iberia, but none of them have focussed specifically on the post-disturbance dynamics (i.e. the type of response) of the vegetation at different space and time scales. To fill this gap, we analysed the record of pollen and non-pollen palynomorphs (NPP) of a 235-cm thick colluvial sequence spanning the last ~13,900 years. The aims were to detect the changes in vegetation, identify the responsible drivers and determine the type of responses to disturbance. To extract this information we applied multivariate statistical techniques (constrained cluster analysis and principal components analysis on transposed matrices, PCA_{tr}) to the local (hydro-hygrophytes and NPP) and regional (land pollen) datasets separately. In both cases the cluster analysis resulted in eight local and regional assemblage zones, while five (local types) and four (regional types) principal components were obtained by PCA_{tr} to explain 94.1% and 96.6% of the total variance, respectively. The main drivers identified were climate change, grazing pressure, fire events and cultivation. The vegetation showed gradual, threshold and elastic responses to these drivers, at different space (local *vs.* regional) and time scales, revealing a complex ecological history. Regional responses to perturbations were sometimes delayed with respect to the local response. The results also showed a ecosystem resilience, such as the persistence of open *Betula*-dominated vegetation community for ~1700 years after the onset of the Holocene, and elastic responses, such as the oak woodland to the 8200 cal yr BP dry/cold event. Our results support the notion that palaeoecological research is a valuable tool to investigate ecosystem history, their responses to perturbations and their ability to buffer them. This knowledge is critical for modelling the impact of future environmental change and to help to manage the landscape more sustainably.

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

1. Introduction

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

Carrión et al. (2010a) outlined the patterns of vegetation change for the Late Quaternary in the Iberian Peninsula, emphasising the strong regional differences, mainly related to the Eurosiberian and Mediterranean biogeographical regions. While in the Mediterranean region a large heterogeneity in vegetation change has been pointed out, in the Eurosiberian one, comprising the north and northwest, as well as in other areas with Atlantic influence, a more homogeneous picture has emerged. Moreover, in the Eurosiberian area the vegetation change generally follows the Central European floristic model, where a rapid spread of mesophytic species occurred at the onset of the Holocene. Overall, the last ~14,000 years of palaeoenvironmental and vegetation changes in NW Iberia have been investigated using a variety of proxies, including pollen, non-pollen palynomorphs (NPP), charcoal, plant macroremains, diatoms, geochemistry and molecular markers, in several types of archives such as lacustrine deposits (Allen et al., 1996; Santos et al., 2000; Muñoz Sobrino et al., 2001, 2004; Leira and Santos, 2002; Jalut et al., 2010; Moreno et al., 2011; López-Merino et al., 2011a), mires (Muñoz Sobrino et al., 1997; Martínez Cortizas et al., 1999, 2005; Mighall et al., 2006; López-Merino et al., 2010a, 2011b; Morales-Molino et al., 2011; Schellekens et al., 2011), colluvial soils (Kaal et al., 2008, 2011; Costa Casais et al., 2009; Carrión et al., 2010b), coastal sediments (Santos and Sánchez-Goñi, 2003; García-Amorena et al., 2007), marine sediments (Desprat et al., 2003; Muñoz Sobrino et al., 2007a), and archaeological deposits (López-Sáez et al., 2003, 2009; López-Merino et al., 2010b). These studies were mainly undertaken in mountain areas and showed complex histories where climate, fire, vegetation change and human activities, e.g. animal husbandry, agriculture and mining, were ultimately responsible for past and current landscape configuration (Ramil-Rego et al., 1998; Muñoz Sobrino et al., 2005, 2007b; Martínez Cortizas et al., 2005, 2009). Briefly, from the onset of the Holocene to ~2000 years ago forests expanded and were important in the landscape. Indicators of human impact started to appear around ~7600 years ago, increasing at ~4500 years cal BP with widespread phases of deforestation since Roman times onwards (Jalut et al., 2010). But despite the many studies focussing upon past vegetation, climate trends and impact of human activities, investigations comparing vegetation composition and post-disturbance dynamics are lacking. The same is true for other parts of the Iberian Peninsula, with notable exceptions for the SE of Iberia. Firstly, the study of the pollen record of Siles Lake by Carrión (2002), which covers the last ~20,300 years, showed gradual, rapid and threshold responses, which involved complete changes in forest composition, as well as abrupt shifts at the local scale, pointing towards hydroclimatic variations. Moreover, lags in vegetation development in comparison with limnological stages were identified at the centennial scale. Secondly, in another study carried out by Carrión et al. (2001) in the Villaverde Lake, timelags in vegetation response to environmental change were detected, especially in response to climate amelioration at the beginning of the Holocene, pointing towards the resilience of established *Pinus* populations during ~2200 years, as well as decadal shifts in the pollen record since the mid-Holocene. Finally, Gil-Romera et al. (2010a) defined ecosystem functioning and resilient behaviour at long-term time scales at two sites. At Zoñar, it seems that disturbance promoted changes in biodiversity and landscape structure, shifting from one state to another; while in Gádor several stable phases linked to arid conditions and the spread of the grassland were detected.

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

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

2. Materials and methods

2.1. Study area

The PRD-4 sequence is located in the Rock Art Park of Campo Lameiro (42º32'N 8º31'W, Pontevedra, NW Spain, Fig. 1), in a local depression on the isolated hill Monte Paradela (260-320 m a.s.l.). The area is located in the Atlantic/Eurosiberian climate region, with mild (mean annual temperature of 15 °C) and humid (mean annual precipitation of 1200 mm) climatic conditions (Martínez Cortizas and Pérez Alberti, 1990). Currently, *Pinus pinaster*, *Quercus robur, Pteridium aquilinum* and heathlands with different species of *Erica* and *Calluna vulgaris* are the main components of the vegetation, with remnants of *Eucalyptus globulus* plantations, *Ulex* and *Cytisus*, which are periodically eliminated since 2003 with the setting up of the archaeological park. In the valleys, the riparian vegetation is composed of *inter alia Alnus glutinosa*, *Corylus avellana*, *Fraxinus excelsior*, *Ulmus glabra*, *Populus*, *Betula alba* and *Crataegus monogyna*.

2.2. Sampling and palynological analysis

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

2.3. Radiocarbon dates and chronology

Six samples were selected for ^{14}C dating using the AMS technique. The ^{14}C dates (Table 1) were calibrated using the IntCaL09.14C calibration curve (Reimer et al., 2009). The age-depth model was obtained using the Clam software developed by Blaauw (2010), using a smooth-spline solution. According to this model, the 235 cm represents the last ~13,900 years (Fig. 3).

2.4. Separating local and regional taxa

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

2.5. Statistical analyses

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

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

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

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

3. Results and interpretation

3.1. Local signal

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

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

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

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

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

From 100 to 45 cm, corresponding to zones LAZ-5 to LAZ-7, charcoal concentration increased (Fig. 2), most of which originated from deciduous *Quercus* (Kaal et al., 2011). **LAZ-5** (100-70 cm; ~4800-3400 cal yr BP) is characterised by the second principal component ($PC2_L$), which explains the vast majority of the variance in the pollen composition of this zone (71-94%; Fig. 5). *Polypodium vulgare* type has a large positive score, while *Coniochaeta xylariispora* has a moderate positive score (Fig. 6). The increase in charcoal fragments in this zone is not associated to grazing activities, as they are not recorded in tandem with synanthropic pollen and coprophilous fungal spores (Figs. 4 and 7), but could be climate-induced, although human activities with purposes other than animal husbandry could have also been important.

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

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

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

3.2. Regional signal

Eight Regional Assemblage Zones (RAZ) were detected with the cluster analysis (Fig. 7) while four principal components explained 96.6% of the total variance. The percentage of the variance explained by each principal component can be seen in Table 3, and the fractionation of the communality and the factor scores are given in Figs. 8 and 9, respectively.

In **RAZ-1** (235-210 cm, ~13,900-12,370 cal yr BP) the second principal component ($PC2_R$) explains most of the variance (91-98%; Fig. 8). *Betula* has the largest positive factor score, while Poaceae and *Cytisus/Ulex* type also have positive scores and deciduous *Quercus* a moderate negative score (Fig. 9). Although these pollen types are the taxa that show the largest statistical association to this zone, *Artemisia*, Chenopodiaceae and *Juniperus* are also present (Fig. 7) and they are indicative of dry, cold conditions.

In **RAZ-2** (210-185 cm; ~12,370-10,670 cal yr BP) the $PC2_R$ still explains most of the variance (79-89%), indicating the persistence of the *Betula* open woodland, but with increasing loadings of $PC1_R$ (6-10%) and $PC3_R$ (4.5-10.4%; Fig. 8). In $PC1_R$ deciduous *Quercus* has a large positive factor score, while other mesophytes such as *Corylus*, *Alnus* and *Betula* have moderate ones, while Poaceae has a negative moderate score (Fig. 9). In $PC3_R$, Poaceae shows the largest positive factor score; deciduous *Quercus* and *Cistus ladanifer* have moderate scores, while *Betula*, *Corylus* and *Pinus* show moderate negative scores. Both $PC1_R$ and $PC3_R$ would be indicative of a slight incipient spread of both closed ($PC1_R$) and open oak ($PC3_R$) forests.

In **RAZ-3** (185-155 cm; ~10,670-8620 cal yr BP), while $PC2_R$ still explains part of the variance (25-48%), $PC1_R$ becomes more important (49-71% of the variance; Fig. 8). In contrast, in the top sample of the zone (~8920-8620 cal yr BP) $PC1_R$ only explains 13% while the $PC2_R$ 73% of the variance. In general, this zone shows a gradual replacement of *Betula* by deciduous *Quercus* forest, but by the end of this zone open *Betula* woodland becomes more important. As found for the local vegetation, the latter could be related to a short-term abrupt shift in environmental conditions.

RAZ-4 and -5 represent the consolidation of the deciduous oak forest. In **RAZ-4** (155-130 cm; ~8620-6870 cal yr BP) $PC1_R$ explains most of the variance (81-90%), with $PC2_R$ accounting for only a minor part (3-14%; Fig. 8). This implies that the deciduous *Quercus* forests were extensive and only some remnants of the “cold vegetation”, more abundant in previous stages, still persisted. In **RAZ-5** (130-100 cm; ~6870-4800 cal yr BP), $PC1_R$ continues to explain most of the variance (86-93%; Fig. 8). It is noteworthy that, although in RAZ-5 the oak forest is well developed, indicators of human pressure such as *Plantago lanceolata* type, *Plantago major/media* type, *Urtica dioica* type and *Rumex acetosella* type were also detected (Fig.7). Additionally, at a local scale, an increase in coprophilous fungi was also detected at 140 cm (~7580 cal yr BP).The local vegetation underwent some changes (see above), but apparently these were minor at the regional scale as they did not affect the overall composition of the regional forest and it seems that only a small reduction of the arboreal cover occurred (Fig.7).

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

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

4. Vegetation composition and post-disturbance vegetation dynamics

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

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

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

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

An abrupt short-lived change in the structure of the vegetation has been detected at ~8920-8620 cal yr BP. At a local scale *Pteridium aquilinum* spread as the main taxon ($PC3_L$), while at regional scale the open landscape with *Betula* ($PC2_R$) became re-established (Fig. 10). Both are considered to be short-term disturbances in which the vegetation showed an elastic response, as its composition (both local and regional) completely recovered thereafter (Fig. 10). This short-term perturbation is likely to be related to the cold 8200 cal yr BP event. Although the chronology in PRD-4 is somewhat older, the difference can be assumed within the uncertainty of the age-model. In fact, in other pollen records of NW Iberia similar short-term forest reductions have been detected and related with this cold event (i.e. Muñoz Sobrino et al., 2004, 2005, 2007b). At the regional scale, the oak forest ($PC1_R$) had expanded after the short-term perturbation and the remnants of the open-landscape with *Betula* ($PC2_R$) almost disappeared.

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

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

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

Multiple responses were identified at PRD-4 after ~3400 cal yr BP. At the regional scale a more open oak forest was dominant between ~2510 cal yr BP and ~1200 cal yr BP (PC3$_{\mathrm{R}}$, Fig. 10), the period with the lowest percentages of arboreal pollen of the whole record (Fig. 7), and for which the maximum concentration of charcoal was found (Fig. 10). In general, a renewed increase in grazing (indicated by coprophilous fungi, *Plantago lanceolata* type, *Plantago major/media* type and *Urtica dioica* type) occurred accompanied by increased soil erosion (*Pseudoschizaea*, PC5$_{\mathrm{L}}$). *Pteridium aquilinum* (PC3$_{\mathrm{L}}$) expanded even though *Polypodium vulgare* type (PC2$_{\mathrm{L}}$) remained the dominant taxon, providing further evidence of local grazing impact. Furthermore, by ~1830 cal yr BP the intensity of the fire regime strongly diminished, although not disappearing, and at the local scale an internal, post-disturbance restructuring of the vegetation took place in three stages: i) *Polypodium vulgare* type / *Pseudoschizaea* (i.e. erosion), ii) *Pteridium aquilinum* / *Polypodium vulgare* type, iii) Cyperaceae / *Pteridium aquilinum*. In the last stage (top sample), the palynological composition is dominated by Cyperaceae (PC1$_{\mathrm{L}}$) and *Pteridium aquilinum* (PC3$_{\mathrm{L}}$), which were the main taxa prior to the period characterised by an intense fire regime, indicating an elastic response of the local vegetation. However, at the regional scale there was no such immediate shift in the system, although by ~1200 cal yr BP a threshold response is characterised by the abrupt spread of heathland (PC4$_{\mathrm{R}}$) coeval with the decrease in grazing indicators and greater importance of pine and, somewhat later (~800 cal yr BP), cereal crops (Figs. 4 and 7). This delayed response at the regional scale could be explained by the fires being localised and/or by the oak woodland showing resilience until other drivers amplified the effects of the changing environmental conditions (e.g. lower grazing pressure and perhaps the start of crop cultivation). Heathland is a common feature of the current landscape of NW Iberia, but there are significant differences in the chronology and intensity of the replacement of deciduous woodlands by heathlands. In PRD-2, fire and grazing induced forest regression and Ericaceae/Fabaceae shrubland expansion was significant by around ~5500 cal yr BP, and the complete colonisation of the area by heathland was detected in the pollen record at ~1880-1695 cal BP (Carrión et al., 2010b). In other palynological studies in nearby areas the spread of heathlands was found since the initial stages of the Iron Age (~2800 cal yr BP; van Mourik, 1986), while in PRD-4 it was detected during the Medieval Period (~1200 cal yr BP).

5. Conclusions

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

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

The application of principal component analysis on the transposed data matrices (PCA_{tr}) of palynological data seems to be appropriate to obtain information on the structure of the variance of the palynological composition of the samples, resulting in lower dimensions/groupings than the constrained cluster analysis. PCA_{tr} proved to be a valuable tool to identify the type of responses of the vegetation to environmental change. Nonetheless, a systematic comparison with other techniques is necessary to fully understand the advantages and drawbacks of this approach. Moreover, in the studied record the responses usually coincided with the boundaries of the palynological zones, although some of the boundaries did not reflect a real change or reorganization in the composition of the vegetation.

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Tables and table captions

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

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 ± 0.4 pM	modern	~
PRD-4-06	25-30	Beta-297739	850 ± 30	690 – 797	89.4
				820 – 820	0.1
				871 – 897	5.4
PRD-4-14	65-70	Beta-299229	3080 ± 30	3219 – 3231	2.9
				3238 – 3368	92
PRD-4-20	95-100	Beta-299230	4090 ± 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 ± 40	6286 – 6403	100
PRD-4-39	190-195	Beta-240963	9760 ± 50	10910 – 10911	0.1
				11096 – 11258	94.9

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

Table 2

PCA Local taxa						
	Initial Eigenvalues			Rotation Sums of Squared Loadings		
Component	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.

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

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.

Figure captions

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

Figure 2. PRD-4 soil stratigraphy (courtesy of Manuela Costa Casais) and charcoal concentration (Kaal et al., 2011).

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

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

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

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

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

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

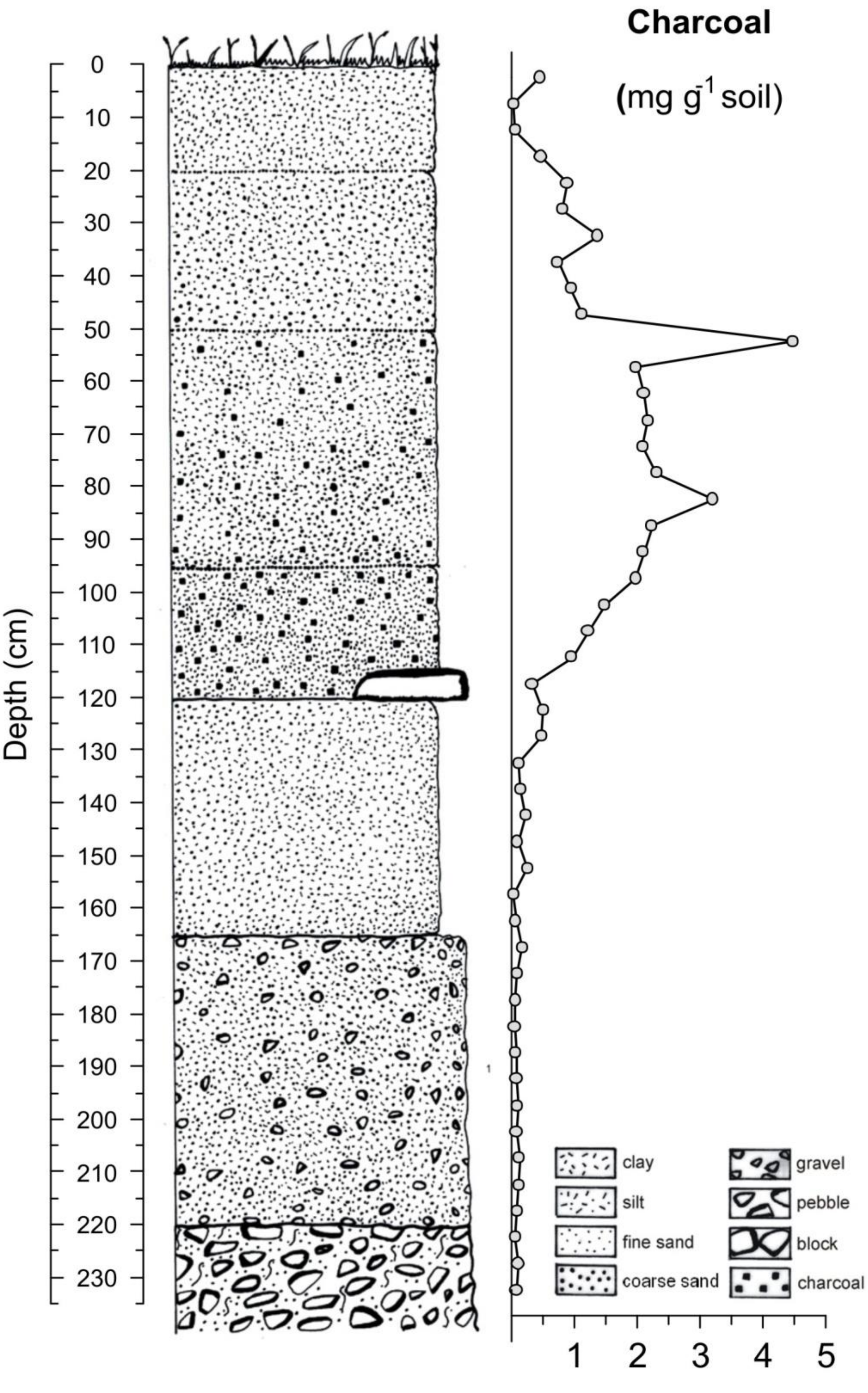
Figure 9. Factor scores of the four regional principal components (transposed matrix) obtained for the regional signal of PRD-4 soil sequence.

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

Figure 1

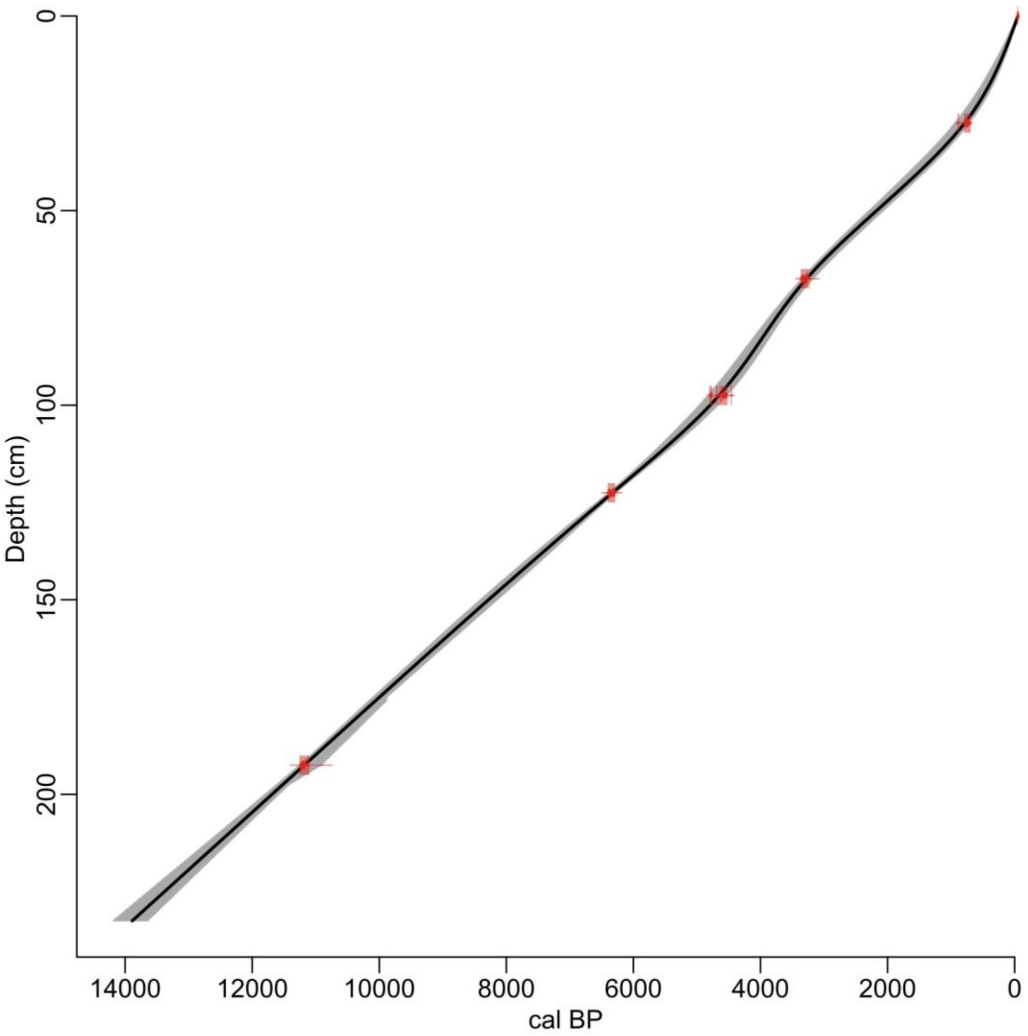

Iberian Peninsula
France
EUROSIBERIAN REGION
MEDITERRANEAN REGION
ATLANTIC OCEAN
Spain
Portugal
MEDITERRANEAN SEA
N
0 50 100
km

799 Figure 2



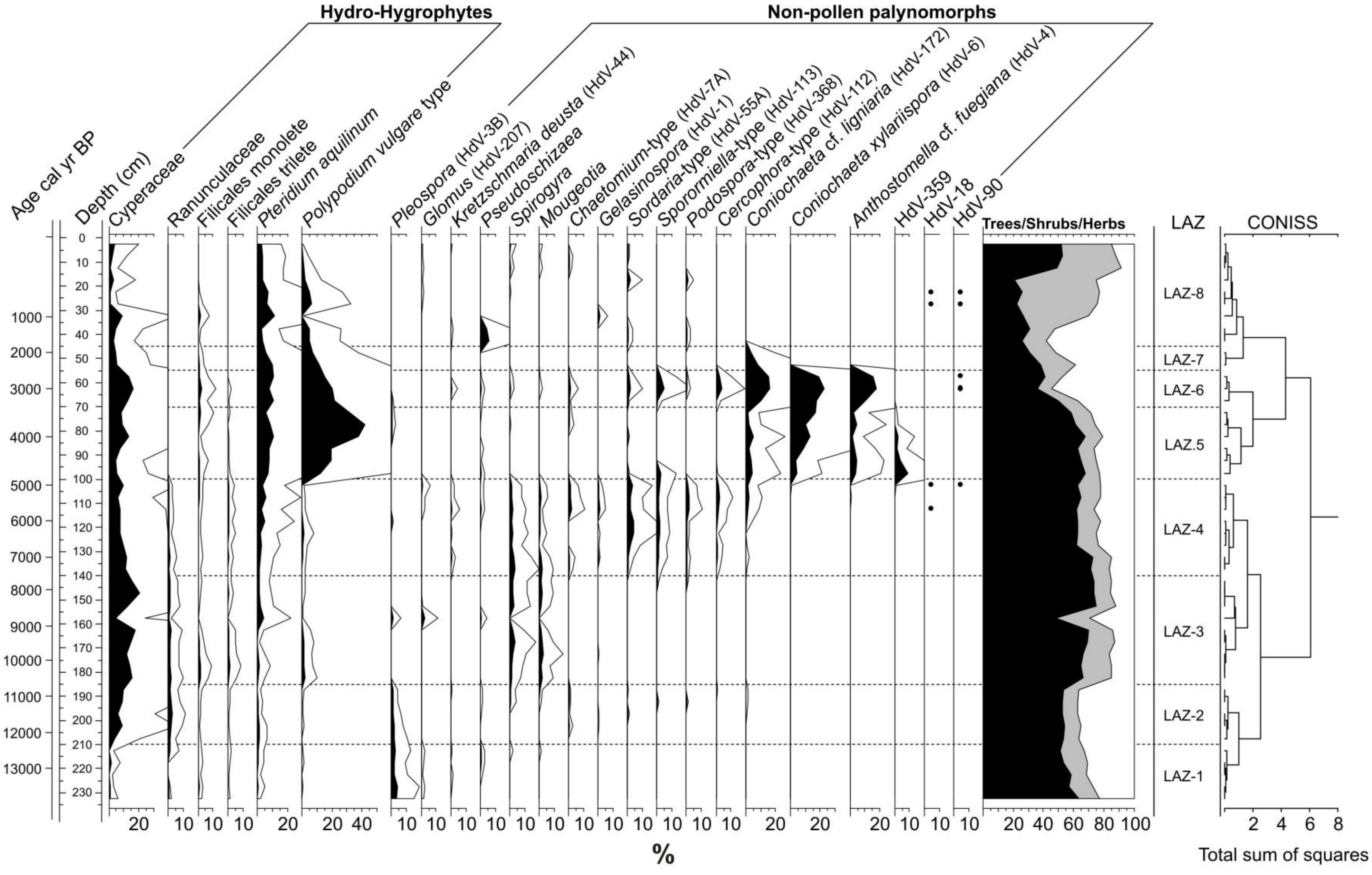
800
801

Figure 3



0
50
100
150
200
Depth (cm)
14000
12000
10000
8000
6000
4000
2000
0
cal BP

Figure 4



Hydro-Hygrophytes
Non-pollen palynomorphs
Age cal yr BP
Depth (cm)
Cyperaceae
Ranunculaceae
Filicales monolete
Filicales trilete
Pteridium aquilinum
Polypodium vulgare type
Pleospora (HdV-3B)
Glomus (HdV-207)
Kretzschmaria deusta (HdV-44)
Pseudoschizaea
Spirogyra
Mougeotia
Chaetomium-type (HdV-7A)
Gelasinospora (HdV-1)
Sordaria-type (HdV-55A)
Sporormiella-type (HdV-113)
Podospora-type (HdV-368)
Cercophora-type (HdV-112)
Coniochaeta cf. ligniaria (HdV-172)
Coniochaeta xylariispora (HdV-6)
Anthostomella cf. fuegiana (HdV-4)
HdV-359
HdV-18
HdV-90
Trees/Shrubs/Herbs
LAZ
CONISS
LAZ-8
LAZ-7
LAZ-6
LAZ.5
LAZ-4
LAZ-3
LAZ-2
LAZ-1
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190
200
210
220
230
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
11000
12000
13000
20
10 10 10
20
20 40
10 10 10 10 10 10 10 10 10 10 10
20 20
20 10 10 10
20 40 60 80 100
%
2 4 6 8
Total sum of squares

Figure 5

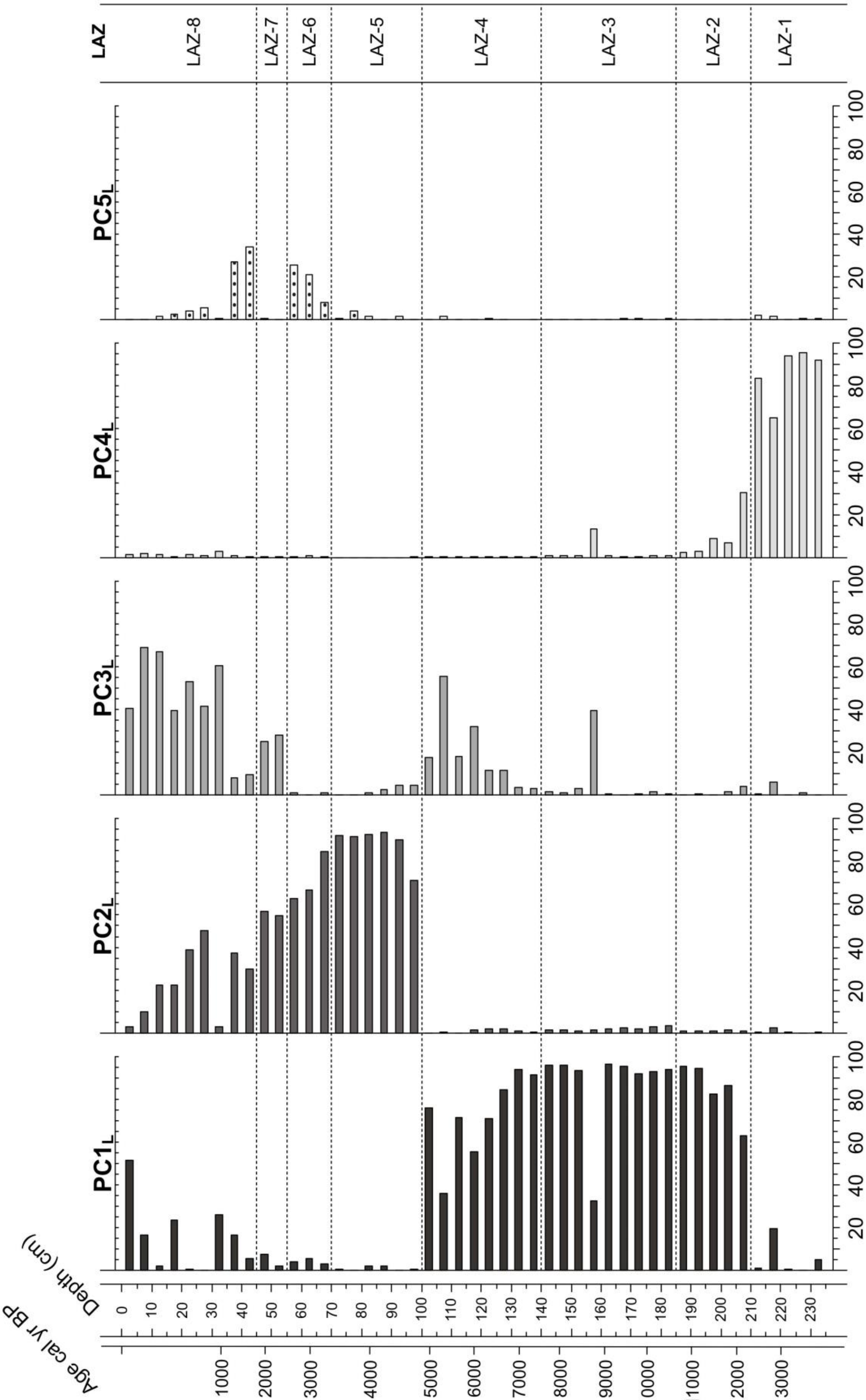

LAZ
LAZ-8
LAZ-7
LAZ-6
LAZ-5
LAZ-4
LAZ-3
LAZ-2
LAZ-1
$\mathrm{PC1_L}$
$\mathrm{PC2_L}$
$\mathrm{PC3_L}$
$\mathrm{PC4_L}$
$\mathrm{PC5_L}$
20
40
60
80
100
Depth (cm)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190
200
210
220
230
Age cal yr BP
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
11000
12000
13000

Figure 6

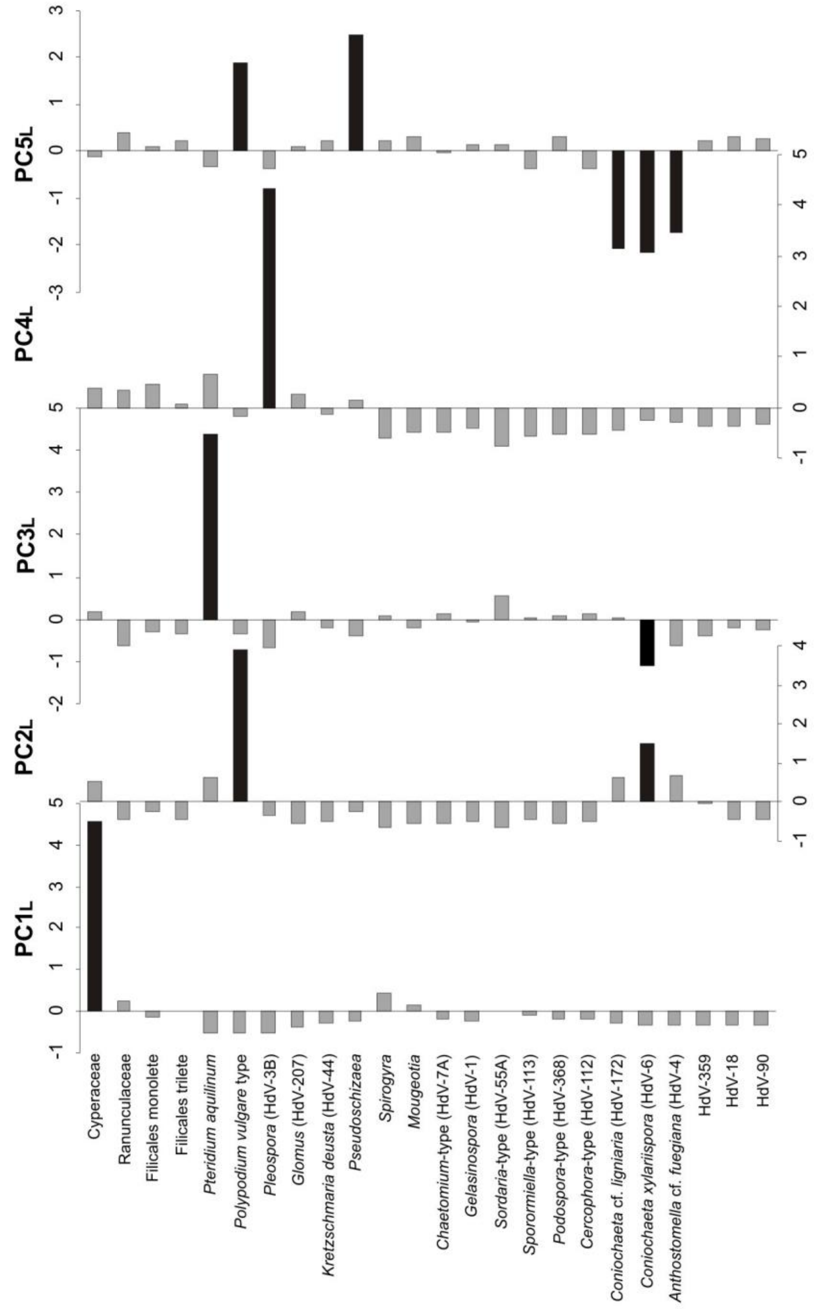

PC1L
PC2L
PC3L
PC4L
PC5L
-1
0
1
2
3
4
5
-2
-3
Cyperaceae
Ranunculaceae
Filicales monolete
Filicales trilete
Pteridium aquilinum
Polypodium vulgare type
Pleospora (HdV-3B)
Glomus (HdV-207)
Kretzschmaria deusta (HdV-44)
Pseudoschizaea
Spirogyra
Mougeotia
Chaetomium-type (HdV-7A)
Gelasinospora (HdV-1)
Sordaria-type (HdV-55A)
Sporormiella-type (HdV-113)
Podospora-type (HdV-368)
Cercophora-type (HdV-112)
Coniochaeta cf. *ligniaria* (HdV-172)
Coniochaeta xylariispora (HdV-6)
Anthostomella cf. *fuegiana* (HdV-4)
HdV-359
HdV-18
HdV-90

Figure 7

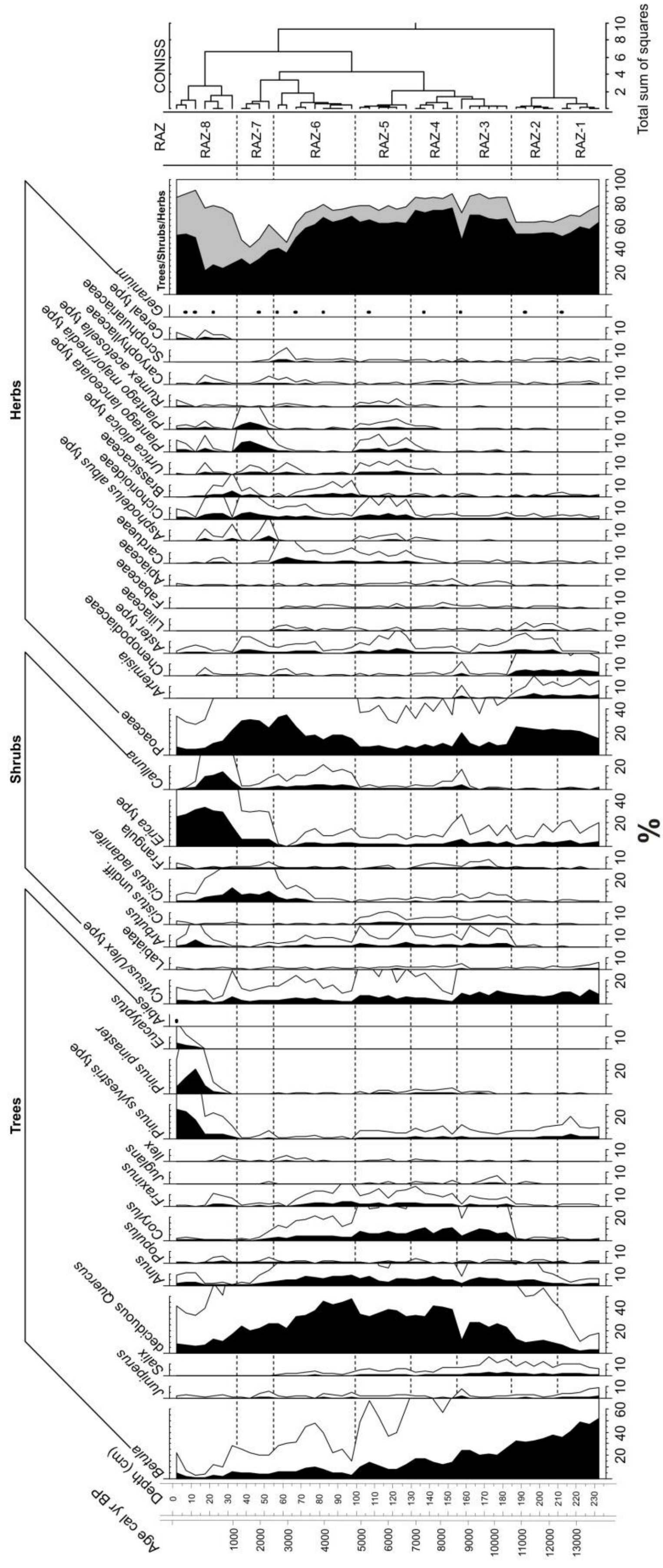
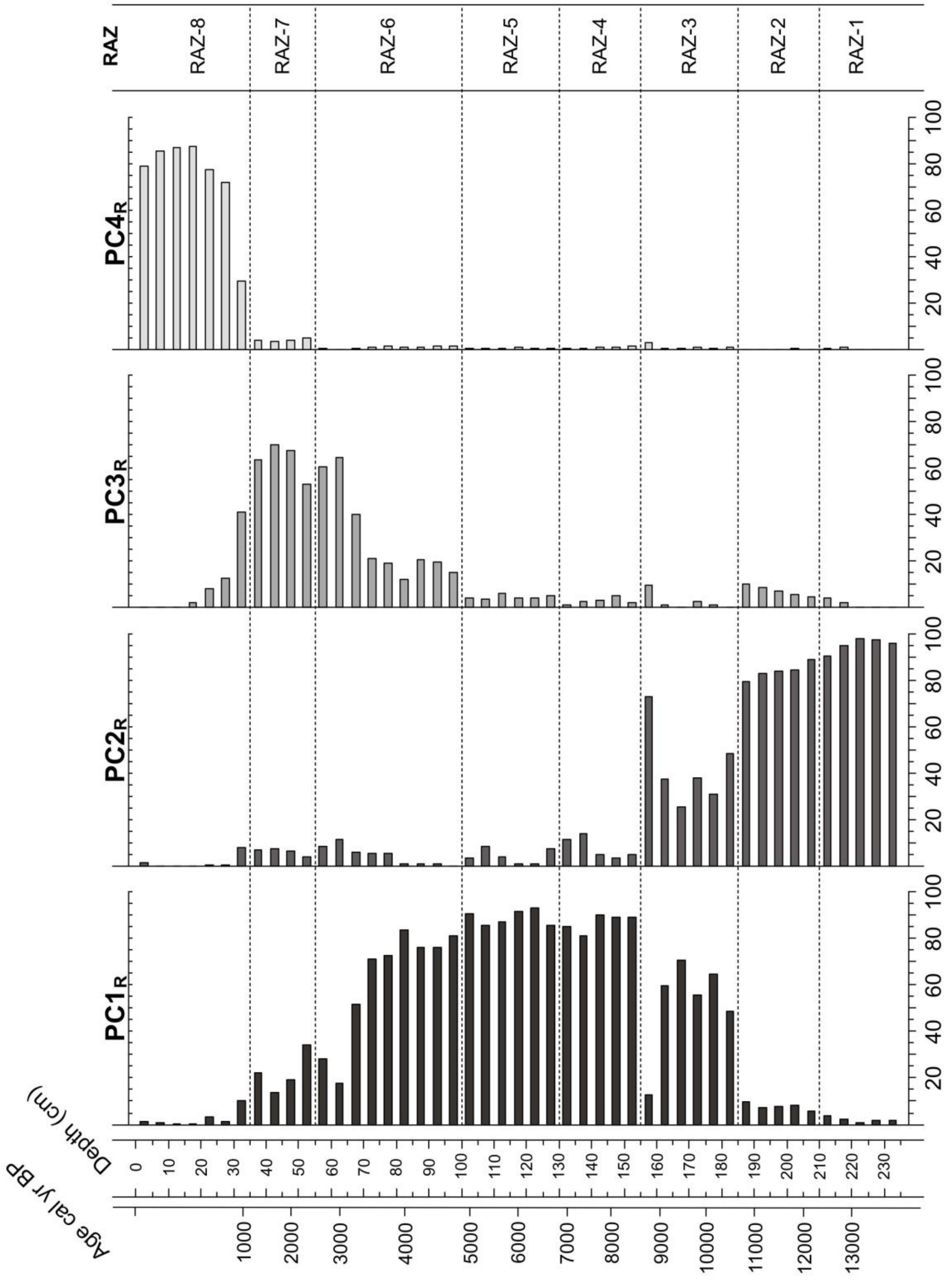
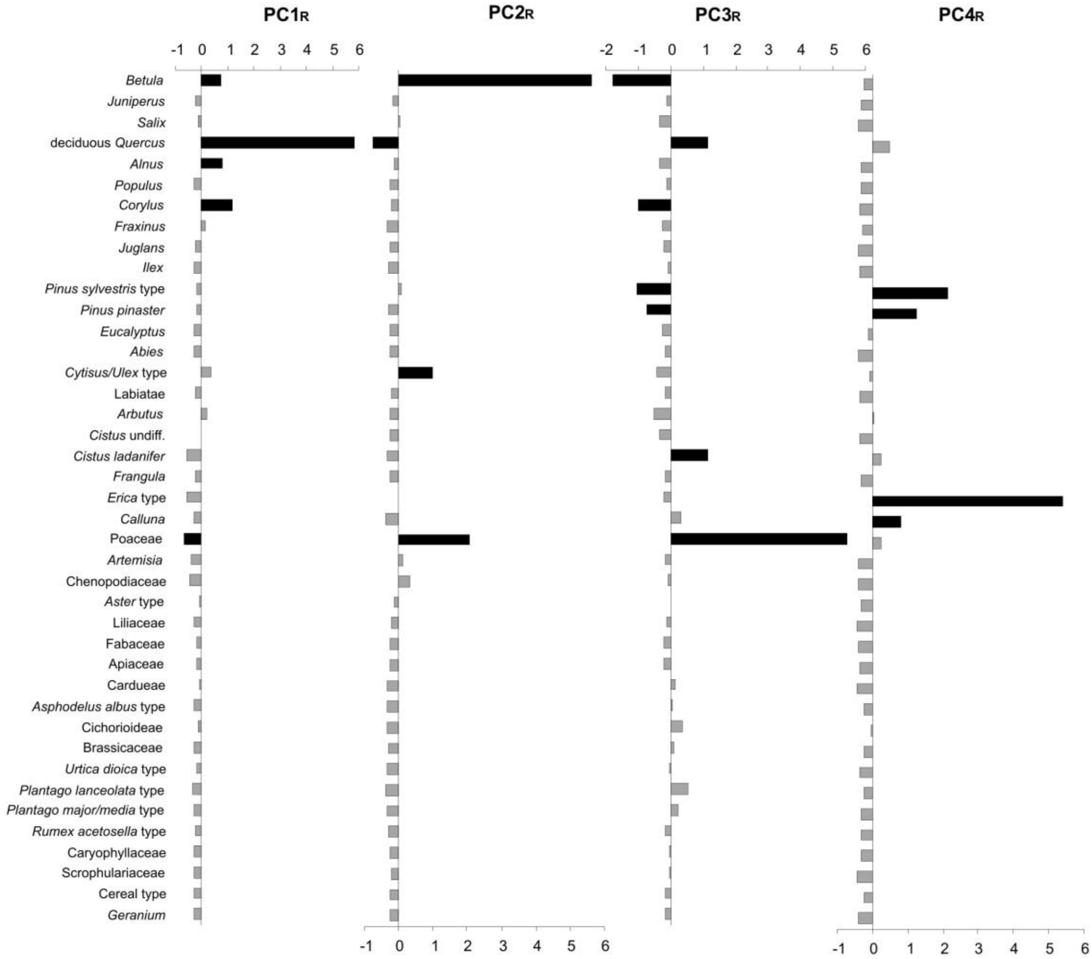

Trees
Shrubs
Herbs
Age cal yr BP
Depth (cm)
Betula
Juniperus
Salix
deciduous Quercus
Alnus
Populus
Corylus
Fraxinus
Juglans
Ilex
Pinus sylvestris type
Pinus pinaster
Eucalyptus
Abies
Cytisus/Ulex type
Labiatae
Arbutus
Cistus
Cistus undiff
Cistus ladanifer
Frangula
Erica type
Calluna
Poaceae
Artemisia
Chenopodiaceae
Aster type
Liliaceae
Fabaceae
Apiaceae
Cardueae
Asphodeae
Asphodelus albus type
Cichorioideae
Brassicaceae
Urtica dioica type
Plantago lanceolata type
Plantago major/media type
Rumex acetosa/acetosella type
Caryophyllaceae
Scrophulariaceae
Cereal type
Geranium
Trees/Shrubs/Herbs
RAZ
RAZ-8
RAZ-7
RAZ-6
RAZ-5
RAZ-4
RAZ-3
RAZ-2
RAZ-1
CONISS
Total sum of squares
%

Figure 8

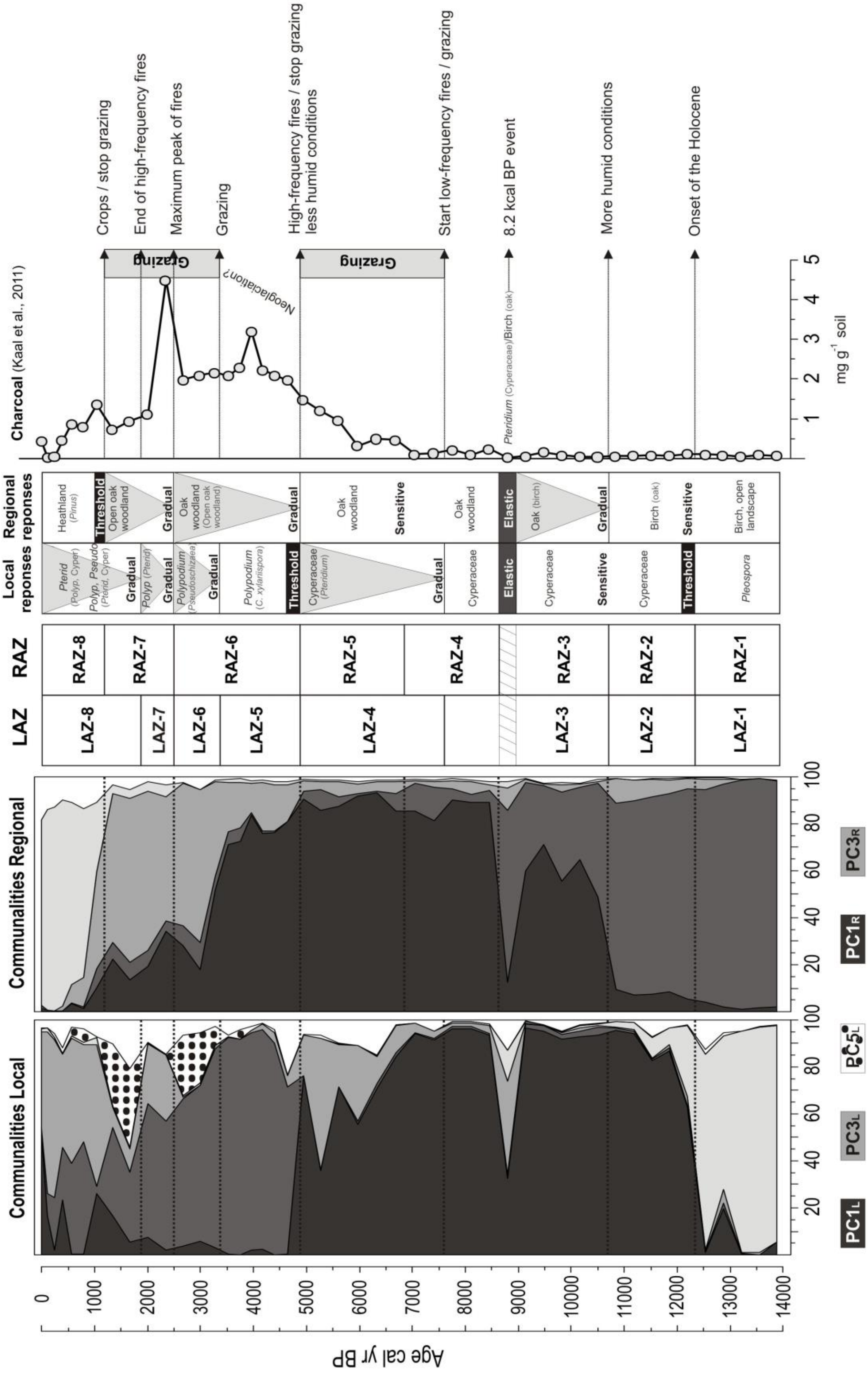

RAZ
RAZ-8
RAZ-7
RAZ-6
RAZ-5
RAZ-4
RAZ-3
RAZ-2
RAZ-1
PC4$_R$
PC3$_R$
PC2$_R$
PC1$_R$
20
40
60
80
100
Depth (cm)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190
200
210
220
230
Age cal yr BP
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
11000
12000
13000

819 Figure 9



820
821

Figure 10


Communalities Local
PC1L
PC2L
PC3L
PC4L
PC5L
Communalities Regional
PC1R
PC2R
PC3R
PC4R
20
40
60
80
100
Age cal yr BP
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
11000
12000
13000
14000
LAZ
LAZ-8
LAZ-7
LAZ-6
LAZ-5
LAZ-4
LAZ-3
LAZ-2
LAZ-1
RAZ
RAZ-8
RAZ-7
RAZ-6
RAZ-5
RAZ-4
RAZ-3
RAZ-2
RAZ-1
Local reponses
Pterid (Polyp, Cyper)
Polyp, Pseudo (Pterid, Cyper)
Gradual
Polyp (Pterid)
Gradual
Polypodium (Pseudoschizaea)
Gradual
Polypodium (C. xylarispora)
Threshold
Cyperaceae (Pteridium)
Gradual
Cyperaceae
Elastic
Cyperaceae
Sensitive
Cyperaceae
Threshold
Pleospora
Regional reponses
Heathland (Pinus)
Threshold
Open oak woodland
Gradual
Oak woodland (Open oak woodland)
Gradual
Oak woodland
Sensitive
Oak woodland
Elastic
Oak (birch)
Gradual
Birch (oak)
Sensitive
Birch, open landscape
Charcoal (Kaal et al., 2011)
1
2
3
4
5
mg g-1 soil
Pteridium (Cyperaceae)/Birch (oak)
Neoglaciation?
Grazing
Grazing
Crops / stop grazing
End of high-frequency fires
Maximum peak of fires
Grazing
High-frequency fires / stop grazing / less humid conditions
Start low-frequency fires / grazing
8.2 kcal BP event
More humid conditions
Onset of the Holocene