Portada y contraportada por Carlos de Miguel Chaves

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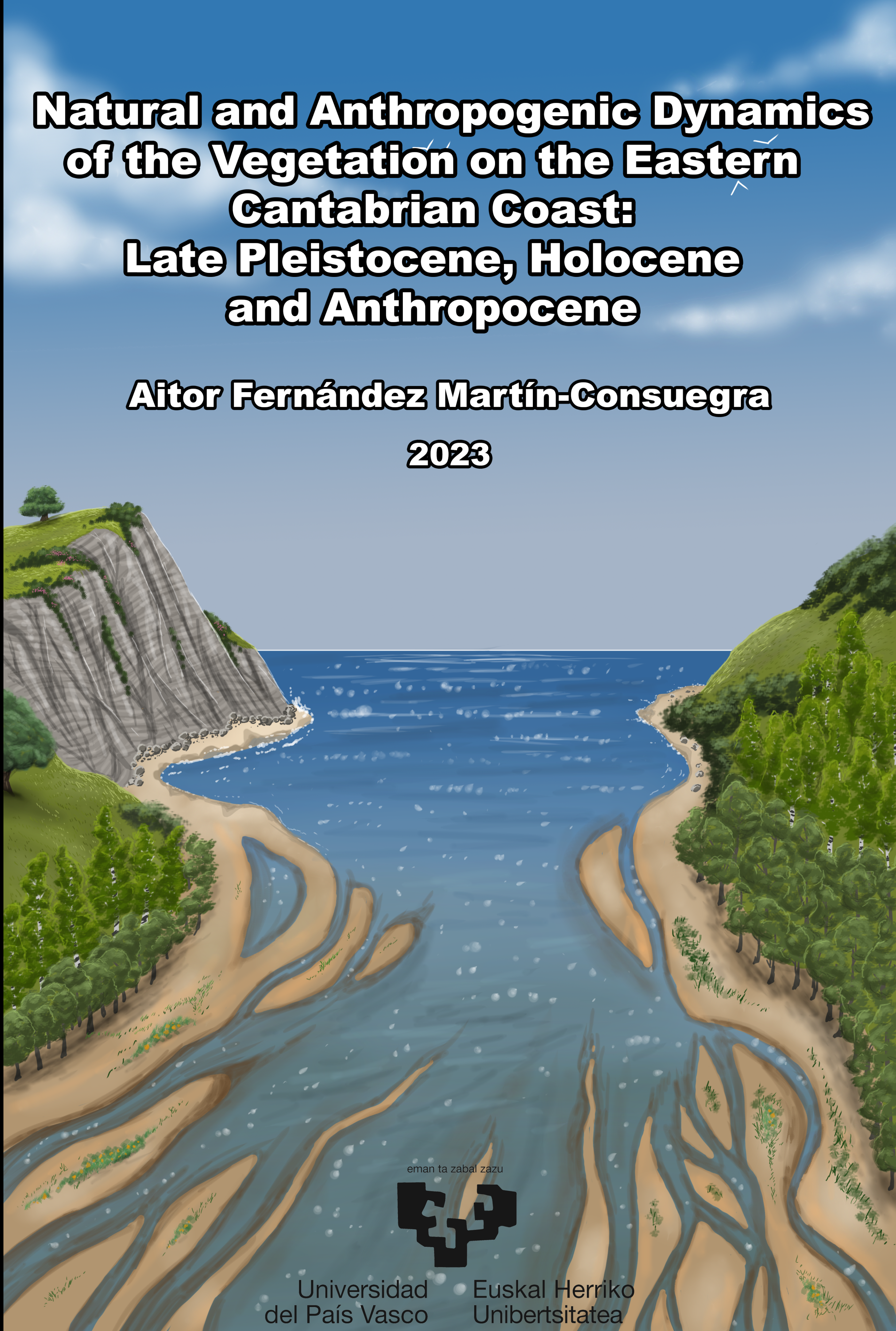
Late Pleistocene, Holocene and Anthropocene

Aitor Fernández Martín-Consuegra

2023



# Natural and Anthropogenic Dynamics of the Vegetation on the Eastern Cantabrian Coast: Late Pleistocene, Holocene and Anthropocene

## Aitor Fernández Martín-Consuegra

2023

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Universidad
del País Vasco

Euskal Herriko
Unibertsitatea

“*El sol brilla de otro modo, el aire es distinto, el agua no es la misma agua que era antes. Todo lo que antes comíamos, lo que usábamos, muere, se empequeñece, se echa a perder. Nosotros nunca cultivábamos la tierra, no la heríamos con la azada y el arado, al contrario que vosotros. A vosotros la tierra os paga un sangriento tributo. A nosotros nos lo regalaba. Vosotros arrancáis a la tierra sus tesoros por la fuerza. Para nosotros, la tierra misma los criaba y florecía, porque nos amaba.*”

Filavandrel en el El último deseo, Saga de Geralt de Rivia
Andrzej Sapkowski

*“A veces hay que darle vuelta a la hoja y comenzar de nuevo, aunque cueste o duela.”*

Dolores Ibárruri

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# Abstract/Resumen

## Natural and anthropogenic dynamics of the vegetation on the Eastern Cantabrian Coast: Late Pleistocene, Holocene and Anthropocene.

Coastal ecosystems have always been characterized by their dynamism and continuous exposure to natural changes, such as climate oscillations or the geophysical activity of the Earth. However, through their technological and evolutive development, humans have also become a very aggressive agent of transformation and alteration of these ecosystems.

Coastal ecosystems, specifically estuaries, have proven to be excellent sites for the study of both natural and anthropogenic changes thanks to their sedimentary record. In reference to the latter, humans have used these places as preferential zones for settlement and development of their activities. The great wealth of these coastal ecosystems from a biological point of view, as well as the development of natural resources around these areas, has turned estuaries into one of the ecosystems with the greatest human pressure.

Vegetation is one of the elements within these ecosystems that best reflects the changes that have occurred throughout the history of our planet. For this reason, in this doctoral dissertation a study of five long boreholes has been carried out, four of them in estuaries and one in an ancient karst lake near the coast. Additionally, another five short cores were analyzed, three of them in estuaries and two of them marine, all with the aim of recording the broadest possible chronological framework while analyzing more incisively the historical moments of greatest human impact. These boreholes have allowed us to go back in time to the Pleistocene and Holocene, while also reaching recent chronologies in the Anthropocene.

Thanks to the sensitivity of these ecosystems to natural and anthropogenic changes, the main objective of this doctoral dissertation was to characterize the natural environmental conditions on the Cantabrian Coast and to evaluate the environmental impact of anthropogenic origin on coastal ecosystems from the Pleistocene to the Anthropocene. For this purpose, we have analyzed the pollen content of the samples taken along the eastern Cantabrian coast. This allows us to know the past and present plant assemblages, evaluate the evolution of estuaries as coastal systems affected by both natural and anthropogenic dynamics, and identify the different processes and evolutionary stages that estuaries have experienced as a result of historical episodes of environmental impact.

During the Pleistocene, in the Liendo borehole (89 m long) we observed dynamics of change in the vegetation, with alternating dominance of arboreal and herbaceous vegetation. The $^{14}C$ dating has allowed us to characterize only a small part of the borehole, which could belong to the climate oscillations of MIS 3. These oscillations recorded in the vegetation would correspond to very cold and dry events (Heinrich/H-

E events) prior to the intervals of rapid warming known as Dansgaard-Oeschger (D-O) events. This would explain how the arboreal vegetation seems to recover at the same time as the humidity-indicative taxa increase.

The vegetation dynamics shown by the Requejada (15 m long), Anbeko (4.6 m), San Kristobal (4.5 m) and Ozollo (5.3 m) boreholes, chronologically framed in the Holocene, generally show a recovery of forest-type vegetation, especially since the beginning of the Holocene. This could be due to the climatic improvement occurred after the Younger Dryas with a very rapid increase in temperatures (Holocene Climate Optimum) leading to the Early Holocene (~10,000 – 8200 cal yr BP). This progressive increase in temperatures, which led to a rise in sea level, was one of the factors that most conditioned the formation of the current estuaries and therefore determined the changes in the vegetation near the estuarine zones that were colonized by mixed deciduous forest-type vegetation and herbaceous taxa acclimatized to humidity and salinity. This climatic improvement also meant that tree species isolated in small refugia during intervals of glacial cold, such as *Fagus sylvatica*, expanded along the Cantabrian coast. Around ~6000 cal yr BP, human activity started to become more noticeable in the estuarine sedimentary records. Pollen analyses show the appearance of taxa such as *Cerealia* type and NPP indicators like *Sordaria* sp. that reveal pastoral activity in the area.

Finally, the short cores at Miengo (49 cm long), Axpe (49 cm), Zumaia (45 cm) and KI03-KI06 (20 cm) show the evolution of the vegetation during the last 200 years. The human impact on estuarine areas has intensified since the 19th century, mainly due to the Industrial Revolution. In the specific case of the Iberian Peninsula, it is precisely on the Cantabrian coast where the industrialization process had its greatest development. Previously, during the Middle Ages, these areas began to be systematically deforested to create open fields for grazing and agriculture. Herbaceous plants were the dominant vegetation group or were fairly equal to the percentages of the arboreal group. Typical marsh vegetation appeared along with the presence of cereal pollen and NPP indicators of fire, erosion and grazing, confirming the development of these human activities in the estuarine area. All the Anthropocene cores show a change in the predominance of plant assemblages. Arboreal pollen indicates a great recovery of forest areas, especially since the beginning of the 20th century. This is the result of the intensive reforestation processes that began in the 19th century and culminated in the reforestation of the "Plan Nacional de Repoblaciones" (PNR, National Reforestation Plan) in the 1940s. These reforestations were characterized by a marked economic interest, prioritizing taxa of rapid growth.

## Dinámica natural y antrópica de la vegetación de la Costa Cantábrica Oriental: Pleistoceno final, Holoceno y Antropoceno.

Los ecosistemas costeros se han caracterizado siempre por su dinamismo y su continua exposición a cambios de carácter natural, como las oscilaciones climáticas o la actividad geofísica de la Tierra. Sin embargo, el ser humano se ha convertido gracias a su desarrollo evolutivo y tecnológico en un agente muy agresivo de transformación y alteración de estos ecosistemas. De los ecosistemas costeros, los estuarios, han demostrado ser enclaves idóneos para estudiar tanto cambios de carácter natural como antrópico. En referencia a estos últimos, el ser humano ha utilizado estos lugares como zonas preferenciales para el asentamiento y desarrollo de sus actividades. La gran riqueza de estos ecosistemas costeros desde el punto de vista biológico, así como el aprovechamiento de los recursos naturales que se desarrollan entorno a estas zonas, ha convertido a los estuarios en uno de los ecosistemas que más presión humana soporta.

Dentro de estos ecosistemas, la vegetación es uno de los elementos que mejor refleja los cambios que se han producido a lo largo de la historia de nuestro planeta. Por eso, en esta tesis doctoral se ha realizado el estudio de 5 sondeos largos y 5 sondeos cortos, 7 de ellos en estuarios, 2 de ellos marinos y 1 en un antiguo lago kárstico con el objetivo de registrar el marco cronológico más amplio posible a la vez que analizamos de manera más detallada los momentos históricos de mayor impacto humano. Estos sondeos nos han permitido retroceder en el tiempo hasta el Pleistoceno y el Holoceno llegando hasta cronologías recientes del Antropoceno. Gracias a la sensibilidad de estos ecosistemas ante los cambios naturales y antrópicos, este trabajo de tesis se planteaba como objetivo principal caracterizar las condiciones ambientales naturales de la Costa Cantábrica y evaluar el impacto ambiental de origen antropogénico en los ecosistemas costeros desde el Pleistoceno hasta el Antropoceno. Para ello, se ha analizado el contenido polínico de los sondeos extraídos a lo largo la costa cantábrica oriental para conocer la evolución de los conjuntos vegetales pasados y presentes, evaluar la evolución y transformación de los estuarios como sistemas costeros afectados tanto por dinámicas naturales como antrópicas, e identificar los diferentes procesos y etapas evolutivas que han experimentado los estuarios como consecuencia de episodios históricos de impacto ambiental.

Durante el Pleistoceno, en el sondeo de Liendo (89 m de longitud) se observan dinámicas de cambio en la vegetación, con alternancia en la dominancia de la vegetación arborea y herbácea. Las dataciones obtenidas por $^{14}C$ nos han permitido caracterizar temporalmente solo una parte del sondeo cuyas oscilaciones climáticas podrían relacionarse al MIS 3. Estas oscilaciones climáticas registradas en la vegetación se corresponderían con eventos muy fríos y secos (eventos Heinrich/H-E)

previos a los intervalos de calentamiento rápido conocidos como eventos Dansgaard-Oeschger (D-O). Esto explicaría cómo la vegetación arbórea parece recuperarse a la vez que aumentan los taxones indicativos de humedad.

La dinámica de la vegetación mostrada por los sondeos de Requejada (15 m de longitud), Anbeko (4,6 m), San Kristobal (4,5 m) y Ozollo (5,3 m), encuadrados cronológicamente en el Holoceno, muestran generalmente una recuperación de la vegetación de tipo boscoso, sobre todo desde inicios del Holoceno. Esto podría deberse a la mejora climática ocurrida tras el Younger Dryas con un aumento muy rápido de las temperaturas (Optimo Climático Holoceno) que da lugar al Holoceno Inicial (~10.000 – 8.200 años cal BP). El aumento progresivo de las temperaturas, que conllevó al aumento del nivel del mar, fue uno de los factores que más condicionaron la formación de los actuales estuarios y, por tanto, que determinó los cambios en la vegetación próxima a las zonas estuarinas que fueron colonizadas por vegetación de tipo bosque caducifolio mixto y taxones herbáceos aclimatados a la humedad y la salinidad. Esta mejora climática también supuso que especies arbóreas aisladas en pequeños refugios durante los intervalos de frío glacial, como *Fagus sylvatica*, se expandieran a lo largo del litoral cantábrico. En torno al ~6.000 años cal BP, la actividad humana se empieza a hacer más notable en los registros sedimentarios estuarinos. Los análisis polínicos muestran la aparición de especies como *Cerealia* tipo e indicadores NPPs como *Sordaria* sp. que nos revelan actividad pastoral en la zona.

Finalmente, los sondeos cortos de Miengo (49 cm de longitud), Axpe (49 cm), Zumaia (45 cm) y KI03-KI06 (20 cm) muestran la evolución de la vegetación durante los últimos 200 años. El impacto humano en las zonas estuarinas desde el siglo XIX se intensificó, debido fundamentalmente a la Revolución Industrial. En el caso concreto de la Península Ibérica, es precisamente en la Cornisa Cantábrica donde el proceso industrializador tiene su mayor desarrollo. Previamente, durante la Edad Media, estas áreas comenzaron a ser sistemáticamente deforestadas para crear campos abiertos para el pastoreo y la agricultura. Las plantas herbáceas eran el grupo de vegetación dominante o estaban bastante igualadas con los porcentajes del grupo arbóreo. La vegetación típica de marisma aparece junto con la presencia de polen de cereal y los indicadores NPP de fuego, erosión y pastoreo, confirmando el desarrollo de estas actividades humanas en las zonas estuarinas. Durante el Antropoceno, el polen arbóreo indica una gran recuperación de las zonas forestales, especialmente desde principios del siglo XX. Esto es resultado de los procesos de reforestación intensivos iniciados a partir del siglo XIX y que culminaron con las repoblaciones del “Plan Nacional de Repoblaciones” de 1940. Estas repoblaciones se caracterizaron por un marcado interés económico, priorizando taxones de rápido crecimiento

# Abbreviations

# ABBREVIATIONS

| | |
|---|---|
| **$^{14}C$** | Carbon-14 |
| **$^{137}Cs$** | Cesius-137 |
| **$^{210}Pb$** | Lead-210 |
| **$^{226}Ra$** | Radium-226 |
| **$^{222}Rn$** | Radon-222 |
| **$^{235}U$** | Uranium-235 |
| **$^{238}Pu$** | Plutonium-238 |
| **$^{239+240}Pu$** | Plutonium-239+240 |
| **AP** | Arboreal Polen |
| **AWG** | Anthropocene Working Group |
| **AZSA** | Compañía Asturiana de Zinc S.A. |
| **BCE** | Before the Common Era |
| **BMP** | Basque Mud Patch |
| **BP** | Before Present |
| **Cal** | Calibrated |
| **CIC** | Constant Initial Concentration |
| **CCHS** | Centro de Ciencias Humanas y Sociales |
| **CE** | Common Era |
| **CF** | Constant flux |
| **CF:CS** | Constant flux: Constant sedimentation |
| **$CH_4$** | Methane |
| **CIC** | Constant initial concentration |
| **$CO_2$** | Carbon dioxide |
| **CONISS** | Constrained cluster analysis |
| **CSIC** | Consejo Superior de Investigaciones Científicas |
| **CRS** | Constant rate of supply |
| **D-O** | Dansgaard-Oeschger |
| **E** | East |
| **e.g.** | For example |
| **GS-1** | Greendland Stadial-1 |
| **GSSP** | Global Boundary Stratotype Section and Point |
| **ha** | Hectares |
| **HCl** | Hydrochloric acid |
| **H-E** | Heinrich event |
| **HF** | Hydrogen fluoride |
| **$hm^3$** | Hectometers |
| **Km** | Kilometers |
| **KOH** | Potassium hydroxide |
| **LPAZ** | Local pollen assemblage zone |
| **m** | Meters |
| **$m^3/s$** | Cubic-meters per second |
| **Ma** | Million years |
| **MAR** | Mass accumulation rate |
| **MIS** | Marine isotopic stages |
| **mm** | Millimeters |
| **Mt** | Megatons |
| **MWP** | Medieval Warm Period |
| **N** | North |
| **$N_2$** | Nitrogen |
| **NaOH** | Sodium hydroxide |
| **NAP** | Non-Arboreal Pollen |
| **NE** | Northeast |

# ABBREVIATIONS

| | |
|---|---|
| **NGRIP** | North Greenland Ice Core Project |
| **NNE** | North-northeast |
| **NPPs** | Non-Pollen Palynomorphs |
| **NW** | Northwest |
| **O** | Oxygen |
| **OHO** | Older Holstenian Oscillation |
| **PANN** | Annual precipitation |
| **Pb** | Lead |
| **pH** | Acidity or basicity index |
| **PVC** | Polyvinyl chloride |
| **RMSEP** | Root Mean Square Error of Prediction |
| **Rpm** | Revolutions per minute |
| **SAR** | Sedimentation accumulation rate |
| **SiZer** | Significant zero crossings of derivatives |
| **sp** | Species |
| **SSW** | South-southwest |
| **SW** | Southwest |
| **TANN** | Annual temperature |
| **t/yr** | Tons per year |
| **UNESCO** | United Nations Educational, Scientific and Cultural Organization |
| **y.r.** | Years |
| **MIS** | Marine isotopic stages |
| **UPV/EHU** | Universidad del País Vasco/ Euskal Herriko Unibertsitatea |
| **W** | West |
| **WA** | Weighted averaging |
| **WA-PLS** | Weighted averaging partial least squares |
| **Zn** | Zinc |

# Introduction

# 1. Landscape ecology

The definition of landscape is more intricate than we usually think because a good definition has to take into account different points of view. These were very well expressed by the paintings of the European landscape school in the 16th century, where physical, cultural, human and purely aesthetic characteristics are gathered together (Kupfer, 1995). The complexity is such that, in academia, different definitions of landscape have been made depending on the branches of knowledge from which one wishes to approach the term. In the case of natural sciences, the term was introduced by Pierre Dansereau (Dansereau, 1957) and this debate is due to whether landscape should be conceived and studied as a spatial scale, as a level within the ecological hierarchy or as a functional perspective with its causes and consequences (Wiens, 2002).

The most common use of the term landscape is to refer to the spatial scale of the landscape itself ("landscape scale"). What the landscape scale refers to is the physical dimensions of the entities as well as the phenomena observed. This always implies both spatial and temporal units of measurement. This is where human perceptions of their environment become relevant (Kupfer, 2011). This concept can be criticized because of the subjectivity that is inherent in it, but at the same time, it is understandable since the landscape has always been part of the human worldview.

Another definition related to landscape is "landscape level". In this case, the landscape is understood as another level within an ecological hierarchy. Therefore, the landscape is a biological organization that is larger than an ecosystem but smaller than a biome. It is a set of ecosystems that, on many occasions, is dominated (or emphasized) by one of those ecosystems (as is the case of forest landscapes, agricultural landscapes...) (Kupfer, 1995).

The two definitions are convergent since the principal factor is the role that human perception plays in understanding what the landscape is (Figure I.1). This is something that was already explained by the German geographer Alexander von Humboldt (Farina, 2000a).

Finally, there is a third definition of landscape, somewhat more complex, which is based on the fact that the perception of the landscape and its processes depends directly on the organism of interest (plants, insects...). With this definition, it is recognized, on the one hand, that the scales at which spatial processes are perceived differ depending on the organisms on which the study is focused. On the other hand, it avoids defining landscape through only human perceptions (Bossenbroek et al., 2005; Turner, 2005). This third definition, pioneered in North America, reflects the more biophysical orientation of landscape ecology since the causes and consequences to be taken into account in the landscape depend on a variable broader than human beings. Moreover, it is applicable to all scales and adaptable to different modern topics (land management, research, administration, etc.).

**Figure I.1** - "*Sommernatt*" (1886) one of the most representative paintings of the Norwegian landscapist Kitty (Christine) Lange Kielland.

The geology of the landscape is also a significant factor. However, many of these definitions of landscape barely take it into account. This is because many geological phenomena occur on great time scales that humans cannot experience directly. This is an error because although landscape geology has a role in all of the above definitions, geology has also its own division of the study of the landscape. The strong relationship between landscape formation and geologic time works in both directions. In fact, the view of the landscape from the geological perspective is also organized according to a hierarchical classification system. This typology allows the recognition of areas with a similar landscape character or with an origin related to the same geological process. In summary, there are three categories: 1. General landscape character (e.g., the coast), 2. Large scale terrain or topography (e.g., estuary) and 3. Medium-scale typifying terrain or topography (e.g., saltmarsh, reclaimed saltmarsh/mudflat) (Goudie, 1981; Natural Resources Wales, 2016).

This is precisely where the term "landscape ecology" comes in. Landscape ecology is the study of the relationships between space and ecological processes at different scales, which is, in other words, what the third definition of landscape is referring to. The term "landscape ecology" was first used in 1930 by the biogeographer Carl Troll (Vila-Subirós et al., 2006). The technological advances of the time in aerial photography, together with a growing theoretical interest related to ecological sciences, were able to open new frontiers and approaches to the study of landscape and ecology in general (Kupfer, 2011). At first, landscape ecology and the analysis of human interactions with their environment focused more on studies related to land use. In Europe, slowly, a more transdisciplinary approach began to develop, with the entry of other scientific fields besides geography (Opdam et al., 2002; Metzger, 2008).

In general, landscape ecology tends to focus on the relationship of human activity with the landscape through other areas of ecology, such as ecosystem conservation and management and regional planning. And this is where, from our point of view, studies of fields traditionally attributed to biology, such as palynology, would fit in (Farina, 2000b; Kupfer, 2011).

It is also interesting to note the definition given by the European Union following the European Landscape Convention held in Florence in 2000. In it, landscape is defined as any part of the territory as perceived by the population, whose character is the result of the action and interaction of natural and/or human factors (CEP, 2000).

This doctoral dissertation uses paleopalynology as a tool to study what the landscape was like in the past, related to how it is at present and how it may become in the future. Furthermore, within the timescale in which this study is framed, we have been able to study the relationship between a group of organisms (vegetation) and the landscape, and the changes that it has undergone, attending to the causes and consequences of natural and anthropogenic dynamics.

## 1.1. Landscape environmental changes and anthropization

Landscapes are subject to different types of pressures. For example, changes due to climate fluctuations or the extinction of species will also be transferred to the different landscapes. This is because many of these changes have an impact on the organisms that constitute the ecosystems and, therefore, the landscapes.

These changes are the ones we often mention when talking about environmental alterations. We observe a change in a particular group of organisms (vegetation, meiofauna, etc.) and study the impact it has on the ecosystem. These changes in the ecology and the perception that we, as humans, have of them, are what we call environmental changes. It should be borne in mind that the concept of environment refers to physical, biological and chemical elements, of both natural and artificial origin. That is why we can discuss, inside the same environment, about the natural environment or the artificial environment. The natural environment refers to all biological and physical aspects that have not undergone human intervention. The artificial environment is reserved for those activities or interventions of humans (such as rural, urban or industrial areas). It is also important to keep in mind that the environment also refers to the conditions for the development of life and not only to the living space (Mayewski et al., 2004).

Climate and environmental variability are not new to our epoch. Climate fluctuations, as well as a series of other changes experienced by the planet, have been and will always be present with or without human impact. There are different natural factors that affect the climatic and environmental change of our planet: volcanic eruptions, ocean currents, plate tectonics, changes in the Earth's orbit, solar variation, the internal variability (El Niño-La Niña cycles, Arctic Oscillation…), etc. All of them have been the driving forces of the environmental changes that have occurred throughout the Earth's history, to which we must now add a new one: human impact (Galloway et al., 2008).

The oceans also constitute one of the factors with the greatest impact on environmental changes and climate regulation of our planet. Ocean currents, located both in the shallowest part of the ocean and in the depths (more than 300 m deep). are able to move the water horizontally and vertically. Moreover, these currents operate on global and local scales, since most of these currents are part of a more complex, interconnected system of currents. These currents are influenced by wind, ocean tides, the Earth's rotation (Coriolis effect), solar energy, differences in water density and the topography of both the sea basins themselves and the continental land (Pörtner et al., 2014). The differences in the density of ocean water make the different layers of the water column blend together, resulting in a greater circulation. These changes in density are primarily due to the temperature and salinity of the water. This also makes the different currents differ in scale, speed and energy.

All these currents together are known as the global conveyor belt (Figure I.2). This circulation is possible thanks to the existence of warm surface currents, which transport less dense water from the equator to the poles, and deep ocean currents that carry out the reverse process (Winton et al., 2013). The global circulation system is vital for the distribution of thermal energy, the regulation of climate and weather, and the cycling of different nutrient sources.

Another important factor that has been determinant in the history of our planet and has produced great climatic and environmental variations is the Earth's orbital changes. The displacements and the wobbling of the planet are the cause of glacial and interglacial periods. Also known as Milankovitch Cycles (Figure I.3), these orbital changes have been widely studied in the scientific literature due to their great importance and influence on the climatic changes of our planet (Berger, 1988; Dynesius & Jansson, 2000). For example, the Last Glacial Period (LGP) began

110,000 years ago and ended around 12,000 BCE, leading to the Holocene or post-glacial epoch, in which we are currently immersed (Maslin & Christensen, 2007; Ruddiman, 2006).

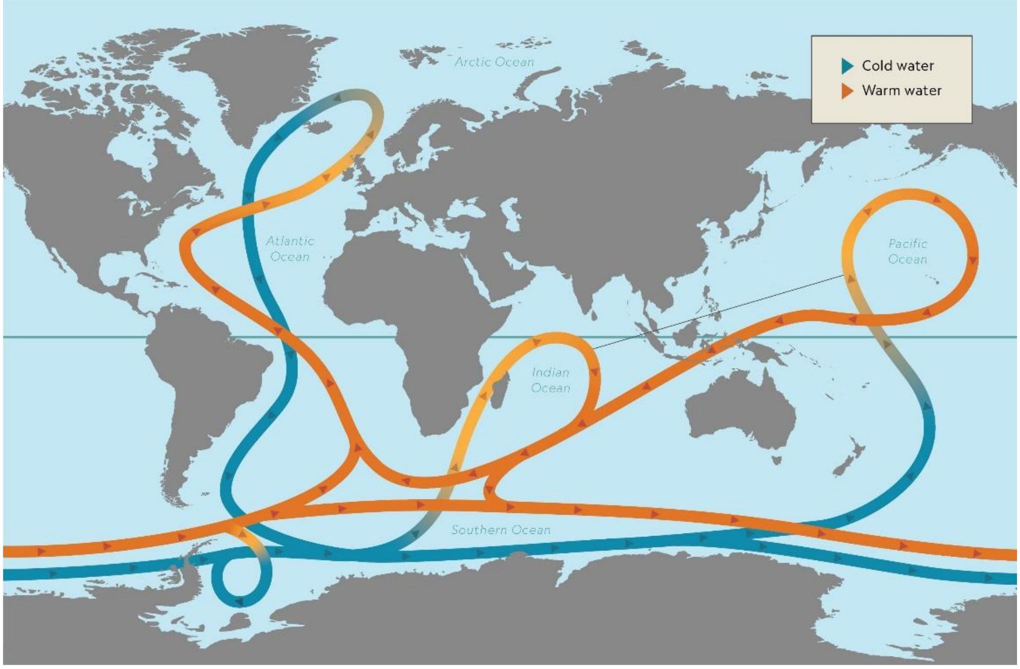


**Figure I.2** - The Global Conveyor Belt. Source: National Geographic Society (https://www.nationalgeographic.org/).

The Sun is undoubtedly one of the most important entities for the appearance of life on our planet. But the Sun has shown, throughout time, not to be completely constant in the amount of energy it emits. Scientific studies have shown that changes in the intensity of solar energy emitted have produced climatic and, consequently, environmental alterations in our planet. One of them, for example, would be the so-called Little Ice Age (1650-1850) that caused the isolation of Greenland by ice and advances in the Alpine glaciers. Even so, the contribution of solar energy and its alterations to current and past climate changes continues to generate controversy. This is because current global warming cannot be explained by solar variations. The average recorded solar energy has remained virtually constant since 1750. If global warming were due to an increase in solar energy, all atmospheric layers would be affected. However, scientific studies show that warming occurs primarily at the Earth's surface in the atmospheric layers closest to the surface (troposphere and stratosphere). This is due to the existence of greenhouse gases, the result of human activities of different kinds, which capture heat between the surface and the stratosphere. This has been observed in climate models devised from the last century to the present day. In these models, the solar irradiance variable is not sufficient to reproduce the warming observed up to the present day (Gray et al., 2010).

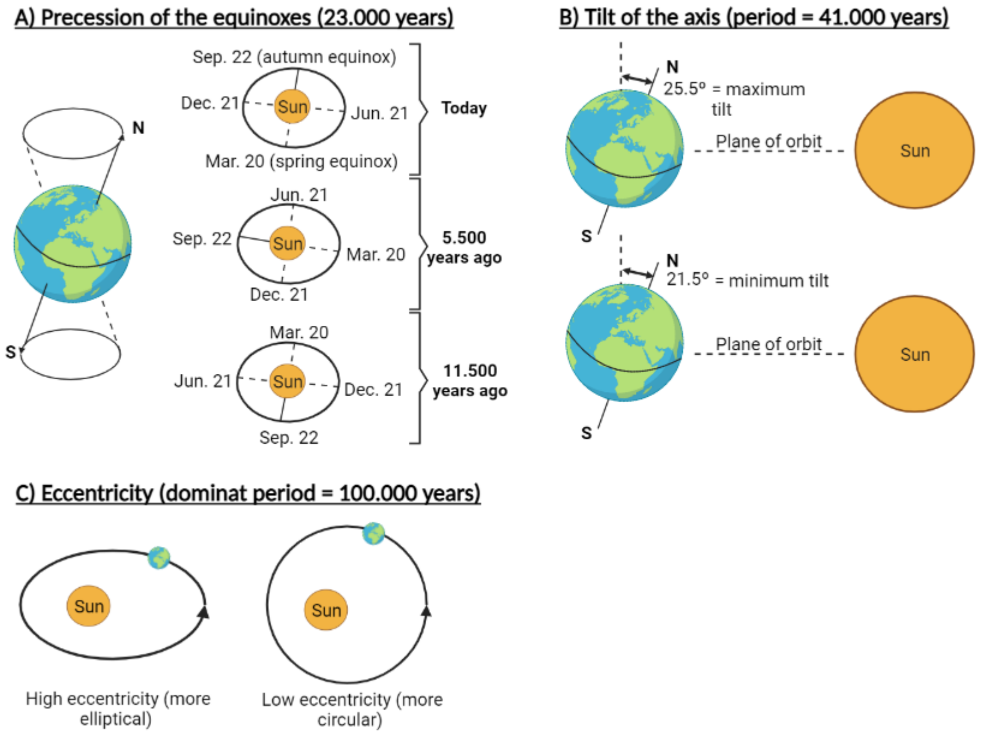


**Figure I.3** - Graphical representation of the three Milankovitch Cycles (Milankovitch, 1920). Precession of the equinoxes (A), the obliquity of the axis (B) and the orbital eccentricity (C). Modified from http://www.detectingdesign.com/milankovitch.html.

Finally, there is a natural internal variability, where some climatic changes are not conditioned by external factors. These are temporary climatic changes, on very short time scales. Some examples of this would be the El Niño-La Niña cycles and the Arctic Oscillation. These are usually phenomena that sometimes produce cooling and warming on a global scale. For example, El Niño increases global temperature, while La Niña decreases it. In both cases, they are part of the previously mentioned oceanic streams, but they have a particularity over the others as they have a cyclic character (Clement et al., 1999). As for the Arctic Oscillation, changes in atmospheric pressure in the northern hemisphere can bring warmer weather to Europe and North America, while the Arctic becomes colder than normal. The opposite may also be the case, with warmer Arctic temperatures and colder subpolar regions.

All these factors mentioned briefly above are involved in the changes that our planet has experienced in recent times. Moreover, we should not forget that they all play the same role today, so they continue to be natural drivers of climate and environmental changes.

However, on our planet, a new agent of change has appeared that bears no relation to the nature of the Earth: human activities. Humanity has acquired the ability to influence the climate and the environment to such an extent that we can modify their nature. This capacity to alter the environment and climate is what we call human impact (anthropization) (Figure I.4). By referring to studies about the impact of humans on the environment or climate, we approach questions such as environmental degradation, desertification, pollution, etc. (Goudie, 2013). The growing interest in studies related to human impact has caused a great number of different scientific disciplines to approach this question from different perspectives and to perform a multitude of different scientific studies. This diversity of scientific studies on human impact leads to the question, therefore, of which are the baselines of human impact.

Anthropization refers to any activity that humans perform in the environment causing an alteration of it. These alterations made by humans have occurred throughout the history of our species and, moreover, have been (and still are today) of different types, on different scales and over different periods of time. That is why we consider it important to take into account some aspects that characterize anthropization and that can help to understand this process within the socio-cultural evolution of our species.

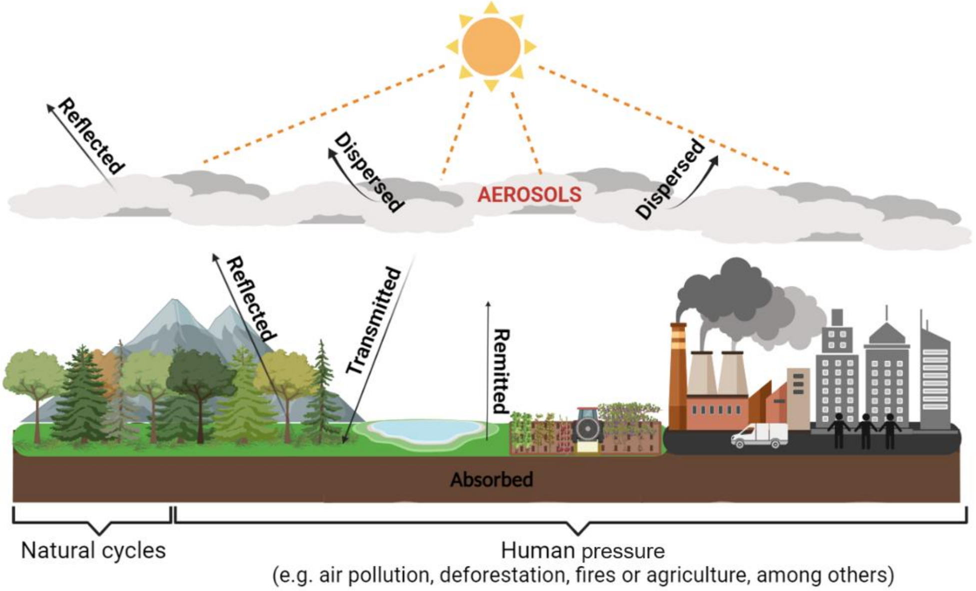


**Figure I.4** - Graphical representation of the effect on solar radiation of aerosol emission into the atmosphere caused by human activity. Adapted from Fúster (2000).

Population growth and cultural development are two of the most important factors in understanding human impact. Our species was able to expand from the African continent to practically occupy the entire planet (Boyle et al., 2011). Population levels during the earliest phases of our civilization are complicated to estimate; some calculations based on studies of hunter-gatherer societies estimate that the world population could have reached 5 million (Ehrlich et al., 1978). It is from the agricultural development (about 10,000 years ago) that a great expansion of the human population occurred, from 200-300 million during the first centuries CE to 500 million people in 1650 (Boyle et al., 2011). Subsequent advances in the fields of medicine and applied industry improved the quality of life greatly, producing an enormous population increase reaching 7 billion in 2012. Although, in summary, it may seem that due to the exponential growth of the population throughout history, the human impact has been greater, this is not entirely true. During the history of humankind there have been periods where population growth has suffered declines mainly due to world wars, epidemics and pandemics. The explanation of why population increases have been so high and why these catastrophic events for population growth have been overcome lies, precisely, in the cultural and technological development that has accompanied humans in evolutionary terms (Goudie, 2013).

Human impact has not been simultaneous in general terms throughout history. Neither in space nor in time. The same environmental impact has not been produced by towns in Europe during the Industrial Revolution as, at the same historical moments, by human settlements in Latin America. For this reason, different aspects must be evaluated separately when studying the anthropogenic impact: richness, the population density and technology. These three terms, together with the study of the social and economic structure of the different societies, are what characterize and act together in the human impact on the environment (Meyer, 1996).

Considering cultural and technical development as one of the most relevant factors in the history of human transformation of the environment, we must emphasize three main phases: the phase of hunting and gathering; the phase of plant cultivation, animal husbandry and metalworking; and finally, modern industry and urban society (Ponting, 2007).

In the hunting and gathering stage, humans began to take advantage of the environment in their activities. These activities consisted mainly of the shaping of stone tools, the exploitation of wild plant resources and hunting animals. This involved the use not only of stone materials but also of wood and bones. The first constructions of shelters and clothing were possible thanks to the mastery of these materials, which allowed early human societies to live in areas that were less favorable environmentally in terms of habitat. The realization of these activities already implied an alteration of the surrounding area, but until then, the impact of hunter-gatherer societies on the environment was local, limited to the extinction of animal species (mainly great mammals) or the spread of seeds and nuts between different regions. With the mastery of fire, especially with the sedentarization of humans and the emergence of agriculture, humans made a considerable leap in their ability to transform the natural environment at regional level (González Urquijo et al., 2000; Gibaja et al., 2003; Goudie, 2013; Peña Chocarro et al., 2013; Ibáñez-Estévez et al., 2019).

The second phase in the cultural and technological evolution of humans is the development of agriculture, stock-raising and the incipient metallurgy (Figure I.5). With sedentarization, humans began to domesticate the first plants and animals, which led to an increase in population density, since the main part of the human diet was obtained in more reduced areas. The domestication of plants and animals occurred asynchronously, as not all human societies developed it at the same time, but we can place this initial domestication at around 10,000 years ago. This “event” would lead to the birth of the first cities in the Middle East. Thanks to the control and domestication of food resources, humans were able to achieve a reliable control of the diet, allowing an increase in population density first, but also greater cultural and technological development by generating vital security (Childe, 1936; Isaac, 1970; Harris, 1996 Diamond, 2002; Mithen, 2007; Ibáñez-Estévez et al., 2019).

These activities and the processes involved were the first to have a major regional impact on the environment (Mannion, 1995). Agriculture, for example, benefited from the advances in the technology of irrigation and river farming, which involved the alteration of areas near rivers to develop different types of irrigation systems, as well as deforestation to open up space for new areas of cultivation. Furthermore, the domestication of animals was soon used as a way to mechanize agriculture, using animal traction to develop these activities faster, thanks to the plow, the farm cart, etc. (Greenfield, 2010). This is also related to the so-called "Revolution of Secondary Products", a process that consists of the use of second-grade animal resources, mainly dairy and textile products, and the aforementioned labor mechanization. Today, and in fact, during the last 300 years, the agricultural sector and arable land have increased sixfold. In addition, one of the great changes that have occurred in the agricultural system is the emergence of the denominated "large-scale monocultures".

Today, only four crops (wheat, rice, potato and corn) are produced in such quantities that they add up to more tonnage than the next 26 crops planted worldwide together (Simmonds, 1976; Goldewijk, 2001; Goudie, 2013). Another technological development that produced great advances in human society but also had and still has a great power of environmental transformation is mining and metallurgy. Metallurgy emerged around the sixth millennium BP (archaeological evidence from

Catal Hüyük, Turkey). But the spread of metallurgical techniques was rapid, especially from the second millennium BP (Muhly, 1997; Craddock, 2000).

**Figure I.5** -Recent agricultural deforestation in the province of Salta (Argentina). Source: Greenpeace (https://www.greenpeace.org/argentina/).

Therefore, the environmental impact that mining and metallurgy have on the environment is extensive and is not only due to the extraction and excavation of minerals and mines, but also to the treatment of metals. Without forgetting that the work of mining requires large amounts of wood, which also influences the deforestation of the areas near the points of mineral extraction.

Finally, the phase of technological and cultural development with the biggest impact on the environment is industrial development and modern urbanization. The cities of antiquity already caused gradual changes in the surrounding landscape. Cities such as Rome grew and achieved splendor thanks to the ability of human beings to transform the surrounding environment (creation of bridges, draining of wetlands, alteration of hills...). But the most powerful impact that these have had (and still do today) has been from the 18th century onwards with the development of major industries (Figure I.6). The evolution of cities has been such that each city has even come to have its own environmental problems, which are not always the same among them, and new terms have appeared for their study (urban ecology, urban geomorphology...) (Gurnell et al., 2007). Some of the most important technological advances are, for example, the steam engine and motor vehicles, which facilitated the access of the general population to fossil energy, which led to a decrease in the dependence on animal force and nature for certain activities, especially agricultural ones. To this must be added the emergence of insecticides, fertilizers, development of selective breeding techniques of animal and plant species... and advances in medicine. All this is what, once again, produced a reduction of the space necessary for the survival of each individual and, at the same time, increased the pressure on the use of the resources (Goudie, 2013). From the Industrial Revolution to the present day, the use of new fuels (coal and oil) began to come on the scene, allowing mining activity to expand to the point that the capacity of this activity to alter the environment is greater than the natural erosive capacity. In fact, some studies show that the total amount of materials moved by this industry is 1.7 times greater than the amount of sediment transported by all the world's rivers combined (Young, 1992).

**Figure I.6** - Industrialization in Spain (Basque Country). “La Basconia” factory in 1920. Source: Municipality of Basauri (www.basauri.net/es).

During the 20th century, the human population grew worldwide from 1.5 billion to 6 billion, energy use multiplied by 13 to 14 times, water use multiplied by 9 times and the overall economy increased by 15 times (Myers & Kent, 2003; McNeill, 2005; Rockström et al., 2009). Some studies claim that the consumption of energy, resources and deforestation in the 20th century was greater than all of these factors during the entire previous history of our species (McNeill, 2003). In general, as technology advances, consumption and pressure on the planet's resources increase, and although this consumption is not balanced (resource consumption varies according to geographical area), the reality is that there is a general increase in per capita resources and in the human impact on the environment (Myers & Kent, 2003; McNeill, 2005). Advances in chemical and nuclear engineering are some of the most relevant "recent" advances and are not exempt from their own impact on the environment. In fact, the impact generated by these advances responded also to warlike causes such as the Second World War or industrial accidents such as Chernobyl. The impact that humans are having is such that it has even altered the natural nitrogen cycles. Humans currently produce more $N_2$ artificially than the whole of the Earth's processes. This is mainly due to fuel burning, biomass burning, legume cultivation and the ammonia industry. All this reactive $N_2$ ends up in the environment, polluting rivers and seas (Galloway et al., 2008; Rockström et al., 2009).

The combination of all these recent drivers means that we can now speak of environmental change on a global scale. The point is that during the last 300 years changes and alterations have gone from taking place in small or regional areas to a global scale. Humans are no longer only capable of altering the vegetation cover of a certain number of hectares. We are now capable of changing the atmospheric composition or modifying the geochemical composition of the planet, for example. We are able to alter the vital and fundamental flows of the Earth's chemicals and energy (Goudie, 2013).

## 2. Pleistocene, Holocene and… Anthropocene

The geologic time scale is the way in which the events of the Earth's history are referenced chronologically. It establishes divisions and subdivisions according to the age and recorded information of the rocks following the stratigraphic principle of rock superposition. Since 1974, the International Commission on Stratigraphy has been in charge of studying, introducing and evaluating possible changes in this scale.

This PhD thesis is framed in the Quaternary Period, formed by the Pleistocene and Holocene epochs. This division is the one formally approved, but the formalization of a possible new epoch, the Anthropocene, is currently under discussion. This is why, throughout this doctoral dissertation, references will be made to the term "Anthropocene".

### 2.1. Pleistocene

The Pleistocene is the first geological epoch in the Quaternary period. It began 2.6 Ma ago and extended until ca. 11,700 cal yr BP. During the Pleistocene, large climatic fluctuations occurred consisting of temperature increases, known as interglacials, and subsequent progressive cooling known as glacials (Dansgaard, 1985; Sánchez-Goñi & D'Errico, 2005). Interglacial intervals are those times when the glacial ice cover is minimal (as at present), whereas glacial intervals are those times when the ice cover is so large that it occupies vast extensions of continental areas in middle latitudes. As mentioned in the previous section, these fluctuations are one of the most important causes of landscape alteration, because of the implications that they globally affect the continental geology as well as the oceans, fauna and flora (Yokoyama et al., 2000; Barnett et al., 2005; Candy et al., 2014) (Table I.1).

The Pleistocene is considered an epoch with a great number of faunal and vegetational changes; animal species that moved or became extinct, replacement of plant taxa by others that were better adapted to the new climatic conditions, etc. This makes the Pleistocene epoch one of the most interesting times for the study of the dynamics of natural change on our planet (Suárez-Bilbao, 2018).

Due to studies carried out in recent years on different proxies and deposits (Greenland ice core, pollen and foraminifera analysis, etc.), it has been possible to study variations in δ18O that have allowed us to identify up to 104 marine isotopic stages (MIS) during the Quaternary period. MISs are ordered according to a classification in which the even numbers in the nomenclature correspond to glacial intervals, while the odd numbers correspond to interglacial intervals. The numbering of the MISs increases with increasing age, so that MIS-104 refers to the earliest MIS. Within each MIS, there are also short and colder intervals (called stadials) within interglacials and other intervals of warmer climate inside a glacial phase (called interstadials) (Preusser, 2004; Sánchez-Goñi, 2005; Sánchez-Goñi et al., 2008; Sakari Salonen et al., 2013; Blakemore et al., 2014; Murray-Wallace et al., 2021).

What marks the transition from the Pleistocene to the Holocene is the end of the last glacial cycle ca. 11,700 years ago. The consequence of the cyclical changes in the climate caused alterations and variations in different factors, among them the hydrochemical ones, which, as mentioned in the previous section, are among the most important climatic regulators of our Earth system. In fact, throughout the Pleistocene, these cyclic changes have been relatively common and their consequences have been observed in several studies (Figure I.7). This profoundly affected the terrestrial landscapes and the ocean environments alike, causing for example new karstic systems, which were filled with sediment of diverse origin, forming many of the Quaternary paleontological and archaeological sites that are studied today or a more complete marine record that registered in detail this climatic transition (Ford & Williams, 2007; Suárez-Bilbao, 2018). Thanks to the appearance of these sites, interdisciplinary studies have been carried out, with different proxies that have provided valuable information for the reconstruction of the Pleistocene climate and the cyclic environmental changes (MIS).

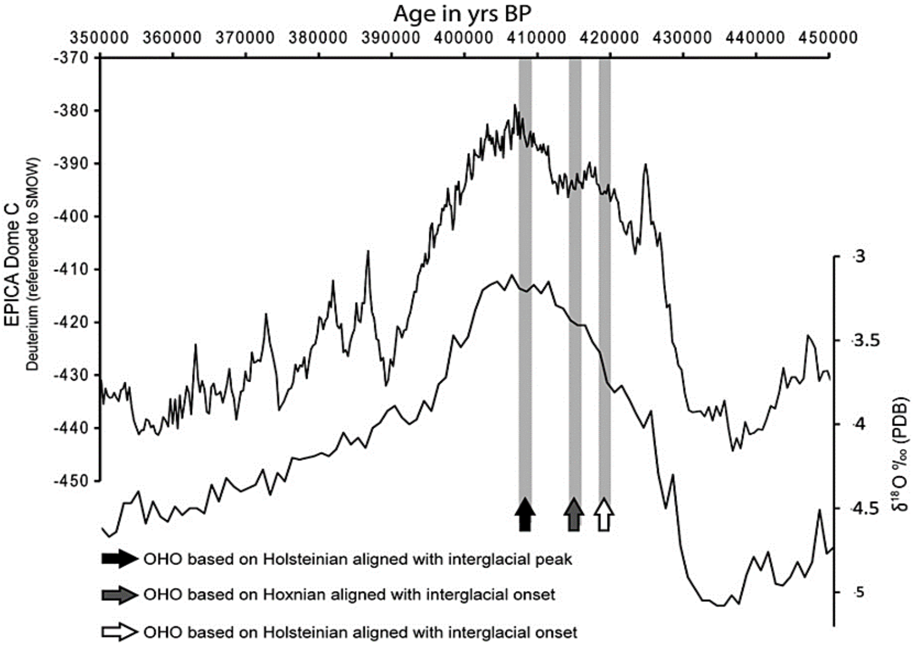


**Figure I.7** - An example of climatic change and regulation. Potential timing of the Non-Arboreal Pollen (NAP) and the correlation of the Older Holsteinian Oscillation (OHO) pollen zones with marine and ice core records. The impact of the meltwater on the oceanic circulation could be a potential trigger for this event (Koutsodendris et al., 2012). Taken from Candy et al. (2014).

## 2.2. Holocene

The term Holocene means "entirely recent". It is the official name for the most recent geological epoch of our planet characterized by the last interglacial interval. Within the Holocene, other terms such as Recent or Postglacial are referred to in different scientific fields, and although they do not have a formal status, they are widely used in the literature. The adoption of the term Holocene meant giving greater importance to the present interglacial, to the different paleoenvironmental records and, above all, to the anthropological record that this epoch preserves (Gibbard & van Kolfschoten, 2005).

The Holocene record and the establishment of its beginning is not located at the end of the last cold stage but with the end of the Younger Dryas or Greenland Stadial (GS-1). This consists of a cooling episode that interrupts the warming characteristic of the current interglacial. This event has been extensively studied and has been dated to between ca. 12,900 and ca. 11,500 cal yr BP (Walker et al., 2009). Hence, the established date for the beginning of the Holocene in the literature is ca. 11,700 cal yr BP. The definition of the Pleistocene-Holocene boundary has always generated much controversy, and was not clear until the study of the Greenland ice cores appeared. Finally, in 2008, the Holocene GSSP was confirmed at 1492.45 m depth in the NGRIP ice core, Greenland (Walker et al., 2009) (Table I.1).

The Holocene is the geological epoch that has attracted the most interest and, therefore, the most scientific studies. This is due, in part, to the great interest that the Holocene generates from the point of view of climate change, geomorphological processes, faunal migrations, changes in vegetation, sea level, etc. Major changes occurred during the Holocene, mostly due to the melting of glaciers that caused a general rise in sea level on a global scale. But, in addition, there were also processes of isostatic uplift of the terrain, causing the sea level to decrease at regional level. These transgressions continuously transformed the coastal landscape, causing lakes and estuaries to appear or disappear. The ice melt, especially in North America, produced in turn, due to the discharge of very cold water, a cooling that altered the oceanic circulation in the North Atlantic 8,200 years ago (Seppä et al., 2009; von Storch et al., 2015).

On the other hand, changes in the Earth's orbit substantially modified solar insolation, which in turn altered the planet's energy balance. First, summers reached their maximum insolation 7,000 - 6,000 years ago. Gradually and after the thaw, a progressive decrease in temperatures began due to lower insolation during the summer season, because of astronomical processes that affect the Earth's orbit. Other factors, such as volcanic activity, natural changes in the concentration of greenhouse gases, marine salinity, etc., also introduced small climatic and environmental variations to the Holocene.

Some examples of this small instability have been traditionally studied, especially in the European context. For example, during the 10th and 11th centuries, conditions in Europe were relatively stable, with hot, dry summers. Indeed, between ca. 900 and ca. 1350 CE, numerous studies record what has been called the Medieval Warm Period (MWP) (*Figure VIII*). During these years, the warm intervals (May-September) exceeded the contemporary warming at the end of the 20th century (Crowley & Lowery, 2000).

There has also been remarkable climatic variability over the last 500 years. A second example would be the so-called Little Ice Age (Figure I.8), which started in the second half of the 16th century and lasted until the early years of the 19th century. The cold periods during these centuries turned out to be considerably longer (Zalasiewicz et al., 2015).

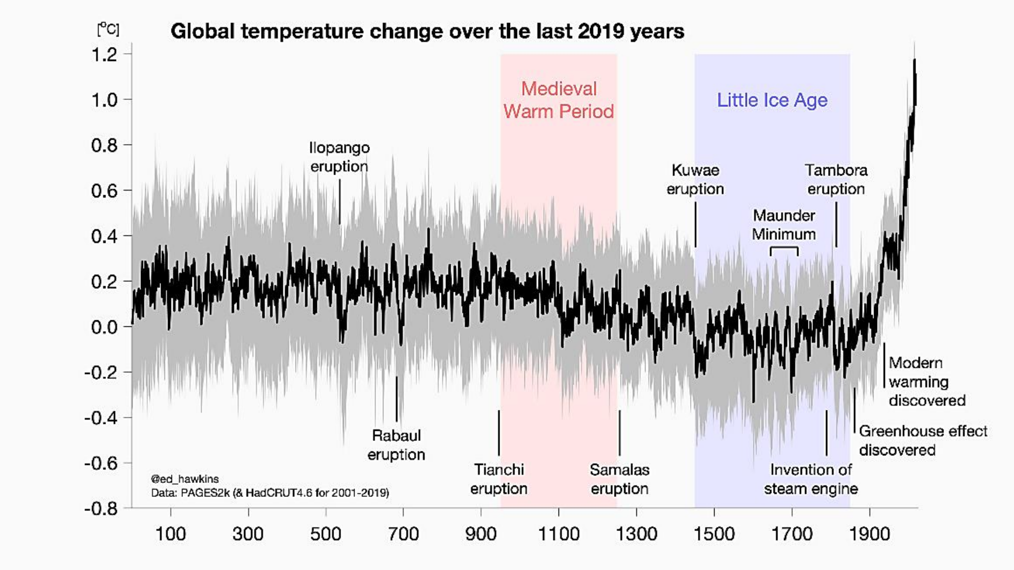


**Figure I.8** - Global temperature evolution over the last 2019 years. The Medieval Warm Period and Little Ice Age periods are indicated. Source: Ed Hawkins, University of Reading (www.climate-lab-book.ac.uk/2020/2019-years/).

## 2.3. Anthropocene

"Anthropocene" is a concept that appeared for the first time in scientific literature when Paul Crutzen, Nobel Laureate in Chemistry, referred to how the natural conditions that characterize the Holocene are being modified at different levels of the Earth System (Crutzen, 2002).

The term arose to give a name to the time interval in the history of our planet characterized by the high velocity and intensity of changes in the Earth's geological processes as a consequence of anthropogenic activities (Crutzen & Stoermer, 2000). This concept is currently used informally and refers not only to geological changes, but also to recent sociological, anthropological and ecological variations.

If we focus on the geological definition of the term, the Anthropocene has not yet been accepted as an official geological epoch, and this term and all the studies included in it are continuously revised. To this end, and as already happened with the Holocene itself, the Working Group on the Anthropocene (AWG) was created, at the invitation of the "Subcommission on Quaternary Stratigraphy", which since 2009 has been working to obtain and review the scientific evidence observed for the approval of the Anthropocene as a new geological epoch that would replace the Holocene as the current epoch, and which would also be located within the Quaternary period (Cearreta, 2017).

The approach of the Anthropocene as a geological epoch entails the need for it to meet a series of particular conditions that fit it into the international stratigraphic system. One of these conditions would be, for example, the alteration of the Earth System by humans, profoundly affecting the most recent sediments and those of new formation. If this were the case, it would be necessary to determine the time at which such alterations are first detected (Steffen et al., 2016; Waters et al., 2016).

For the latter, the scientific literature has brought to light four possibilities: Firstly, the so-called "Early Anthropocene", which would refer to the first human alterations and impacts made through agricultural activities, extensive deforestation, and the resulting increase in atmospheric carbon dioxide ($CO_2$) and methane ($CH_4$) (Ahn & Brook, 2007; Broecker, 2006; Broecker et al., 1999; Ruddiman, 2016). Secondly, the exchange of species that has occurred as a result of the European colonization of the Americas since the 15th century. Thirdly, the beginning of the "Industrial Revolution" from the year 1769 in England. And, fourthly, the so-called "Great Acceleration" initiated in the mid-20th century when factors such as the massive growth of the world population, massive industrialization and the intensive use of minerals and energy come together (Cearreta, 2017).

It is true that, since its appearance approximately 300,000 years ago, *Homo sapiens* has been developing a greater capacity for the alteration of the surrounding environment and that, as mentioned in previous sections, has allowed our species to modify the landscape worldwide (Ellis et al., 2013). This is due, among other reasons, to the expansion of our species around the planet. This process was accelerated by industrial development and mechanization. But in order to consider the Anthropocene as a formal division of geological time, it must meet the requirement that other geological epochs meet: to be global and synchronous. It is at this point that most of the previous proposals on the beginning of the Anthropocene are not adequate. Neither the early agricultural alterations, nor the Columbian exchange of species, nor the Industrial Revolution occurred synchronously in time throughout the planet. Nor were they global-scale events. All these events had different developments geographically speaking and not all human societies experienced technological development in the same way (Ziegler, 2019).

All this makes the "Great Acceleration" (Figure I.9) as the only proposal to establish the boundary for the beginning of the geological Anthropocene. The event with the greatest global and synchronous signal of anthropogenic character in geology and, therefore, in the Earth System, are the atmospheric detonations of atomic bombs between the years 1945 and 1963 (Cearreta, 2017). The radioactive signal resulting from those detonations (e.g., plutonium 239, americium 241, cesium 137 and strontium 90) has been present in sediments ever since 1952-53 CE. Therefore, it is more formally said that the beginning of the Anthropocene could be around 1950 (McNeill & Engelke, 2016; Cundy & Croudace, 2017). To all this, we can add the different types of typically human materials that are being recorded and "fossilized" in the strata of recent formation. A clear example is that of plastics, a highly widespread material that is difficult to disintegrate and that geochemically can leave traces in the rocks and may be geologically identifiable in the future (Table I.1).

There are other views on the Anthropocene, such as the archaeological, which, although not compatible with the purely geological concept, can be complementary to it (González-Ruibal, 2018). The reality is that humans have produced alterations in the landscape since the late Pleistocene, and these have even left a record to the point of naming different temporal units based on technological development (Paleolithic, Iron Age, etc.). Although the human impact generated prior to the first nuclear tests was both local and diachronic in nature, these activities may be an example of the evolution of human beings and their impact, reaching its culmination with the detonation of nuclear bombs capable of altering the geochemical composition of sediments on a global scale (Syvitski et al., 2020; Zalasiewicz et al., 2021).

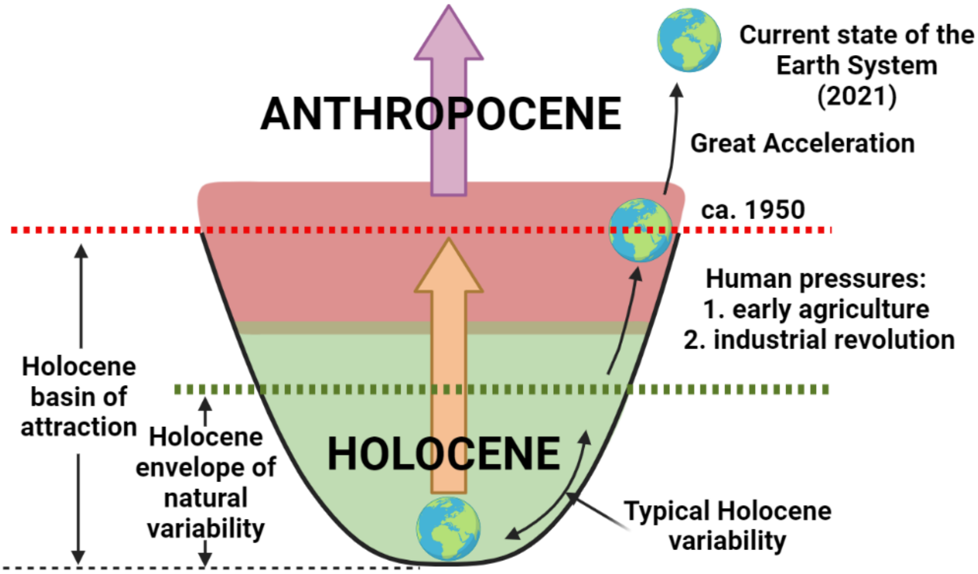


**Figure I.9** - Ball-and-cup diagram showing the natural variability during the Holocene, the first environmental impacts produced by humans and the "Great Acceleration" that would lead to the Anthropocene. Adapted from Steffen et al. (2016).

Humans have caused the Earth and its natural system to be altered. The possible official recognition of the Anthropocene as a geological epoch has implications beyond science. This would mean recognizing humans as a transforming agent of the Earth System, and that the changes produced by humans are comparable in magnitude to other changes that occurred in the geological past. But perhaps the most important thing is that, from the social point of view, the formalization of the Anthropocene would imply the recognition of the consequences that human activities are producing at a planetary scale (Vidas et al., 2015; Cearreta, 2017). Therefore, it could also represent an important global declaration that confronts the current international passivity to remedy or halt this process of anthropogenic change.

The changes that have occurred throughout the Pleistocene, Holocene and Anthropocene in the landscape and the Earth's environment can be approached from different perspectives. This, in many cases, implies the use of different proxies, some of them already mentioned before, as is the case of pollen and paleopalynological studies, the focus of this doctoral dissertation.

## 3. Paleopalynology: history of a discipline

We use here a paleoenvironmental approach with a long tradition in the reconstruction of landscapes: paleopalynology. Paleopalynology is the discipline that studies fossilized pollen and spore remains in sediments. Nowadays, paleopalynology is one of the scientific fields with the greatest applicability for studies of different kinds related to landscape (paleontological, archaeological, paleoenvironmental…). Interest in pollen and spores has always existed, since their biological function as agents of plant reproduction was of major importance for the control of these resources. But, with the invention of the optical microscope, interest in them increased (Burjachs et al., 2003; López-Sáez et al., 2003).

Paleopalynology is a subset of palynology, which differs in the application of palynological techniques to ancient sediments. The first applications of palynology to sediments were aimed at characterizing the dynamics of vegetation over time. This early work emerged in the first decades of the 20th century, led by the Swedish botanist L. von Post. Soon the first differences in applicability to different types of sediments, such as archaeological sediments and non-anthropogenic deposits (peat bogs, rivers and lakes), began to appear (López-Sáez, 2003). Many of these studies also sought to characterize human pressure on the vegetation landscape according to different issues (agricultural activities, deforestation, urban expansion...). The Danish geologist J. Iversen put archaeological palynology in the focus of most archaeological studies, turning it into an auxiliary tool of great relevance (Iversen, 1949). To summarize, the term paleopalynology refers to studies applied to ancient sediments in natural deposits. On the other hand, the term archaeopalynology refers to studies applied to anthropized archaeological sediments.

In the case of the Iberian Peninsula, the first paleopalynological studies were carried out in the 1940s by F. Bellot and E. Vieitez (1945). In the 1970s, the number of researchers in this discipline increased, with the French researchers A. Leroi-Gourhan (1971) and A. Boyer-Klein (1976, 1980) as main representatives. All this ended with the consolidation of paleopalynological studies thanks to the work of Menéndez-Amor & Florschütz P. López García (1977, 1978), M. Dupré (1984), M.C. Peñalba (1989), F. Burjachs (1985, 1990), J.S. Carrión (1992), M.F. Sánchez-Goñi (1991), M.J. Iriarte (1994) and J.A. López-Sáez (1998) among others.

Paleopalynology is a very useful interdisciplinary tool. It has proven to be not only essential for the reconstruction of natural climatic and environmental changes, but it can also provide valuable information on the relationship between humans and the environment (Pérez-Díaz, 2012). It provides information on plant and climatic dynamics, on the anthropization of the environment (causes, consequences and rhythmicity), on the development of economic production activities, on uses of plant materials for various activities (e.g., as biofuels), etc (Zapata Peña, 2001, 2002).

Palynology works with pollen grains and spores that have not fulfilled their reproductive function. The high pollen production of plants combined with the ease of transport of the grains carried by different pollinating agents allows them to be deposited in the sediments in a stratified manner. But, no less important is the resistance to corrosion of the pollen grains, which makes possible their preservation and, therefore, their study. In addition to identifying pollen and spores, palynology studies the so-called non-pollen microfossils, a set of micro-remains that appear in palynological plates, including fungal spores, cyanobacteria, rhizopods and other invertebrates.

Furthermore, paleopalynology allows us to understand the fundamental causes of the current landscape configuration. Owing to the ability of this discipline to discern the origin of the processes of environmental alteration, it also allows us to make hypotheses about the future evolution of plant dynamics and even to establish patterns of environmental and climatic evolution with objectives of environmental restoration and conservation (Girard, 1973; Birks et al., 1988; Dupré, 1988; Galop, 1998; Berglund, 1991; Barbier et al., 2001; López-Sáez et al., 2003).

The relationship between humans and the environment is one of the most interesting questions and can be approached from different scientific branches (archaeology, geology, ecology...). As mentioned above, this possibility of using paleopalynology as an interdisciplinary tool is precisely the greatest value of it. That is why it is one of the most necessary and recurrent scientific methodologies in different fields of the Earth System.

# 4. Justification of the work

Taking into account the information mentioned in the previous sections, the use of palynology is based on two basic principles:

- **(i)** If pollen spectra are a reflection of the current vegetation, a fossil pollen spectrum is evidence of the vegetation that existed in the past.
- **(ii)** The current plant association indicates the existence of certain climatic conditions and, consequently, fossil vegetation allows us to infer past climatic conditions.

## 4.1. The subject

The interest in the study of the vegetal landscape lies mainly in the natural environment changes and, especially, in the landscape-human relationship. In fact, human interactions with the environment are very diverse in nature, as they can range from purely cultural activities to socio-economic interests.

The way in which humans perceive the world is often reflected in the landscape through the alterations made to it (Orejas et al., 2002). The clearing of spaces for the expansion of villages and cities, the construction of infrastructure and new buildings implies the deforestation of forests and the use of wood from them. The same with agricultural activities, where agriculture requires the alteration of some areas to create soils with appropriate conditions for cultivation. We can also mention the selective cultivation of certain species, or large-scale reforestation for economic reasons.

The advantage of paleoenvironmental studies is that they allow us to reconstruct past environmental conditions and that there are a multitude of proxies to do so. Pollen, the main proxy used in this dissertation, provides us with information about changes in the vegetation of the past and how it has evolved over time.

In addition to this, the relationship between humans and vegetation justifies the study of the vegetation landscape. This is of vital importance to understand both synchronic and diachronic anthropogenic dynamics (López-Sáez et al., 2003; Pérez-Díaz, 2012).

## 4.2. The geographic system

Coastal systems have been continuously altered throughout the history of our planet. These changes have been of various types, in which new geomorphological formations, erosion, volcanic formations and, naturally, the oscillations in sea level that move coastal systems back and forth several kilometers or flood previously emerged areas represent the main drivers. All these changes have had an impact on coastal settings, modifying them and causing them to develop new environmental conditions. For example, coastal soils that were once influenced by freshwater can be flooded by sea-level rise, turning them into brackish zones ( Behre, 2002).

Sea-level changes are indicative of global climatic changes. These changes produced naturally are of major importance because in the same way that they have conditioned the fauna and flora to find their spaces in coastal biomes, they have influenced human beings. During the Holocene transgression and the melting of the last glaciers a progressive rise in sea level occurred (Friedman et al., 1992). Some studies indicate that the sea level experienced higher rates during the early Holocene (10,000-7,000 BP), ranging from 6.8 ± 0.5 $mmyr^{-1}$ in central Portugal to 6.3 ± 0.8 $mmyr^{-1}$ in southern France. From 7,000 years BP, the sea level reached a certain stabilization at 5 meters below the present level. Subsequently, the sea level rose again to 2 meters below the present level by 3,700 years BP (Alonso, 2010; Delgado et al., 2012; García-Artola et al., 2018).

Since ancient times, humans have always sought to build settlements near rivers and coastal areas for all the useful resources that these areas can provide (Parfitt et al., 2010). From access to drinking water, to the exploitation of fish and shellfish, to the use of these areas to create easily sustainable agricultural fields. Many early settlements, which later became large population centers, were built on river flood plains and coastal areas. Therefore, it is known that these settlements were often abandoned due to changes in sea level that caused flooding and, therefore, the impossibility of inhabiting these places (DeFrance et al., 2009). The Iberian Peninsula is a clear example of this, where both coastal prehistoric settlements and settlements from Roman, Visigothic, Muslim, etc. times have been found and studied. With the arrival of the Little Ice Age (1650-1850) and the late start of the Industrial Revolution in Spain, an enormous port development and the emergence of new forms of occupation of the coastal areas took place (Morales & Pérez-Alberti, 2019). In fact, the Cantabrian Coast would eventually become the most highly industrialized coastal area of Spain.

The human impact on these coastal areas is a reflection of the evolution of our species and its capacity to modify the surrounding environment. The impact has been such that it has even affected the biodiversity of these coastal and estuarine environments (Cundy et al., 2003; Irabien et al., 2020; Sanz-Prada et al., 2020). In addition, these places act as natural deposits where pollen can accumulate and become buried and fossilized, so the study of the Cantabrian Coast is of great interest if we aim to address issues related to human impact on coastal environments.

## 4.3. The time scale

The Quaternary is of special interest because of the large number of environmental changes that have occurred during it and the quality of its sedimentary record. Whether natural or anthropogenic, environmental and climatic variations are one of the hot topics in scientific literature on the Earth System (Walker et al., 2009). As mentioned above, the Quaternary is formally made up of the Pleistocene and Holocene epochs (Table I .1).

Since the early Pleistocene, more precisely 1.75 Ma ago, humans have been expanding their distribution across the planet from Africa (Ellis et al., 2013; Parfitt et al., 2010). In fact, archaeological sites have been found where early humans began to occupy specific areas, even detecting cyclicity of occupation and subsistence modes (Holdaway & Porch, 1995; Cosgrove, 1990).

Humans generally tended to adapt to environmental and climatic conditions when occupying locations during certain seasons (González-Sampériz et al., 2009). The first major changes in human cultural and technological development occurred during the Holocene (Mannion, 1995). Humans began to carry out activities and settle areas temporarily and permanently, causing alterations in the landscape and environment (Hoelzmann et al., 2001; Méndez & Reyes, 2008).

From the natural point of view, both the Pleistocene and the Holocene are geological epochs that have been shown to display significant climatic and environmental variations (Dansgaard, 1985; Sánchez-Goñi & D'Errico, 2005; Walker et al., 2008; 2009). It is the combination of anthropogenic and natural drivers of change at local, regional and global scales that make them especially interesting and therefore appropriate for framing studies on human impact and climate variability.

**Table I.1 -** Summarized geologic time scale for the last 2.6 Ma. The Anthropocene is included as a new geologic epoch and the onset date based on the geological normative.

| PERIOD | EPOCH | BEGINNING |
|---|---|---|
| Quaternary | Anthropocene | 1950 CE |
| | Holocene | 11,700 BP |
| | Pleistocene | 2.6 Ma |

# Group background

The "HAREA-Geología Litoral" research group (Basque Government, IT1616-22) and the project "ANTROPICOSTA-2: Anthropocene sedimentary record in the coastal and marine areas of northern Atlantic Iberia" (RTI2018-095678-B-C21) (MCIU/AEI/FEDER, EU) have developed an active research agenda. Certain topics of this PhD dissertation arise precisely out of previous studies carried out in the eastern Cantabrian area.

In fact, the Harea-Coastal Geology group has focused on basic and applied research with a multidisciplinary geological approach to the natural and anthropogenic processes that have transformed the Cantabrian coastal environment. From this multidisciplinary approach comes the interest in opening new frontiers such as, in this case, the use for the first time of pollen as the main proxy.

In recent years and closely related to this doctoral dissertation, the estuaries of the Oka, Saja-Besaya and Urola have been studied by other authors. It is true that the perspectives or approaches of those studies have been different, since the use of proxies has not been the same.

Starting in chronological order, in 2013 A. García-Artola studied the salt marshes located in the Oka estuary (Urdaibai) (García-Artola, 2013). Through a series of analyses of short cores and surface samples, she was able to define the criteria to differentiate areas of natural evolution or anthropically influenced. All of this, using multidisciplinary proxies such as benthic foraminifera, analysis of organic matter, sand and heavy metals, as well as radiocarbon dating and short-lived isotopes. However, other Urdaibai cores (Axpe Sur, Busturia, Isla, Isuskiza, Escalante and Carasa) studied by the same author did show an evolution influenced by humans. Regeneration processes after agricultural occupation of the marshes, introduction of large volumes of sediment due to deforestation and anthropogenic introduction of allochthonous sedimentary deposits were observed. All this work concluded, in general terms, that the salt marshes of the Eastern Cantabrian Coast seem to be adapting to the current marine rise, and regenerating recently due to a high regional contribution of detrital deposits. This is also of great interest from the point of view of environmental management, as it allows an optimistic outlook for the regeneration of other salt marshes that are currently occupied. This type of environmental regeneration, known as "coastal managed realignment", allows regeneration to be more economical than the application of other techniques, being only efficiently applicable in those coastal areas where the sediment supply is high.

Furthermore, H. Serrano-García has developed recent work in the Saja-Besaya estuary (Serrano-García, 2020). Two supratidal boreholes and three intertidal short cores were studied as well as twenty-two surface samples. This study concluded that the geochemical quality detected is very low and, in fact, this is confirmed by the scarce appearance of benthic foraminiferal assemblages, which indicate that, despite the reduction of human pressure on this estuary, there is no real improvement yet in its sediment quality.

Finally, recent work has also been carried out in the Urola estuary (Cearreta et al., 2021). This estuary has proved to be one of the least polluted in the Basque Coast Geopark area. In fact, the impact of heavy metals as a factor of anthropization of the estuarine environment is quite low, as can be seen in the abundant assemblages of foraminifera detected, despite the fact that they have been affected by the intense dredging operations historically carried out in the lower part of the estuary.

# Aims

## General aim:

The main objective of this doctoral dissertation is to characterize the natural environmental conditions on the Cantabrian Coast and evaluate environmental impacts of anthropogenic origin on coastal ecosystems from the Pleistocene to the Holocene and the Anthropocene.

## Specific Aims

1. To analyze the pollen content of boreholes and cores extracted from estuaries on the eastern Cantabrian coast, in order to understand the past and present plant assemblages.

2. To study the evolution of estuaries as coastal systems that have been affected by human occupation of their domains, chemical deterioration generated by polluting discharges and biological replacement by plantations or invasions of allochthonous plant taxa.

3. To identify the different processes and evolutionary stages (both natural and anthropogenic) experienced by estuaries as a consequence of historical episodes of environmental impact.

4. To calibrate, as precisely as possible, the processes and stages recorded in the pollen analysis in order to generate a clear and defined spatio-temporal context.

5. To contribute with this research and results in the Cantabrian coastal zone to the achievement of the objectives established in the mandate of the Anthropocene Working Group (AWG).

# Study area

# 1. The Cantabrian Coast

The Cantabrian Coast extends from the estuary of the river Eo (Galicia-Asturias border) in the west to the Basque frontier with France in the east. The Cantabrian Mountain Range runs close and parallel to the coast. Although they are not of high altitude (average 40 m), numerous sea cliffs characterize the Cantabrian Coast. These cliffs are not homogeneous but are conditioned by their constituent geological materials due to important geographical variations (Morales & Pérez-Alberti, 2019).

In addition, these cliffs are interrupted by a large number of estuaries. From west to east the most important are: Eo, Navia, Nalón, Villaviciosa, Deva, Nansa, Escudo-Gandarilla, Saja-Besaya, Asón, Barbadun, Nervión, Butroe, Oka, Deba, Urola, Oria, Oiartzun and Bidasoa. These rivers are characterized by being short, shallow and with an important Holocene sedimentary filling, which has led these estuaries to create sand barriers at their mouths (Rivas, 2000) (Figure I.10).

Beaches, on the other hand, are generally developed in front of these sand barriers and below the surrounding cliffs. The latter remain more natural and less managed than the former. This is due to the low accessibility due to their steep relief. In general, the most popular beaches on the Cantabrian Coast are those located near the estuaries, not only because of their accessibility, but also because of their longer extension, particularly those located on the bays, such as Berria, Santander, Zarautz and San Sebastian (Morales & Pérez-Alberti, 2019).

As already mentioned, human activities have been very present on this coast due to its rich geological ores that allowed early development of economic activities, especially industrial types. This has caused a very intense transformation of this coast, especially the estuarine areas, since the 19th century. With the construction of ports and breakwaters for the control of maritime-river navigation, many of these estuaries are nowadays profoundly modified. A clear example is the Nervión estuary. Areas of marshland and sand dunes were eliminated in order to facilitate the construction of various infrastructures, many of which were intended for the touristic development of the coast. All this had a strong impact on the coastal ecosystems of this region, and its biodiversity was consequently highly affected (Remondo et al., 2005).

In this doctoral dissertation, all the sedimentary deposits studied are of natural character (not archaeological), and the majority of them belong to the estuaries located in the eastern Cantabrian area, such as the Saja-Besaya estuary (Suances, Cantabria), the Oka estuary (Mundaka, Biscay) and, finally, the Urola estuary (Zumaia, Gipuzkoa). The geographical and geological characteristics of this area will be introduced in this section and in Figure S.1, but the specific localization of the boreholes/cores analyzed will be described in detail in the Material and Methods section. Other deposits studied on this eastern Cantabrian coastal area are Liendo (Cantabria) and the Basque Mud Patch (inner continental shelf), of lacustrine and marine origin respectively.

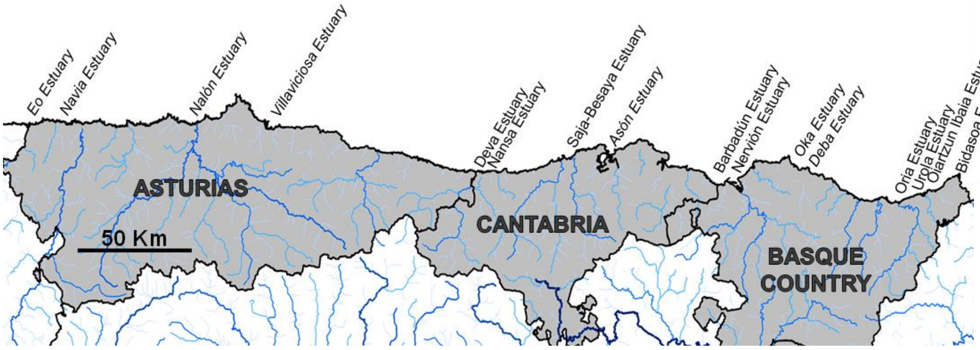


**Figure S.1** - Main estuaries on the Cantabrian Coast (N. Iberian Peninsula).

## 2. Geomorphology

The eastern Cantabrian coast is located in the geological domain of the Basque-Cantabrian Basin. At the same time, the Cantabrian Mountain Range represents a western extension of the Pyrenees. It was uplifted during the Eocene-Miocene as a result of tectonic activity between the European and Iberian plates. The predominant factors responsible for the current geomorphological processes on the Cantabrian Coast are eustatic changes of sea level, lithology and geological structure, wave orientation and, in addition, human impact (Bruschi & Remondo, 2019).

It is formed by abrupt cliffs developed on hard rocks. The cliffs usually alternate between flat-topped and slightly sloping cliffs. The erosive character of these geomorphological features is due, among other factors, to their strong karstification. The predominant rocks in the eastern region of the Cantabrian coast are limestones (Morales & Pérez-Alberti, 2019; Rivas, 2000).

The continental shelf of the Bay of Biscay is well structured, with its seabed characterized by various geomorphological elements, such as erosive rocky outcrops, coastal terraces, fluvial paleochannels, etc. (Galparsoro et al., 2010). Marine terraces (rasas) form some of the emerged cliffs. Some of these terraces have originated since the Eocene, and we find them today well above sea level. The origin of some of these terraces is doubtful, as not all of them show clear evidence of having been formed by waves, such as beach deposits (Gutiérrez et al., 2014; Bruschi & Remondo, 2019). Some of them are lithologically controlled where ancient marine levels, known as wave-cut platforms, were developed by erosion as a result of the Miocene uplift of the Cantabrian Cordillera. In general, these marine terraces are higher on the eastern Cantabrian coast due to more intense continental uplift (Fillon et al., 2016).

All this is related to tectonic uplift movements and eustatic changes in sea level, which have been considerable during the last 50 Ma. This not only affected the erosive processes and the formation of terraces mentioned above, but also caused the effect of hydro-isostasy and glacio-isostasy produced by deglaciation (Kominz et al., 1998; Leorri et al., 2012).

The Cantabrian Coast is affected also by numerous fluvial and alluvial, karstic and slope processes. All these have caused alterations in the relief. Some of these, such as mass movements, are caused both by the tides and waves modifying the coast by the retreat of the cliffs and by heavy rains in the estuarine valleys. These slope processes are a constant geomorphological hazard, and are very characteristic of this coast, where numerous landslides and erosive processes are found (Corominas et al., 2018).

The flysch type outcrops that are particularly present in the Basque coastal sector are also remarkable due to the low resistance of their lithology and the arrangement of their stratigraphic layers. In fact, in the case of areas of soft rocks, like Zumaia, displacements and landslides are much more common (Bruschi & Remondo, 2019).

Karst-type processes are also important on the Cantabrian coast. The karstic landscape in the coastal area of the Bay of Biscay is related to the Atlantic climate and limestone lithology, with the consequence that numerous cave systems have formed (Aranburu et al., 2015; Bruschi & Remondo, 2019). Additionally, the alteration of the relief by wind action is present on beaches such as those of Barrika, La Arena or Zarautz, where aeolian sand deposits can be found (Cearreta et al., 1990) (Figure S.2).

During the last centuries, anthropogenic activity has become an agent of important transformation of the coastal relief in the Cantabrian region. From the construction of new elements, such as port breakwaters, to the elimination of coastal ecosystems to support other economic activities (urbanization, industry, agriculture), which have caused an increase in both erosion and sedimentation, and modified other geomorphological processes (changes in the water-sediment balances, linear or marginal erosion in estuarine channels...). Moreover, global climate change is already having an impact on the landforms, with recurrent damage caused by storm surges (Remondo et al., 2005).

Despite all these human changes on the Cantabrian coastal relief, its natural features make this region one of the most interesting from a geological point of view. Hence, many places have been declared of regional, national or international interest, and form part of the National Inventory of Geosites or International Biosphere Reserves, as is the case of Urdaibai, or Geoparks like the Deba-Zumaia area (Bruschi & Remondo, 2019).

**Figure S.2** - Barrika (Biscay), an example of Cantabrian coastal geomorphology (northern Iberian Peninsula).

## 3. Hydrological network: The estuaries and the Basque Mud Patch

One of the main characteristics of the Cantabrian coast is, as mentioned above, the presence of estuaries that interrupt the cliffy coastline. Estuaries are mixed systems of marine and fluvial influence. As a consequence of global Holocene transgression, modern estuaries began to develop during this epoch (Flor & Flor-Blanco, 2014; Domínguez-Cuesta et al., 2015).

The rivers related to these estuaries are varied in length and size, although they are predominantly short with small fluvial catchments. In the case of the Basque rivers, these are fundamentally catalogued as high or mountainous rivers (Monge-Ganuzas et al., 2019).

It should be emphasized that the Cantabrian estuaries represent incised valleys drowned by the rising sea during the Holocene. Furthermore, most of these estuaries have developed sandy barriers at their mouths, forming beach-dune systems, with salt marshes of great ecological value in their middle and upper areas (Morales & Pérez-Alberti, 2019).

In the easternmost part of the Cantabrian coast, the swell is particularly strong and this affects the dynamics of the estuary mouths during both high and low tides, producing the transport of sand from the adjacent beaches to the lower part of the estuary. These beaches are usually small (Monge-Ganuzas et al., 2019).

The Cantabrian tides are semi-diurnal. On the Basque coast, the average tidal amplitude varies between 1.5 m and 4 m. This makes it a meso-tidal area. Waves come mainly from the NW while the main wind components are NW, SW and NE. In addition, the Cantabrian coast is exposed to large storms, produced by low-pressure systems in the North Atlantic. During sea storms, strong NW swell dominates, with some waves exceptionally reaching heights of more than 14 m (Morales & Pérez-Alberti, 2019).

Sea-level changes must also be considered, since a relative rapid rise in sea level is observed from ca. 10,000 to 7000 years cal BP, and a relatively slow rise in sea level is detected from then to the present day. These rises would be controlled mainly by eustatic factors (Leorri et al., 2012; García-Artola et al., 2018; Monge-Ganuzas et al., 2019).

In order to understand the recent evolution of the Cantabrian coast, it is essential to study also the anthropization processes it has undergone.

## 3.1. Estuaries

The most important sedimentary environment in this doctoral thesis is represented by the estuaries. As mentioned above, estuaries are mixed systems with both fluvial and marine influences. Additionally, throughout human history, estuaries have been places of settlement and development for human populations from prehistoric times to the present day.

For this reason, it is convenient to take into account both the natural and historical characteristics of these places in order to have a better background on which to base new scientific studies.

Three estuaries are studied in this dissertation: the Saja-Besaya (Cantabria), the Oka (Biscay) and the Urola (Gipuzkoa).

### 3.1.1. Saja-Besaya

#### 3.1.1.1. Geographical and geological context

The Saja-Besaya estuary is a meso-tidal environment located along the municipalities of Miengo, Polanco and Suances in the Province of Cantabria. It has an average width of 150 m and its length is 5.5 km. Its total area is 389 ha (Figure S.3).

One of the most representative characteristics of this estuary is that 75% of it is made up of intertidal flats, with freshwater supplied by the Saja and Besaya Rivers with an average annual freshwater flow of 24.2 $m^3/s$ ("http://dmacantabria.cantabria.es/")

**Figure S.3** - Oblique aerial view of the lowermost Saja-Besaya estuary (Cantabria). Source: https://www.cantabriarural.com

The estuary is located in the northwestern sector of the Basque-Cantabrian Basin within the Santillana del Mar anticline whose orientation is NNE-SSW and which was generated during the Alpine orogeny (Serrano-García, 2020). The geological record is formed by Mesozoic and Cenozoic materials. It is important to point out the materials belonging to the Upper Cretaceous, as they are made up of a succession of detritic and carbonaceous rocks whose erosion is responsible for the configuration of the eastern Cantabrian coastline (Bustillo & Fort, 1990).

Additionally, the Pb and Zn sulfide mineral deposits exploited at the mining complex of Reocín are located within the Lower Cretaceous sequence. These deposits are catalogued as one of the largest Pb-Zn ore deposits in Europe (Bustillo & Ordóñez, 1985) and are linked to an extensively developed karst system. The paragenetic sequence of mineralization consists of sphalerite, wurtzite, galena, marcasite, pyrite with dolomite and calcite (Velasco, 2003; Serrano-García, 2020).

#### 3.1.1.2. Historical context

The history of the Saja-Besaya estuary is closely linked to the exploitation of the Reocín deposits. As far back as Roman times, there are records that the area at the mouth of the estuary was an enclave mentioned as *Portus Blendium* (Serrano-García, 2020).

The rediscovery of the deposits in 1856 really marks the beginning of their intensive exploitation. The following year, the Real Compañía de Minería Asturiana, took control of the exploitation and started the work, first in the open air and then, in the 20th century, the extraction of minerals began to be carried out through galleries (Castro et al., 2001). After the economic crisis derived from the 1973 Oil Crisis, the exploitation rights of the mine were transferred to “Compañía Asturiana de Zinc S.A.” (AZSA), which continued the works until 2003, when the exploitation was interrupted due to the exhaustion of the resources. With the closure of the mine, the galleries were flooded and cut open, forming a lake of 36 $hm^3$ (Serrano-García, 2020) (Figure S.4).

The exploitation of the mine during 150 years recorded the extraction of 62 Mt of ore consisting of 8.7% Zn and 1% Pb. Intense mining activity also promoted the modification of the estuary with the objective of facilitating ore transport, which resulted in the drastic reduction of the hydrodynamic energy level in the estuarine intertidal flats. This provoked enhanced muddy sedimentation and, therefore, the deposition of large quantities of highly contaminated fine sediments (Velasco, 2003; Symons et al., 2009).

The activity of other industries in the area also affected the estuary. In the surroundings of Torrelavega, the main urban center near the upper estuary, the industrial complex of the Solvay Company was established and dedicated to the production of sodium carbonate, sodium bicarbonate and salt. Other industrial activities were the “AZSA” plant at Hinojedo, specialized in the processing of Zn concentrates, and the “Sniace group”, producer of cellulose, fibrane and lignosulphonates (Serrano-García, 2020).

**Figure S.4** - A) Reconditioning works at the Reocín Mine (1994-2001) modified from the Mineralogía Topografía Ibérica (MTI) archive. B) Inundated Reocín Mine, 2017. Photograph modified from El Diario Montañes (2017).

The intense industrial activity in the area has been responsible for the discharge of huge amounts of pollutants into the estuarine waters and sediments, creating currently one of the most polluted coastal ecosystems in northern Spain (Irabien et al., 2008; Serrano-García, 2020).

## 3.1.2. Oka

### 3.1.2.1. Geographical and geological context

The Oka estuary has a total length of 12 km and constitutes one of the main hydrographic basins in the Province of Biscay. The Oka River begins at an altitude of 450 m and is characterized by steep slopes in its initial stretch, which gives it an intense erosive capacity. In the middle stretch, the slopes are moderate and flood plains are developed. The estuary stands out for its rapid runoff response to precipitation, where the increase in flow is rapid, especially in the most saturated soils. The salt marshes in this estuary cover an area of 300 ha (García-Artola, 2013) (Figure S.5).

Its N-S orientation and position make it exposed to intense waves that persist even in situations of local calm. Tides are semi-diurnal, but due to the morphology of the estuarine bed, the tidal cycle is asymmetrical, with less flow phase than reflux phase (Ruiz et al., 1994). During the Quaternary, sea-level rises have been responsible for the formation of diverse coastal morphologies along the Cantabrian coast, but in the case of the Oka fluvial valley, it is possible to observe a series of relict structures such as elevated abrasion platforms (rasas) that are indicative of tecto-eustatic restructuring throughout the Cenozoic era (Pascual & Rodriguez-Lazaro, 2006).

**Figure S.5** - Oblique aerial view of the Oka estuary, also known as Urdaibai Estuary. Modified from Deia newspaper (2013), photograph by Zigor Alkorta.

Holocene sedimentary infilling of the lower Oka estuary began more than 8,500 years ago. At that time, the sea was 42.8 m below present sea level, and the river valley was developing but eventually it was flooded by the rising sea level. This generated the estuary in a transgressive sequence that produced progressively more marine environments. The alternation of marine and brackish materials deposited along the estuary allowed the development of salt marsh environments from 4580 cal yr BP onwards (Cearreta & Monge-Ganuzas, 2013).

Today, the Oka estuary is also known as the Urdaibai estuary and was designated a Biosphere Reserve in 1986 by UNESCO for its great natural values (Monge-Ganuzas et al., 2008).

### 3.1.2.2. Historical context

Human presence in the Oka estuary has been documented from prehistoric times. Initially, mollusk harvesting for both aesthetic and nutritional reasons did not have an impact on the natural evolution of the estuary. This changed with the closure of the reed beds in the 17th century, preventing tidal influence, which accelerated the drying up of the salt marsh areas (Zapata-Peña, 2005).

The objective of the salt marsh draining was the creation of farmlands, and represented a common practice between the 18th and the mid-19th centuries, in response to the food needs of a constantly growing population (Figure S.6). It was also common to extract sand from the lower estuary for the different agricultural reclamations. With the arrival of the Industrial Revolution in the 20th century, the rural exodus began, the farmlands were gradually abandoned and the walls that prevented the tidal influx into the agricultural fields were demolished as they were not properly maintained. As a result, these areas gradually regenerated as marshland once again. Later, in the 1980s, there were a series of reinforcements of the agricultural walls, some of them without legal authorization, which delayed the natural regeneration of the salt marsh environment in some areas, such as Anbeko in the middle estuary (Zapata-Peña, 2005; Monge-Ganuzas et al., 2013, 2015).

**Figure S.6** - Vertical aerial view of the lower Oka estuary (American flight, 1945-1946). A large number of agricultural fields can be observed bordering the estuary. Source: GeoEuskadi (https://www.geo.euskadi.eus/)

More recently, navigation along the estuary has been one of the reasons to justify anthropogenic works. The Oka estuary was navigable as far up as Gernika-Lumo for small vessels, as made clear by the denomination of "port" for the town of Gernika in different documents since 1366 (Cearreta et al., 2006).

All this, together with intense dredging and deposition of sediments in the lower estuary and railway occupation, has caused the total reduction of the estuarine surface by 58%. This is why the rapid environmental regeneration observed in the salt marshes of the Oka estuary has been a reference of great interest to establish adaptation measures both for the maintenance and management of this natural space under a climate-change scenario and for its extrapolation to other regional estuaries (García-Artola et al., 2011, 2015).

### 3.1.3. Urola

#### 3.1.3.1. Geographical and geological context

The Urola estuary is 5.7 km long and up to 10 m deep. Therefore, it is a short and shallow estuary, whose total surface area is 0.81 km$^2$. The Urola River is 60 km long and supplies fresh and torrential water (flow rate of 8 m$^3$/s) to the estuary. As is the case along the whole Cantabrian coast, this is a cliff area highly exposed to waves and mesotidal and semi-diurnal tides (<1 m at neap tides and 4.5 m during spring tides). Together with the Deba estuary, the Urola estuary is the only brackish environment within the Basque Coast Geopark (Cearreta et al., 2021).

This geopark was listed by UNESCO in 2010, extends over 90 km$^2$ and has a 13 km long coastal front formed by an almost continuous outcrop of marine turbiditic rocks from the Lower Cretaceous to the Lower Eocene (Figure S.7).

The most important urban center is Zumaia. It is a tourist town founded in 1347. Since then, anthropogenic activities began to alter the lower part of the estuary (Cearreta et al., 2021).

#### 3.1.3.2. Historical context

Initially, the inhabitants of the town of Zumaia dedicated themselves to agricultural work, but technological development soon led to the emergence of the first professional and industrial activities. In fact, since the end of the 14th century, ships were already being built, as a high percentage of the population was dedicated to fishing work. With the reclamation of the salt marshes at the end of the 17th century, agricultural production could be increased and the town of Zumaia grew economically and in terms of population (Cearreta et al., 2021).

Between the 16th and 18th centuries, Zumaia stood out for its activity related to the ironworks and iron trade, which favored the early construction of port facilities, attracting active maritime traffic to Zumaia (Benito-Domínguez, 2012).

In the 19th century the cement factories became the economic engine of the town, and these in turn boosted the commercial activity of the port. Terrestrial transport also improved at this time, the road linking Zumaia to San Sebastian was built and in 1900 the train connecting Deba with Zarautz arrived (Odriozola, 1996).

**Figure S.7** - Oblique aerial view of the mouth of the Urola estuary and the village of Zumaia. Source: Adobe Stock (https://stock.adobe.com/).

The deposition of sand at the mouth of the estuary forced intense dredging, which began in 1914 and had to be reinforced with the construction of a seawall and a channeling breakwater in 1928, 1948 and 1995. This favored the accretion of the Santiago beach-dune system. All this, together with the presence of a shipyard and harbor, plus the smelting and galvanizing industries, represent the greatest human impact on the recent estuary (Belzunce et al., 2004; Cearreta et al., 2021). Moderate levels of trace metals and organic contaminants from both domestic and industrial discharges have been detected, but thanks to the presence of a wastewater treatment plant, the discharges into the intertidal system have recently been reduced (Tueros et al., 2009; Legorburu et al., 2013).

## 3.2. Basque Mud Patch

### 3.2.1. Geographical and geological context

The Basque Mud Patch (BMP), located on the continental shelf of the Bay of Biscay in front of San Sebastian city, is narrow and elongated, between 7 and 20 km N-S, and approximately 150 km W-E. To the east, it is bounded by the Aquitanian shelf and coast and to the south and west by the so-called North-Iberian margin and the Cantabrian coast. To the north, it opens to the Atlantic Ocean and the presence of tributary canyons of the Capbreton Canyon and the interfluves produced by these canyons makes it possible to reach depths of between 300 m and 800 m (Jouanneau et al., 2008).

The Basque continental shelf is characterized as a passive margin sedimentary basin and receives about 1.57 x $10^6$ t/yr$^{-1}$ of sediment from twelve different river systems (Pascual et al., 2004; Uriarte et al., 2004; Irabien et al., 2020). Considering the grain size of the sedimentary deposits on the Basque continental shelf, it can be divided into two distinct regions. The western region, whose sediments are made up of coarse sands concentrated along ancient Quaternary coastlines. In the eastern region, also called "Vasière de Loï Gunea", the major accumulation of sediments is fine-grained and is found in two areas, one in front of San Sebastian and the other in front of Bayonne (Jouanneau et al., 2008; Galparsoro et al., 2010).

Regarding the oceanography, the Bay of Biscay has some particular characteristics conditioned by its location, which causes it to be affected by the subpolar and subtropical gyres coming from the North Atlantic current. The influence of the subtropical gyre on the Basque continental shelf, although present in the Bay of Biscay, is generally very weak (Koutsikopoulos & Le Cann, 1996; Fontán et al., 2008). The hydrography of the area has a marked seasonality, highly conditioned by the presence of a branch of the North Atlantic Current. The current enters the Bay of Biscay in a clockwise circulation (Cabal et al., 2008). The influence of currents such as the North Atlantic current is compounded by the climatic characteristics of the Basque shelf, where the wind blows from the southwest in autumn-winter, causing currents to the north and east. The main current is from west to east except in summer when it is inverted (Fraga et al., 1982). In spring-summer, the change in the circulation of water masses and the prevalence of north-westerly winds induce currents to the south, following the French coast, and to the southwest near the Basque shelf (Ferrer et al., 2009). Moreover, cold water masses are driven through the San Sebastian Canyon, one of the tributary canyons of the main Capbreton Canyon, by upwelling events that create cold water streams (Fernández Martín-Consuegra, 2018).

### 3.2.2. Historical context

Human impact has also been recorded throughout history in the Basque Mud Patch. Since the end of the 19th century, the anthropogenic activities developed on the Basque coast, mainly as a result of the great industrialization of the region, resulted in the dumping of factory wastes in the estuaries that channelled them into the waters of the Bay of Biscay (Irabien et al., 2020) (Figure S.8).

Another important regional event was the “MV Prestige” oil tanker disaster, which introduced some 63,000 metric tons of heavy fuel oil into the Bay of Biscay between November 2002 and February 2003 (Laffon et al., 2006; Pascual et al., 2008) (Figure S.9).

**Figure S.8** - Photograph taken in 1931 of one of the Altos Hornos de Vizcaya ships and, in the background, part of the industrial complex in the Nervión estuary. Photographer: L. Roisin.

**Figure S.9** - Photograph of the MV Prestige ship during its sinking in front of the Galician coast (2002). Source: La Voz de Galicia (2020).

# 4. Liendo

## 4.1. Geographical and geological context

The Liendo valley (Cantabria), 2 km from the sea, is a particularly interesting landscape because of its characteristic karstic modeling. This modeling has resulted from the intrusion of a diapir and the development of a circular valley depression and the formation of numerous caves and galleries in the surrounding calcareous rocks. Most of the geological elements that remain visible today primarily originated during much warmer times during the melting of the regional glaciers and the following post-glacial phases (Salvarrey et al., 2005) (Figure S.10).

**Figure S.10** - Panoramic view of the Liendo Valley (Cantabria). Photographer: Miguel de Avendaño.

The karst system of the Liendo valley is formed mainly in carbonate rocks and marls, sedimentary rocks consisting of calcite and organic matter, as well as sandy and clayey material. These rocks are originated by "biochemical precipitation" accumulating calcium carbonate from shells and skeletons of various marine organisms that, once dead, end up accumulating to form carbonate muds and reef formations (Salvarrey et al., 2005).

From the hydrological point of view, Liendo lacks rivers of great flow. The two main watercourses, better known as resurgences because they originate in caverns, are those from the Covacho Cave and the Yesta Cave. However, the longest stream is the Rosveras, which crosses the entire valley from south to north (Salvarrey et al., 2005).

### 4.2. Historical context

The Liendo area is dedicated mainly to agriculture and livestock farming. This was the basis of the local economy although, after the Carlist Wars in 1887, the Liendo Valley stood out for its iron ore reserves and the exploitation of the Mount Candina quarry. The ore was brought down to Sonabia by means of buckets and cables, as the terrain was rocky and difficult to exploit. From Sonabia, the ore was transported by ships to different parts of Spain, mainly to Gijón (Asturias). With the outbreak of World War I, these mines stopped definitively (Barba, 2004; Salvarrey et al., 2005).

Construction increased during the 20th and 21st centuries and transformed the local economy to services and tourism. Most of the resident population work outside the valley or in the service sector (BOC, 2013).

## 5. The coastal climate

The climate in the eastern Cantabrian region is mesothermal and oceanic, with moderate temperatures and abundant rainfall (Uriarte et al., 1996) Winters are mild, with a temperature between 7º and 18º and 390 mm of rainfall accumulated. Summers are temperate (18º - 25º) and wet (110 mm). In autumn the temperatures range between 15º and 24º with an average rainfall of 275 mm. In spring, temperatures vary from 13º to 24º, with accumulated rainfall averaging around 225 mm. It is not surprising that annual rainfall reaches more than 1500 mm (Uriarte et al., 1996; Monge-Ganuzas et al., 2019). Furthermore, temperatures are milder owing to the contact of air masses with the masses of water on the coast, so no great oscillations in temperatures during the day-night cycles occur. The coastal strip is somewhat cooler and rainier to the east in Gipuzkoa than to the west in Cantabria and Biscay.

The region also has high cloud cover which, combined with the rugged terrain and the strong oceanic influence, favors the presence of humidity. The average relative humidity during the year is 78%, and the winds blow predominantly from the northwest and south, with 27.5% of calms (Monge-Ganuzas et al., 2019).

One of the great regional climate influences is the Bay of Biscay. From this oceanic portion come most of the weather situations of both stable and unstable character. An example of this is the importance of the Gulf Stream, which bathes the Cantabrian coast with warm water, tempering the low winter temperatures. This causes sea water to reach 20º in August (Loidi et al., 2011).

## 6. The eastern Cantabrian coastal vegetation

The vegetation of the Cantabrian coast responds to the presence of a temperate oceanic bioclimate. The strong marine influence avoids extreme temperatures and provides abundant annual rainfall. The high proportion of limestone soils and poor substrates also influences the distribution of vegetation in this region. These geological characteristics are also variable and, consequently, two different coastal districts should be considered: the Santanderino-Vizcaino (from the middle of Cantabria to the Deba river basin) in the west and the Vascónico Oriental (from the upper basins of the Deba River to the banks of the Adour River in the French Basque Country) in the east (Fig. S.11) (Loidi et al., 2011).

In the Santanderino-Vizcaino district (including the coastal strips of Zarautz and Zumaia), the predominant arboreal vegetation on acid soils consists of oak groves (*Quercus robur*) followed by stages of forest degradation colonized by birch (*Betula*). Due to pure economic reasons, a large part of the total land corresponds to pine (*Pinus radiata*) and eucalyptus (*Eucalyptus* sp.) plantations. In the more eutrophic soils, there are some ash trees (*Fraxinus* sp.), that are disappearing due to the agricultural value of these soils, the most fertile in the region. In the siliceous and higher altitude substrates of the coastal region, towards the interior of the peninsula, beech (*Fagus sylvatica*) forests dominate. As for the watercourses, these are surrounded mainly by edaphohygrophilous taxa such as alder (*Alnus* sp.), which forms alder groves and gallery forests. Associated with the massive limestone formations, holm oak groves (*Quercus ilex*) develop, creating cliff ecosystems. These, due to their scarcity and uniqueness, justify their inclusion in the Natura 2000 Network, as Habitats of High Priority for Conservation (European Commission 1992) (Aseginolaza et al., 1988; Meaza, 1991, 1997; Loidi et al., 2011).

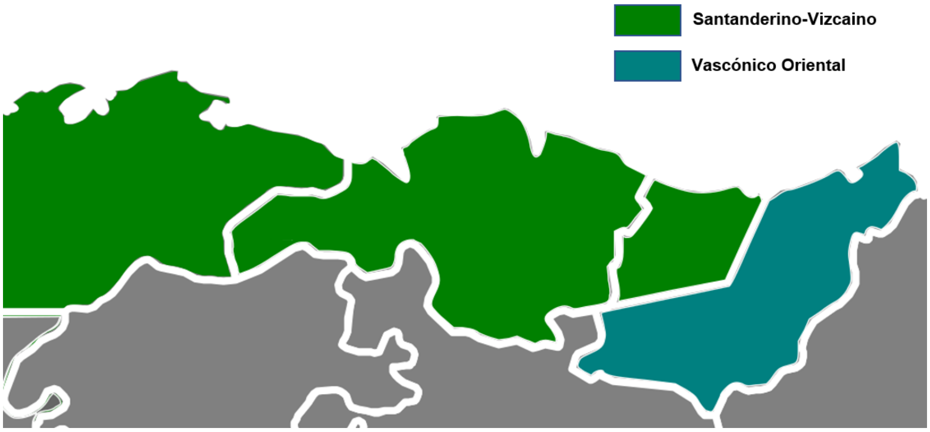


**Figure S.11** - Classification of the vegetation of the Eastern Cantabrian region according to Loidi et al. (2011).

As for shrub vegetation, the flora of the Cantabrian cliffs includes halophyte species exclusive to coastal ecosystems, with very unique adaptations to the marine environment, especially heather (*Erica* type), which covers the margins of the cliffs (Meaza, 1991, 1997; Loidi et al., 2011).

In the east, the Vascónico Oriental district is characterized by a very humid climate and by the predominance of siliceous soils due to the outcrops of Paleozoic materials and red sandstones. The less basic character of the soils in this sector results in some differences in terms of vegetation. The main difference from the previous western district is that, in terms of arboreal vegetation, the more basic substrates are occupied by oak groves (*Quercus robur*) while the more acidic slopes are occupied by *Quercus pyrenaica*. In general, the greater presence of acid substrates means that the main difference between this district and the previous one is the predominance of oak groves, with holm oak groves being much scarcer (Meaza, 1997; Loidi et al., 2011).

Uniformly, in both districts, hydro-hygrophilous vegetation abounds in the areas close to watercourses. As for herbaceous vegetation, it is important to note that, in shallow soils (estuaries and marshy soils), the predominant saline herbs are *Plantago coronopus*, *Chenopodiaceae* or *Cichorioideae* (Loidi et al., 2011; Asensi & Diez-Garretas, 2017).

**Figure S.12** - Some of the trees present in the Santanderino-Vizcaino and Vascónico Oriental areas: A) Alder, B) Eucalyptus, C) Oak and D) Beech.

# Materials and methods

This PhD dissertation presents the paleopalynological study of 10 sedimentary records. Seven of them correspond to estuarine deposits, two are from marine cores collected in the Basque Mud Patch, and one was retrieved from a former karst lake environment (Figure M.1). These records are located along the Cantabrian Coast, in the territories of the Autonomous Communities of Cantabria and the Basque Country (northern Spain).

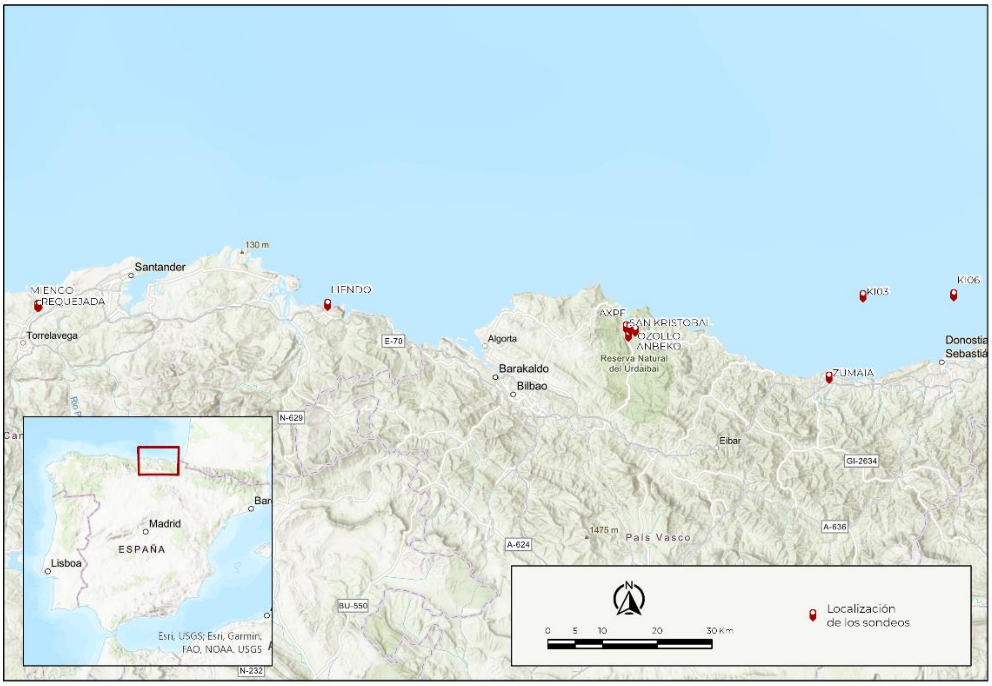


**Figure M.1** - Location of the studied boreholes and cores in the eastern Cantabrian coast.

The paleopalynological records studied in this work range from the Pleistocene epoch to the Anthropocene. This is due to the main objective that motivated this project: to reconstruct the natural and anthropogenic evolution of the vegetation along the eastern part of the Cantabrian Coast and the transformation that its main estuaries underwent during the Quaternary until the present. The records studied have been divided into Long Boreholes and Short Cores, as their length and coring methodology are diverse. Boreholes are several meters long while cores are ±50 centimeters long (Table M.1).

Palynological methodology consists of a series of phases that are highly standardized among specialists. This is why the existing bibliography, due to the long tradition of palynology as a scientific branch, is exhaustive (Girard, 1975, 1985; Bryant & Holloway, 1983; Dimbleby, 1985; Birks et al., 1988; Pearsall, 1989; Moore et al., 1991; Horowitz, 1992; Richard, 1999; Bui-Thi, M. & Girard, 2002; Burjachs et al., 2003; López-Sáez et al., 2003).

The working methodology in paleopalynology has the versatility to be applied to any sedimentological context. Firstly, the fieldwork, also known as sampling; Secondly, the chemical processing of the samples in the laboratory and their subsequent preparation for observation under the optical microscope to identify the palynomorphs, pollen and non-pollen present in each sample analyzed; Finally, the graphic representation of the results, through pollen diagrams that allow us to visualize and interpret the data obtained. In this case, all these phases have been carried out using the facilities of the University of the Basque Country (UPV/EHU) in Leioa (Biscay) and the Centre for Human and Social Sciences (CCHS) of the CSIC in Madrid.

**Table M.1 -** List of boreholes (grey) and cores (white) studied

| BOREHOLE/CORE | ENVIRONMENT | LENGTH (cm) | AGE |
|---|---|---|---|
| Miengo (Suances, Cantabria) | Estuarine | 49 | 1855-2018 CE |
| Requejada (Suances, Cantabria) | Estuarine | 1500 | 7980±30 BP-1970 CE |
| Liendo (Cantabria) | Karst lake | 8900 | Pleistocene |
| Ozollo (Urdaibai, Biscay) | Estuarine | 531 | 2470±30 BP-2004 CE |
| Anbeko (Urdaibai, Biscay) | Estuarine | 464 | 3770±30BP-3480±30 BP |
| San Kristobal (Urdaibai, Biscay) | Estuarine | 450 | 1978-1979 CE |
| Axpe Norte (Urdaibai, Biscay) | Estuarine | 49 | 1773-2018 CE |
| Zumaia (Gipuzkoa) | Estuarine | 45 | 1816-2018 CE |
| K103 (Basque Mud Patch) | Marine | 17 | 1873-2004 CE |
| K106 (Basque Mud Patch) | Marine | 20 | 1866-2004 CE |

## 1. Sampling

Sampling is one of the most important phases of paleopalynological work. Although it is true that this phase is not very complicated, several factors that are of vital importance must be taken into account, especially for the success of the following phases.

There are many different types of natural deposits, including peatlands, karst lakes, estuaries and continental shelf. In these deposits the conservation of palynomorphs is usually exceptional allowing a high-resolution analysis. The choice of one type of deposit or another depends on the objectives that are being sought. That is why estuaries were chosen as the main sedimentary deposit, although it is true that samples from other settings such as marine surveys have been studied.

The sampling, therefore, is closely linked to the type of sedimentary deposit to be studied. For the long boreholes, ROLATEC RL-46, a percussion/rotary drill mounted on self-propelled tracks was used (Figure M.3). The long boreholes correspond to: Requejada (43º23.572 N, 4º01.146 W), Liendo (43º23.548 N, 3º21.595 W), Ozollo (43º21.128 N, 2º39.405 W), Anbeko (43º21.430 N, 2º40.122 W) and San Kristobal (43º22.027 N, 2º41.276 W) (Figure M.5). The Requejada borehole was obtained in September 2017. In the case of Liendo, the borehole recovery was carried out in April 2019. The boreholes of Ozollo, Anbeko and San Kristobal were extracted during February 2019 (Table M.1). In the Requejada borehole, sampling was carried out so that 1-cm thick samples were obtained every 30 cm. In the case of Liendo, samples were collected from the most organic levels with the objective of carrying out a preliminary study due to the great length of this borehole. For Ozollo, the resolution used was a 1-cm sample every 7 cm. The Anbeko and San Kristobal samplings were carried out with a high resolution of 1-cm of sample every 5 cm.

**Figure M.2** - A) Photograph of the landscape surrounding the Axpe Norte core (Urdaibai). B) The Miengo (Suances) PVC tube prepared to be inserted for the extraction of the core.

**Figure M.3** – A and B) Core extraction with a Kullenbeg corer during the EUSKASED (Euska2) campaign on board the R/V Côtes de la Manche cruise ship in 2004. C) Drilling boreholes with ROLATEC RL-46 a percussion/rotary drill in Liendo (Cantabria).

In the estuaries, the extraction of the short cores was done manually, introducing 50-cm long and 12.5-cm diameter PVC tubes in each salt marsh or tidal flat (Figure M.2). These are the Miengo (43º24.586 N, 4º01.430 W), Axpe Norte (43º22.516 N, 2º41.150 W) and Zumaia cores (43º17.129 N, 2º14.466 W) (Figure M.5), all of them collected between March and December 2018 (Table M.1). The sampling frequency consisted of 1 cm thick intervals, obtaining from 45 to 49 samples respectively.

In turn, the marine sedimentary cores were obtained during the EUSKASED (Euska2) campaign carried out in July 2004 (Figure M.4). The coring was carried out on board the R/V Côtes de la Manche cruise ship. The objective was to obtain cores in the central area (opposite the city of San Sebastian) in the Basque Mud Patch (BMP). Core KI-03 (43°25.69 N, 2°09.18 W) was retrieved at 135 m depth using a Kullenbeg corer. Core KI-06 (43°25.424 N, 1°57.747 W) was obtained at 119 m depth (Table M.1) using an interface corer (Champilou, 2005; Irabien et al., 2020) (Figure M.3). Both cores were later divided into 1-cm thick samples at the University of Bordeaux (France).

Different sampling resolutions depended on the conditions and properties of the cores obtained (length, age, type of sediment...).

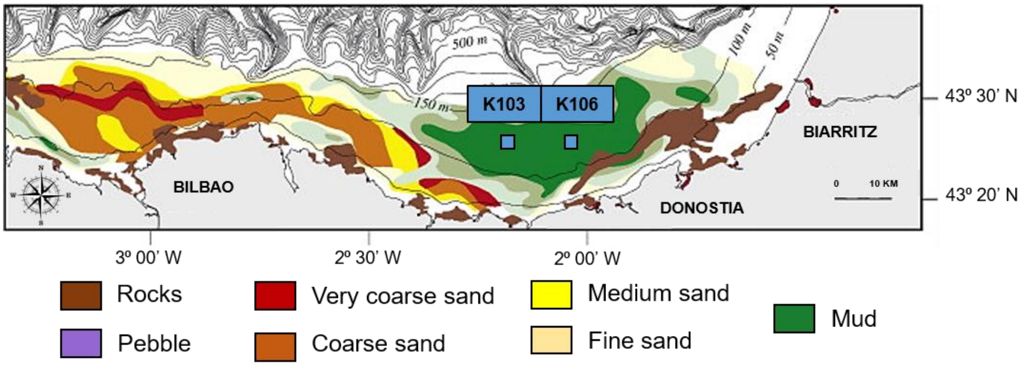


**Figure M.4** - Geographical location of the cores studied on the Basque Mud Patch.

Once the samples required for the corresponding pollen analyses were taken from each borehole or core, they were introduced in individual sterilized plastic bags and properly labelled. Finally, they were stored in the refrigerators in the UPV/EHU (Leioa) and the CCHS-CSIC (Madrid) until they were processed.

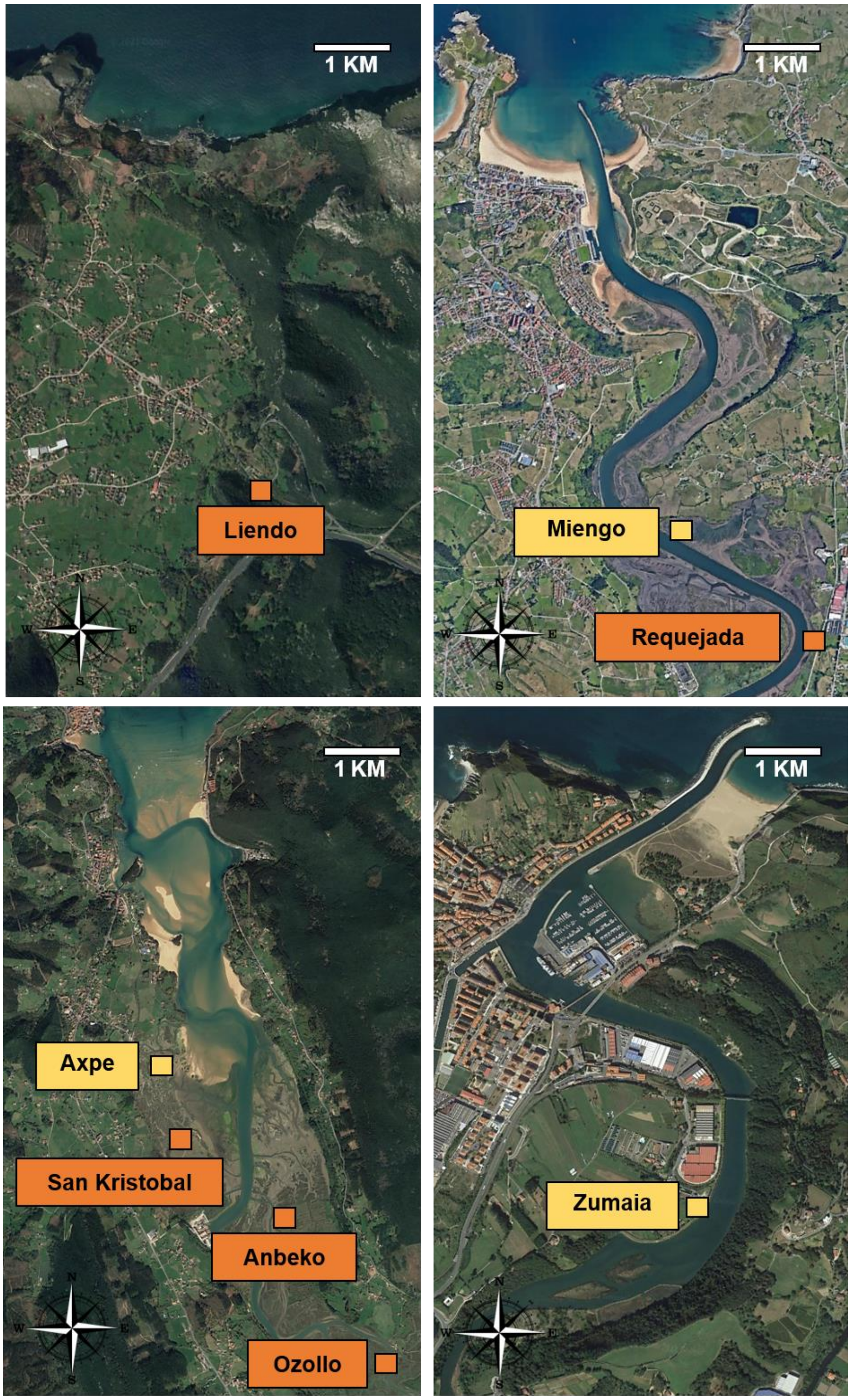


**Figure M.5** - Geographical location of the studied boreholes and cores in the different coastal settings (Liendo, Saja-Besaya, Urdaibai and Urola). In orange, the long boreholes and in yellow, the short cores.

## 2. Chemical treatment

The method consists, firstly, of washing the sediment samples and, secondly, of exposing the sediment to a series of chemical attacks with acids and bases to eliminate successively the carbonates, silicates and organic matter present (Girard & Renault-Miskovsky, 1969; Goeury & Beaulieu, 1979; Faegri & Iversen, 1989; Moore et al., 1991; Burjachs et al., 1990, 2003; López-Sáez et al., 2003) following a series of steps for the correct extraction of the spore-pollen content:

**(i)** Each sample is first collected in separate and correctly identified beakers (about 10 g). Distilled water (covering the sediment sample) is poured in and diluted until no lumps remain. Following this, a tablet of *Lycopodium*, an exogenous element normally used to estimate the pollen concentration, is added. Afterwards, hydrochloric acid (HCl) is added to remove the carbonates and, in addition, break up the *Lycopodium* tablet. When the tablet has been dissolved, the sediment should be washed with distilled water. In order to do this, successive centrifuges of 5 minutes at 2500 revolutions per minute (rpm) are used. The sediment should be left with a neutral pH.

**(ii)** Once the pH is neutral, sodium hydroxide (NaOH) is added. It must be diluted to 20%. Then, each sample is placed in a hot water bath for 20 minutes to make the sediment and the NaOH react (Figure M.6) to eliminate the silicates. Once 20 minutes have passed, we again proceed to perform successive washings of the sediment with distilled water and centrifugation (2500 rpm) until the sediment pH is neutralized. Once the washings are completed, in the last one, it is recommended to add a drop of HCl so that the sample acquires some acidity. This is to ensure that in the process of leaving the sample to dry (the tubes are left upside down to drain off all the water), the sediment is well stuck to the bottom and does not pour out. It is important that the sediment does not crack so as not to lose any portion of the sample.

**(iii)** The third step is the most important of all. The aim is to separate the pollen content from the sediment definitively using the densimetric difference. For this, we use Thoulet's liquor (made from potassium iodide, cadmium iodide and distilled water). We add this liquor to each sample, and this will give us a density of 2 $g/cm^3$ (Girard & Renault-Miskovsky, 1969; Goeury & Beaulieu, 1979). Each sample should be agitated, in this case, in an ultrasonic cell disintegrator (Sonifer 450 CE with threaded micro tip) for 8 seconds. Then, it is centrifuged for 10 minutes at 2500 rpm. The pollen will be concentrated in the floating liquor, so the liquor should be decanted into small crystal glasses, again, correctly listed and identified. Finally, this liquor is filtered through glass fiber filters, where the pollen content of each sample is adhered. These filters are stored in new tubes to which hydrofluoric acid (HF) is added to remove remaining unwanted organic matter and the glass filter filters, leaving the samples to react for at least 12 hours.

**(iv)** After 12 hours, each sample is washed until the pH is neutral, a little potassium hydroxide (KOH) diluted to 10% is added, and it is again neutralized. After this the sample is ready to be observed under the microscope.

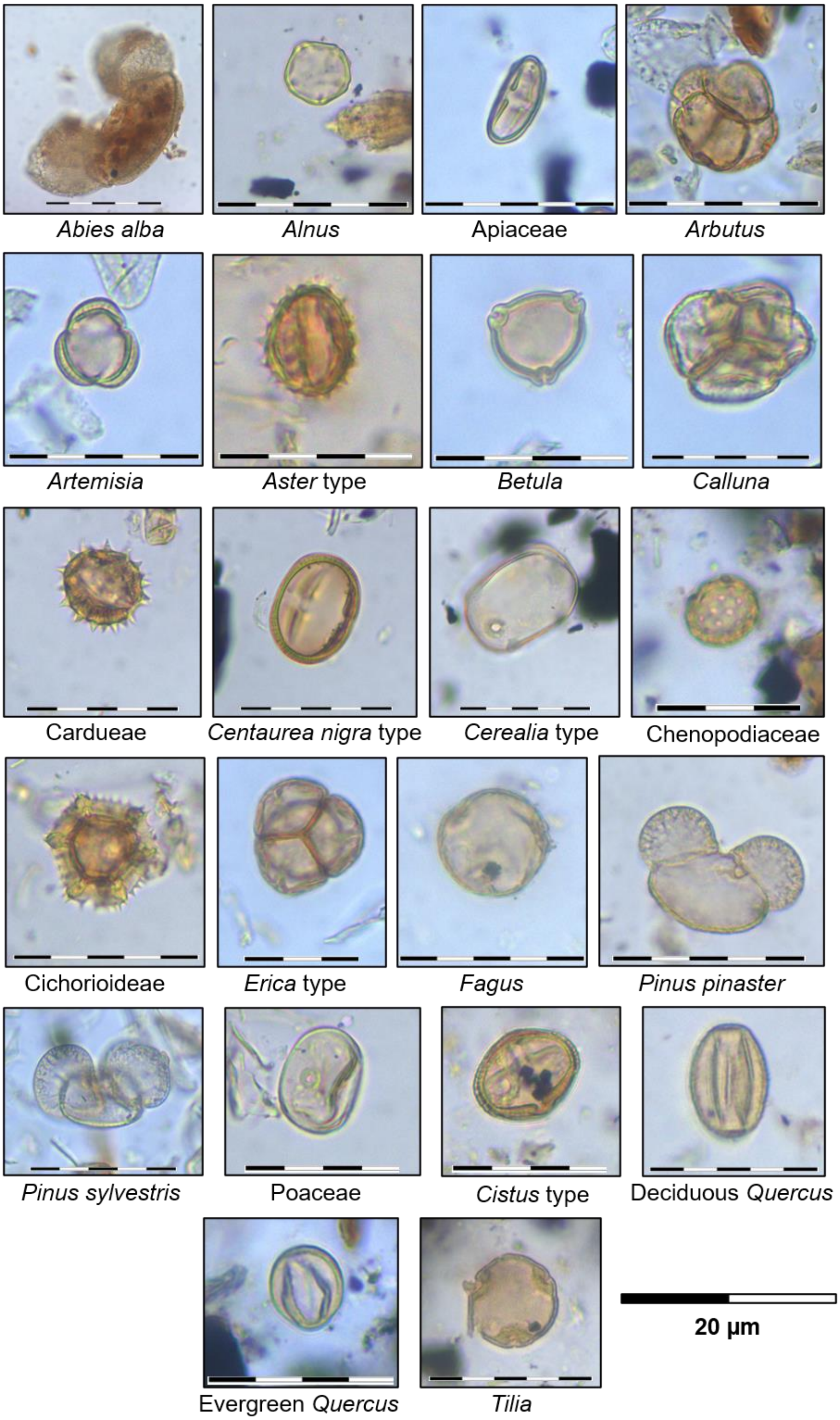
**(v)** For better preservation, samples are stored in *Eppendorf* tubes with gelled glycerine (Figure M.6).

**Figure M.6** - A) Laboratory for chemical treatment of pollen samples at CCHS (CSIC) in Madrid. B) Pollen samples prepared for HF treatment. C) Samples stored with glycerine in *Eppendorf* tubes. Photographs by Reyes Luelmo-Lautenschlaeger.

## 3. Microscopic identification

After chemical processing, each sample is mounted directly from each *Eppendorf* tube, using micropipettes, on optical microscope slides 76 x 26 mm in size and 1 mm thick. Cover plates of 24 x 60 mm are placed and sealed with *hystolaque*. The analysis has been carried out by optical microscopy, with a Nikon Eclipse100 optical microscope -objectives x40 and x60- (Figures M.7 and M.8).

**Figure M.7** - “Nikon Eclipse100”, the microscope used for pollen identification.



*Abies alba*
*Alnus*
Apiaceae
*Arbutus*
*Artemisia*
*Aster* type
*Betula*
*Calluna*
Cardueae
*Centaurea nigra* type
*Cerealia* type
Chenopodiaceae
Cichorioideae
*Erica* type
*Fagus*
*Pinus pinaster*
*Pinus sylvestris*
Poaceae
*Cistus* type
Deciduous *Quercus*
Evergreen *Quercus*
*Tilia*

**Figure M.8** - Most common pollen taxa identified in this doctoral dissertation.

## 3.1. Pollen Microfossils

The identification of pollen is possible thanks to the external structure of the grain. Pollen grains have two cell wall layers, called intine and exine. It is the second, the external exine, which ensures the good preservation of pollen, as the internal intine is made of cellulose and it is not preserved in buried sediments. Exine is composed of sporopolenine, a polyterpene with a high carbon content. This makes it resistant to oxidation and microbial destruction, allowing the preservation of the structural characteristics of the pollen grains over time and exposure to chemical attacks to which we subject the samples in paleopalynological studies. For microscopic identification, the reference collection in the Laboratory of Archaeobiology at the Centre for Human and Social Sciences (CCHS) of the Spanish National Research Council (CSIC, Madrid) has been used together with bibliography on the morphometric characteristics of palynomorphs (Bonnefille & Riollet, 1980; Moore et al., 1991; Reille, 1992, 1995, 1999).

The structural and diagnostic characteristics of pollen are (Figure M.9):

- Number of grains: The pollen, in the anthers of flowers, are united in 4 (tetrads) but, when they are released, they usually separate individually (monads). Also, in some cases, they can be in pairs (dyads), again in fours, or together with more grains (polyads).

- Ornamentation and structure of the exine: The exine (outer layer of the pollen grain) is in turn formed by several sub-layers, of which the ectexine is the outermost one. Ectexine can have a smooth or unadorned appearance, baculate (elements of more than one micron and rounded), equine (with pointed elements of more than 3 microns), etc.

- Distribution and shape of the openings: In the exine we can sometimes find areas where it becomes thinner or even disappears. The objective of these apertures is to favor the exit of the pollen tube through which the fertilization of the ovocyte takes place. They are a diagnostic element depending on the number of openings, their distribution and their shape. Depending on the number of apertures, the pollen grains can be: mono-(1), di-(2), tri-(3), tetra-(4), penta-(5), hexa-(6) and poly-(>6) aperture. Depending on the shape, pollen grains are classified as colporated (the aperture is twice as long as the width), pororate (aperture equal in length and width) and colporoidated (when the shape of the apertures is combined). Finally, if the distribution of the pores is on the equator of the grain, they are called zona-colporated and if they are located on the whole surface they are named as panto-colporated.

- Shape and size of the pollen: These parameters are only taken into account as a guideline, because once outside the flower, the pollen grains can undergo exogenous variations.

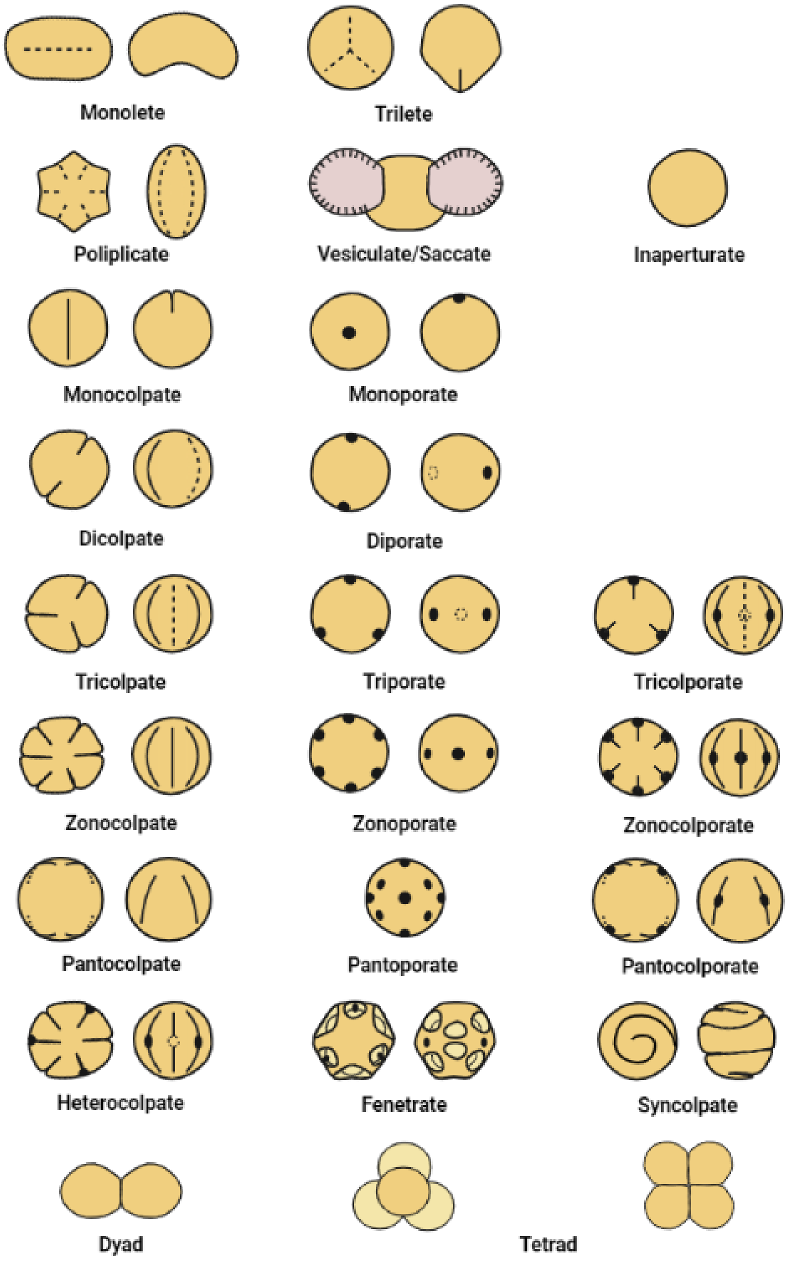


**Figure M.9** - Full spectrum of possible pollen types. Re-adapted from Lang (1994).

### 3.2. Non-Pollen Palynomorphs (NPPs)

Non-pollen palynomorphs (NPPs) are a group of elements that can be found in the pollen residue after treatment. Their composition can be diverse (cyanobacteria, fungal spores, animal micro-residues, bryophytes, foraminiferal organic linings, etc). Using the same chemical treatment to concentrate pollen microfossils, we can have access to additional important information about paleoenvironmental aspects of the samples that are difficult to detect with traditional pollen microfossils (van Geel, 1972, 1976a, 1976b, 1978; van der Hammen et al., 1973; van Geel et al., 1981, 1983, 1984, 1989, 1996; Bakker & van Smeerdijk, 1982; Brinkkemper et al., 1987; Haas, 1996; Kuhry, 1997; Carrión & van Geel, 1999; López Sáez et al., 1998, 2000; van Geel, 2001; Galop & Lopez-Saez, 2002)

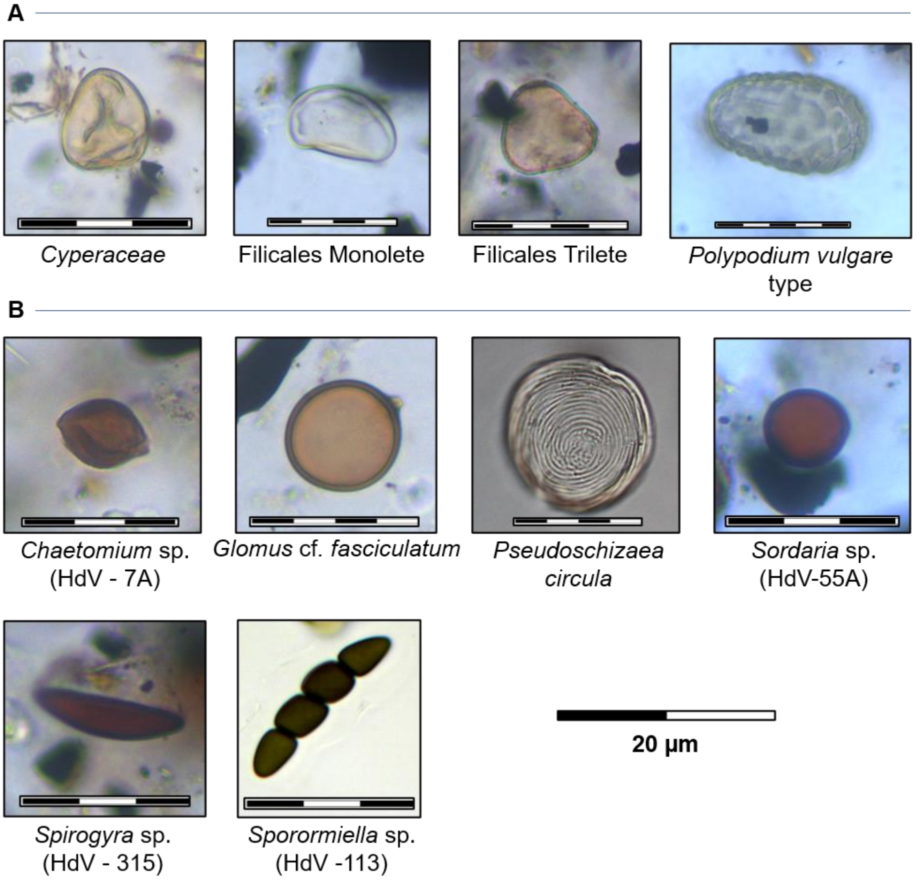
Some of these paleoenvironmental aspects that we can reconstruct through NPPs are: the degree of water pollution, the selective use of fire, the natural or anthropogenic origin of fire, the relationship between periods of humidity and dryness, the variations in the water table, the degrees of erosion, etc (Carrión & Navarro, 2002).

Specialized literature has been used to identify NPPs in our samples (van Geel, 1976, 1978; van Geel et al., 1980, 1983, 1989; López-Sáez et al., 1998, 2000; Carrión & van Geel, 1999; van Geel et al., 2003; López-Sáez & López-Merino, 2007). In most cases the identification (Figure M.10) was made possible by the assignment of a number that determines the type of NPP following the typology established by the school of Dr. van Geel (University of Amsterdam, Netherlands).

## 4. Statistical representation

In paleopalynology, two different concepts must be clearly understood in order to determine if a sample is representative: the sum of the pollen base and the taxonomic diversity.

The pollen sum (PS) consists of the number of palynomorphs counted for each sample. It should be noted that, in general, hydro-hygrophytes, cryptogam spores and NPPs are excluded from the pollen sum because of their over-representation in aquatic deposits. The relative percentage of these palynomorphs excluded from the pollen sum is calculated separately. This is because pollen analysis must take into account different factors, such as the nature of each taxon, the type of pollination, the dispersion index and the sedimentary deposit (López Sáez et al., 1998, 2000).



*Cyperaceae*
Filicales Monolete
Filicales Trilete
*Polypodium vulgare* type
*Chaetomium* sp. (HdV - 7A)
*Glomus* cf. *fasciculatum*
*Pseudoschizaea circula*
*Sordaria* sp. (HdV-55A)
*Spirogyra* sp. (HdV - 315)
*Sporormiella* sp. (HdV -113)

**Figure M.10** - A) Most common hydro-hygrophilous taxa identified and B) most common NPP taxa identified in this doctoral dissertation.

In paleopalynology, depending on the original sedimentary context, different pollen counts are considered as representative. In the case of this doctoral dissertation, where the sedimentary contexts studied are all natural (karst lakes, estuaries and marine settings), the necessary sum of the pollen base must be 500 terrestrial pollens per sample to be considered as representative. This is because pollen preservation in natural contexts is usually excellent (Burjachs, 1990; Moore et al., 1991; Horowitz, 1992).

Taxonomic diversity is the second criterion to be taken into account when dealing with statistical representativity in paleopalynology. This term refers to the minimum number of different palynomorphs identified for each pollen spectrum. In this work, it has been considered that the number of different palynomorphs for each pollen spectrum should be 20 (McAndrews & King, 1976; Pons & Reille, 1986; Sánchez-Goñi, 1993a, 1993b; Pérez-Díaz, 2012; López-Sáez et al., 2003).

Therefore, a sample is considered to be representative of its depositional environment when:

**(i)** The base sum is 500 pollen grains discounting hydro-hygrophytes, spores and NPPs.

**(ii)** 20 or more different taxa are present. With the exception of specific studies in contexts such as monocultures or other contexts with high human impact.

**(iii)** The percentage of indeterminable pollens does not exceed 50% of the base sum.

## 5. Graphical representation of the results

Any pollen analysis should result in a graph showing how the taxa develop during the diachronic temporal sequence. In this dissertation, data processing and graphical representation have been performed using Tilia, Excel and C2 programs.

Raw data collection was performed with Excel and transposed to Tilia in order to produce pollen diagrams and pollen zones (with CONISS included in the Tilia program) (Grimm, 1987, 1992, 2004).

ClamR has been used to perform the age-depth models of the studied boreholes. For this purpose, it is necessary to have the free software R installed and to download the Clam content package. The code is able to perform age-depth models, hiatus detection, different modelling and extrapolations (Blaauw, 2010).

The other R package used here is SiZer (Significant Zero crossings of derivatives). This has been used to detect the significance of change values and trends in the pollen data obtained. The results can range from significantly negative, possibly zero or significantly positive, always taking into account a range of smoothing bandwidths. The graphical representation is quite visual as it allows this significance to be observed in a colored graph (Chaudhuri & Marron, 1999). Analyses were performed with the SiZer package (Sonderegger et al., 2009) for R (version 4.0.2, R Development Core Team, 2018).

Finally, C2 program was used for the enhancement of paleoclimate modelling and reconstruction. This software presents a wide range of resources and procedures allowing a multimodal approach (Juggins, 2007).

# 6. Interpretation of paleopalynological results

Once the data are obtained and treated statistically, their interpretation should take place. For this, we must try to see all the information the pollen diagram provides and attempt to propose an explanation. In order to interpret a pollen diagram, we must take into account the following (Iriarte & Zapata Peña, 1996; Iriarte, 2002; Pérez-Díaz, 2012):

**(i)** The buried pollen rain reflects the vegetation of the past just as the current pollen rain reflects the current vegetation cover.

**(ii)** The precision, meticulousness and rigour of the method used determine the veracity of the results obtained.

**(iii)** The comparison between the past plant species (Pleistocene-Holocene) and the present ones has not produced significant variations in their morphology or ecology.

**(iv)** The original location of the extracted core confers certain sedimentological and environmental characteristics which, consequently, influence the vegetation by creating specific living conditions.

## 6.1. Pollen dispersion

The pollen dispersion factor must also be taken into account when interpreting pollen data. The graphical representation of the data, by means of the pollen diagram, is the result of a percentage analysis of each pollen taxon present. However, comparisons of the percentage presence of pollen taxa are not always meaningful because this percentage value depends on the value of the other taxa in the pollen sum (Davis, 1969; Hicks & Hyvärinen, 1999). On the other hand, there are situations in which pollen may be the only reliable way to demonstrate the presence or absence of a species at a site (Hyvärinen, 1975; Hicks, 1994) and therefore, the mere presence of pollen may already have some significance depending on the interest of the study being carried out.

This doctoral dissertation has the particularity that it works with estuarine and marine deposits, and is not only focused on the study of estuarine evolution (Woodroffe et al., 1989; Armour & Kennedy, 2005;) but also on the study of the paleoenvironment and paleoclimate (Kraus & Matthiessen, 2003; Malamud-Roam et al., 2006; Ellison, 2017).

In the case of estuarine deposits, the distance a pollen grain can travel depends on the depth of the water and the level of turbulence. These estuarine characteristics are determined by the geomorphology of the estuary. Also, continental drainage and tidal water flows are key factors (Stutz & Prieto, 2003; Fontana, 2005; Stuart et al., 2006; Clark & Patterson, 2016; Medeanic et al., 2016). In general, pollen representation in studies of estuarine sediments shows the pollen spectrum of regions adjacent to the estuary (Brush & DeFries, 1981; Deng et al., 2006). Another feature to consider is the morphology of the pollen grain itself. There are species that have developed, for example, aerial sacs that allow them to be transported over longer distances by wind pollination (Moore et al., 1991). This characteristic can produce a differential sorting in the pollen population and distort the sedimentary record, for example, by the floating of these species, mainly conifers, and the faster sinking of the rest. Floating pine pollen may, therefore, produce concentrated deposits of this taxon in areas where there is no nearby pine vegetation. It should also be taken into account that herbaceous pollen, being taxonomically smaller, is more susceptible to long-distance transport in estuarine systems. Moreover, the information provided by herbaceous pollen in estuarine records can be very interesting, as they may indicate salinity or freshwater conditions (Hopkins, 1950; Traverse & Ginsberg, 1966; Byrne et al., 2001; Beecher & Chmura, 2004; Ellison, 2017).

Regarding the marine cores, there are also some specific conditions for the interpretation of data. Pollen deposited in marine sediments comes from adjacent continental areas. The distribution of pollen grains can cover great distances, and it is important to know the agents responsible for this distribution. In general, the predominant pollen is that which is transported by wind, but fluvial discharge of sediments also plays an important role in the concentration of pollen grains in marine sediments, especially in those closer to the coast. Ocean currents may be influential, but they are not the major contributor of pollen in marine sediments (Heusser, 1988; Heusser & Balsam, 1985; Dupont & Wyputta, 2003). This issue is related to the same problematic as that of estuaries in terms of percentages and overrepresentation of tree species that possess a greater ease of dispersal (Ganne et al., 2016; Clément et al., 2017; Penaud et al., 2020).

## 6.2. Pollen indicators of anthropization

Anthropization is defined as the process of human transformation of the vegetal landscape. This process can manifest itself in different ways (construction, deforestation, reforestation, and arable and livestock processes) but is almost always closely linked to the human populations that inhabit that landscape or its surroundings. Thanks to the pollen diagrams, the consequences of these human activities can be detected in the sedimentary records.

There are more factors of anthropization, but from the palynological point of view, the evidence of these activities is obtained through the "pollen indicators of anthropization" (Behre, 1981, 1986, 1988; Jalut, 1991; Brun, 2007, 2011; Carrión & Navarro, 2002; Chambers et al., 2011; Cugny et al., 2010; Echazarreta, 2020; Ejarque et al., 2011; López-Sáez & López-Merino, 2007; Mercuri et al., 2013; Miola, 2012; Richard, 1994b, 1994a, 1995, 1997). These indicators can be classified into two groups: the evidence of pollen microfossils and the evidence of non-pollen palynomorphs (NPPs).

The evidence that pollen microfossils can provide about human activities are very diverse: appearance of cultivated plants, appearance of anthropogenic vegetation, decrease of tree pollen, etc. The evidence of anthropization observed through the record of NPPs is also very useful because it can indicate presence of fire, erosive processes and pastoral pressure. For example, the development of pastoral activities can be identified relatively easily with the appearance of pollen clusters such as Chenopodiaceae, *Urtica dioica* type, *Plantago* sp., etc. or through coprophilous fungi (Brun, 2007, 2011; Carrión & Navarro, 2002; Chambers et al., 2011; Cugny et al., 2010; Ejarque et al., 2011; Galop, 1998, 2000; Galop & Lopez-Saez, 2002; Mercuri et al., 2013; Miola, 2012; López-Sáez et al., 2003).

## 6.3. Cereal, *Eucalyptus* sp. and Pine representativeness and pollination.

There are also other taxa whose presence, depending on spatio-temporal conditions and historical contexts, can indicate anthropization or directly show evident anthropogenic dynamics. In this doctoral dissertation this applies to taxa such as *Cerealia* type, *Eucalyptus* sp. and *Pinus pinaster*.

In the case of cereals, their relationship with the development of pastoral and agricultural activities is usually clear. As mentioned above, there are other taxa that can be interpreted as markers for the development of these activities over time. It is important, for example, to note that cereals of the genera *Avena*, *Hordeum* and *Triticum* are autogamous. This means that they are self-pollinating, which implies a rather low aerial dispersal (Heim, 1970; Bottema, 1992; Bower, 1992). The low dispersion of cereal pollen also results from the large size of its grains, which makes them very heavy and difficult to be transported by the wind. A clear example of this would be rye (*Secale cereale*), an allogamous species (cross reproduction between genetically different individuals) with high pollen productivity (13,200-19,000 grains per anther), but due to its size, its pollinating capacity is significantly affected (Vuorela, 1973; Subba Reddi & Reddi, 1986; Vicent et al., 2000). This implies that, very often, the absence of *Cerealia* type pollen taxa is not indicative of the absence of crops.

However, the presence of *Cerealia* type pollen that could indicate the development of agricultural practices in a place bases its representativeness on its presence in significant percentages. It was therefore important to determine what percentage of this palynomorph is sufficient to demonstrate the existence of agricultural activities near the study site. Numerous studies have been carried out with modern pollen rain and the results have been mixed. Some studies claim that percentages around 10-15% reflect the proximity of crop fields, others argue that at distances of less than 100 m the percentages of cereal pollen do not exceed 1% and disappear at greater distances (Heim, 1970; Beaulieu, 1977; Diot, 1992).

However, the representativeness of *Eucalyptus* sp. in the pollen record is affected by its mainly entomophilous/ornithophilous character (pollination preferentially by insects or birds). The pollen concentration in the air is highly variable and is negatively affected by average temperatures, rainfall and humidity (FAO, 1981; Rodríguez-Rajo et al., 2001). In the case of the Iberian Peninsula, this species is a replanted species and, therefore, a translocated taxon. This implies some control over the localization and expansion of the species, which also limits the colonizing capacity and reproductivity of *Eucalyptus* sp. These factors may influence the limited occurrence of this taxon in the sedimentary record. Even so, its mere appearance in the sedimentary record already indicates its presence and, therefore, it has representative potential in a spatio-temporal context such as that of the eastern Cantabrian Coast during recent decades.

Finally, the case of *Pinus* is precisely opposite to that of *Eucalyptus* sp. since pollen production and dispersal of pine pollen is very high. Pine is a genus of anemophilous nature which, thanks to the structure of its pollen grain (aerial sacs), has a dispersal capacity of even hundreds of kilometers. Although within the genus *Pinus* there are numerous species, all of them have in common a similar pollen morphology that allows a very effective aerial transport of pollen grains over long distances (Benkman, 1995; Jato et al., 2000). This means that we can sometimes find an overrepresentation of the genus *Pinus* in the sedimentary records. For this reason it is important to discern between the different types of pine species in our records, although it is sometimes impossible. In addition, pine is a strong colonizing species, adapting quite well to different types of soils, and not allowing other species to grow in its domain.

All these taxa must be taken into account when interpreting the data obtained in the recent pollen records, as these factors condition in susceptible ways the dynamics of the vegetation, of both natural and anthropogenic character.

# 7. Dating methods

## 7.1. Natural radioisotopes ($^{14}C$ and $^{210}Pb$)

Radiocarbon dating is based on the use of the natural radionuclide $^{14}C$ because its lifespan ($T_{1/2}$ = 5,730 ± 40 years) allows it to be used for dating throughout the Holocene and part of the Late Pleistocene (up to ±43,500 yr BP). The method, developed by Libby in 1952, uses the unstable $^{14}C$ isotope which is the result of the interaction of neutrons from cosmic radiation with the atmospheric $^{14}N$. Because $^{14}C$ is part of the environmental $CO_2$, it is constantly absorbed by living organisms during their lives. After death, this contribution to the organism of $^{14}C$ ceases, and that which remains in the organism gradually disintegrates. Due to this process of disintegration and to the proportion of $^{14}C$ that remains, the age of the organic matter analyzed can be estimated. However, it should be noted that the contribution of $^{14}C$ is not constant and is linked to other factors. Some examples are the variation in the intensity of cosmic radiation, anthropogenic processes (such as the emission of large quantities of $CO_2$ into the atmosphere and the bomb spike) and, especially, the existence of reservoirs of organic matter in the oceans. The ocean floor is deficient in $^{14}C$ since it is not in direct contact with the atmosphere and, in addition, these reservoirs modify their flow of carbon as a function of the Earth's climate (Alejandre, 2018). In fact, the difference between radiocarbon data obtained from marine and terrestrial samples is approximately 400 years (Stuiver et al., 1998). In addition, the data must be calibrated. Calibration is also different if the samples are of marine or terrestrial origin. In terrestrial samples the calibration is done by curves from dendrochronological studies while in marine samples, coral and planktonic foraminifera data are used (Reimer et al., 2013, 2020; Heaton et al., 2020; Stuiver et al., 2020).

For the most recent records, the analysis of the natural radioisotope $^{210}Pb$ has been used. $^{210}Pb$ is a short-lived radioisotope ($T_{1/2}$ = 22.3 years) that results from the disintegration of $^{222}Rn$ after its escape from the Earth's surface into the atmosphere. The $^{210}Pb$ is continuously deposited back to the Earth's surface. This process is known as fallout (Appleby, 1992; Appleby & Oldfield, 1978). Furthermore, there is a fraction of the $^{210}Pb$ that appears from the disintegration of $^{226}Ra$ in the sediment. The result of this disintegration is known as "$^{210}Pb_{equilibrium}$". The quantitative difference between the $^{210}Pb$ fraction coming from fallout and the one disintegrating in the sediment is known as "$^{210}Pb_{excess}$". This $^{210}Pb_{excess}$ is used in geochronological studies based on depth and distribution of recent sedimentological records (Cundy et al., 2003). Using various geochronological models already established (CIC: constant initial concentration; CF: constant flux, CF:CS constant flux: constant sedimentation, CRS: constant rate of supply) and according to the $^{210}Pb$ disintegration constant, it is possible to estimate the sedimentation rate over periods of less than 100-120 years (Robbins, 1978; Sanchez-Cabeza & Ruiz-Fernández, 2012; Serrano-García, 2020).

Radioisotope analyses for this study were performed at the Department of Medical and Surgical Sciences of the University of Cantabria (UC) by Dr. José Gómez Arozamena.

## 7.2. Artificial radioisotopes ($^{137}Cs$, $^{238}Pu$ and $^{239+240}Pu$)

The rate of sedimentation calculated with $^{210}Pb$ can be used to indicate precisely the dates of the analysed sediment. The problem is that, like all sedimentary records, these can undergo mixing or bioturbation processes that can disturb the stratigraphical order of the materials, especially in lake, marine and estuarine sediments. This is why it is necessary to validate the results obtained from $^{210}Pb$ with the use of at least one independent tracer that separately provides an unambiguous stratigraphic time horizon (Smith, 2001).

Some of the radionuclides that have been used here to validate the $^{210}Pb_{excess}$ datation are $^{137}Cs$, $^{238}Pu$ and $^{239+240}Pu$. $^{137}Cs$ is an artificial radioisotope that arises from nuclear fission of $^{235}U$ expelled into the atmosphere after the detonation of nuclear bombs between the 1950s and 1960s. The life of this radioisotope is very short ($T_{1/2}$ = 30.1 years). Its detection in the atmosphere, goes back to 1952 while in the sediments, it begins to be detectable from 1952-53 CE onwards. Its maximum concentration signals the year 1963 CE, because from this date atmospheric nuclear tests were banned and the presence of $^{137}Cs$ began to decrease. The use of $^{137}Cs$ as a tracer of $^{210}Pb_{excess}$ is useful, but its short half-life makes it increasingly difficult to measure, since its current disintegration from sediments is at 70% (Hewitt, 2000).

On the other hand, Pu radioisotopes, also resulting from atmospheric nuclear detonations, are used more frequently especially in recent years and in view of the need to complement the decaying $^{137}Cs$. What makes the difference between the Pu radioisotopes and the $^{137}Cs$ is that Pu has a longer half-life ($T_{1/2}$ $^{238}Pu$ = 88; $^{239}Pu$ = 24,110; $^{240}Pu$ = 6500 years). This makes them more useful in the long term and, also, some studies indicate that their mobility in the sediment is lower due to their high reactivity, producing a bond with the sediment much stronger than that of $^{137}Cs$ (Crusius & Anderson, 1995; Everett et al., 2008; Casas et al., 2015).

# 8. Other data processing

## 8.1. Age Models

For the long continuous sedimentary records from the boreholes (~±3m), age models have been performed to obtain greater precision in the specific age of the different samples. Depending on the case, different modeling approaches (linear interpolation, smooth spline...) have been applied with the aim of achieving the point of highest probability of the correlation interval (in BP dates) of each radiocarbon date (ClamR has been used for this purpose). This has made it possible to obtain age-depth models that chronologically assign each cm of the record to an approximate age (Blaauw, 2010).

## 8.2. Paleoclimatic reconstruction

Environmental reconstructions are currently the most important way of using paleoecological information if environmental purposes are involved. Reconstructions based on biological fossil remains preserved in sediments provide vital historical information for solving specific environmental issues (Seppä, 2018). Reconstructions have shown the recent human-induced acidification, eutrophication or pollution of lakes and estuaries in industrialized regions and also the utility of these for biodiversity conservation, ecosystem management and restoration plans (Dietl et al., 2015; Chevalier et al., 2020).

In terms of methodology, there are different approaches to the reconstruction of paleoenvironments (Birks, 2014):

**(i)** Approach through indicator species: the past environment is interpreted in terms of the environmental range occupied by some current indicator species. Information is needed, therefore, about the factors that influence the modern distribution and abundance of the species in question. To obtain such data, current distributions are compared with those of different ecoclimatic and geographical areas. If these show a covariant ecoclimatic variable with the distribution of the species in question, the relationship is usually assigned to that species as cause and effect. Sometimes, when reconstructions go back a long time, the species that we find are extinct. This makes the relationship mentioned above ambiguous. To solve this problem, the modern relative is used as a guide taxon, and with it, the environmental conditions of the extinct species are estimated (Mosbrugger et al., 2005).

**(ii)** Assemblage approach: fossil assemblages are considered as a whole. The interpretation of these is based on species composition and abundance. This approach, used initially in a non-quantitative way, has developed into a more modern method in which modern and fossil samples are compared numerically. Fossil samples that are most similar to modern samples are interpreted to reflect environmental conditions similar to those of modern samples (Seppä, 2018).

**(iii)** Mathematical transfer functions/calibration function: For reconstructions carried out using weighted averaging-partial least squares (WA-PLS), the term "calibration function" is more appropriate to differentiate it from other types of reconstructions that also use transfer functions. The WA-PLS reconstruction methods consist of a two-way weighted averaging (WA) and weighted averaging partial least squares regression and calibration (WA-PLS) where there are an explicit underlying taxon-climate response model and a global estimation of taxon parameters (Birks & Seppä, 2010). The transfer functions include other approaches such as principal components regression, partial least squares regression and calibration, Gaussian logit regression and calibration, multinomial logit regression and calibration and correspondence analysis regression (ter Braak & Prentice, 1988). The pollen data are quantitative and expressed as percentages based on the total count of the samples, so they are closed composition, multivariate data with a constant sum restriction (ter Braak & Verdonschot, 1995). Furthermore, they usually contain many zero values (taxa not present in some samples but present in others from the same borehole or core). This makes the data complex, showing noise, redundancy and internal correlations (Birks & Seppä, 2010). On the other hand, climate data rarely contain zero values as quantitative climate variables often have normal and linear distributions, with a high correlation between variables. This leads to a great data redundancy.

Therefore, in order to carry out a quantitative paleoenvironmental reconstruction using any of the previous approaches, a series of requirements must be taken into account: 1) a biological proxy that generates many fossil remains and is sensitive to climate/environmental variations; 2) a modern, high-resolution database of the proxy used; 3) fossil data and modern data must be comparable in quality and sedimentary environment; 4) a chronological control of the fossil data that is as clean as possible; 5) fossil data should be statistically and ecologically sound so that they easily fit other data sets (such as the modern database); 6) an estimate of the range of error of the modern data as a whole and of the fossil samples; and 7) the reconstructions obtained should be validated with other reconstructions already validated through comparison and discussion, assessing whether they are ecologically and paleoclimatically significant and reliable (Birks & Seppä, 2010; Chevalier et al., 2020).

## 8.3. SiZer analyses

SiZer (Significant Zero crossings of derivatives) analysis (Chaudhuri & Marron, 1999) has proven to be a useful tool for detecting significant changes in ecological records. The application to time series is particularly interesting from an ecological point of view because it allows the characterization of observed increases and decreases in records over time (Clements & Rohr, 2009; Sonderegger et al., 2009; Clements et al., 2010). By applying SiZer to time series, we are essentially implementing nonparametric smoothing to a signal, in this case, to pollen data. SiZer is a powerful and flexible tool, allowing different parameters and variables to be modified to obtain the most out of our data. Thanks to its flexibility, it is possible to detect trends, and single and multiple trend changes. In addition, SiZer adapts to the error in the time scale distribution. The results obtained by the SiZer analysis can be visualized with the color maps it generates. These maps are formed by an arrangement of axes, where the horizontal axis indicates the temporal scale and the vertical axis the bandwidth level applied to the data.

The application of SiZer analysis and paleoenvironmental reconstructions in this dissertation has been learned during my pre-doctoral research stay at the Department of Geosciences and Geography in the University of Helsinki, Finland, under the tutorship of Prof. Heikki Seppä.

# Results

In this PhD dissertation, as mentioned above, a total of 10 boreholes and cores have been analyzed. Although all sedimentary records are located in a common general geographical framework (Cantabrian Coast), each borehole and core is unique and has its own particularities, from the sedimentology to the pollen results and the radiocarbon and isotopic dates. For this reason, the results obtained for each record will be analyzed and disaggregated according to its chronology.

# 1. Pleistocene

## 1.1. Liendo

### 1.1.1. Pollen analysis

The case of Liendo is particularly different from the others. In the first place, because it is not an estuarine or marine borehole, but was carried out in a possible ancient karst lake. Secondly, it is also a unique case due to its length, which reaches a depth of 89 meters. Furthermore, it was surprising that the 13 samples sent for radiocarbon dating provided dates older than 43,500 years BP (methodological age limit).

For these reasons, the pollen analysis was performed, first with a low resolution, but covering the entire length of the borehole. After analyzing the results, it was decided to carry out a higher resolution study, starting with the uppermost part of the borehole.

A stratigraphic cluster analysis restricted by the incremental sum of squares (CONISS) was performed in order to define the different local pollen assemblage zones (LPAZ). Considering the whole of the Liendo borehole, regardless of its different sampling resolution, which ranges from 282 to 8,865 cm, 11 LPAZ have been established. As the sample resolution at which the upper part of the borehole has been analyzed is much higher than the rest, the pollen diagrams presented in this section are different for the deeper LPAZs and the upper LPAZs. The section with the highest pollen resolution corresponds, therefore, to LPAZ LIE-7, 8, 9, 10 and 11 (Fig. R.1, 2, 3).

**Table R.1 -** Summary of the most representative taxa (relative abundance %) identified in the lower resolution zones of the Liendo borehole. The single value represents the average and those in parentheses give the range. The percentages of hydro-hygrophilous taxa and NPPs are calculated separately together with the rest of the taxa.

| | **LIE - 1** | **LIE - 2** | **LIE - 3** | **LIE - 4** | **LIE - 5** | **LIE - 6** |
|---|---|---|---|---|---|---|
| *Abies alba* | 32 (17.3-48.6) | 1 (0.9-1) | 13 (0-48.9) | 4 (0-12.9) | 0.5 (0-1.2) | 33 (0.6-65.3) |
| *Alnus* | 0.5 (0.2-1.4) | 13 (5.2-21.2) | 23 (0.8-50.5) | 0.5 (0-1.7) | 0.1 (0-0.4) | 1 (0.8-1.2) |
| *Betula* | 10 (1-22.6) | 7 (2.4-12.3) | 19 (4.5-37.4) | 15 (0.4-45) | 5 (1.3-9) | 4 (2.8-5.3) |
| deciduous *Quercus* | 2 (0.7-4.4) | 7 (5.7-8.7) | 7 (0.4-20.6) | 8 (3.6-17.9) | 11 (1-31) | 25 (6.2-44.4) |
| *Pinus pinaster* | 18 (8.7-27.6) | 13 (9.7-15.3) | 14 (3.3-29) | 19 (3.5-53.7) | 34 (9-59.5) | 19 (10.6-8.1) |
| *Pinus sylvestris* type | 16 (5.3-26) | 5 (4.2-6.2) | 6 (0-14.6) | 5 (1.3-12.4) | 9 (1.1-15) | 6 (4.8-7.4) |
| *Calluna vulgaris* | 4 (0.4-10.9) | 25 (15.3-34.8) | 2 (1.3-4.5) | 9 (0-33) | 9 (2.6-21.6) | 0.4 (0-0.8) |
| Apiaceae | 1 (0.4-1.4) | 3 (2.5-3.8) | 2 (0.4-4.2) | 20 (1.5-66.8) | 2 (0.4-2.6) | 0.4 (0.2-0.6) |
| Cichorioideae | 0.1 (0-0.2) | 1 (0-2.3) | 0.3 (0-1.2) | 2 (0-7.8) | 12 (0.4-28.5) | 0.1 (0-0.2) |
| Poaceae | 2 (0.4-5.6) | 17 (15.9-17.2) | 4 (0.8-11.6) | 9 (2-20) | 11 (8.3-15.9) | 2 (1.2-1.8) |
| Cyperaceae | 2 (0-2.7) | 18 (15.8-20.6) | 5 (1.2-9.8) | 13 (3.8-26.4) | 10 (3.4-20.9) | 3 (3.2-3.6) |
| Filicales Monolete | 0.5 (0.2-0.7) | 4 (1.8-5.3) | 13 (1.2-35.4) | 2 (0.8-4.8) | 3 (0.8-3.8) | 11 (7.2-13.9) |
| Filicales Trilete | 3 (0.2-10.9) | 0.5 (0-0.9) | 1 (0.4-2.2) | 1 (0-2.7) | 13 (0.1-36.5) | 4 (0.1-7.1) |
| *Myriophyllum* | 1 (0-4.6) | 2 (0.9-3) | 3 (0.2-6.1) | 12 (0.7-33.5) | 3 (0.5-6.1) | 6 (4.8-6.6) |
| TREES | 87 (74.9-95.4) | 48 (39.2-57.4) | 88 (73.7-95.9) | 54 (21.7-89.8) | 61 (43.3-83.5) | 95 (94.1-96) |
| SHRUBS | 8 (2-21.9) | 28 (18-38.2) | 5 (2.3-10) | 11 (0.8-39.6) | 12 (5.6-23.8) | 1 (0.4-2.6) |
| HERBS | 5 (1.9-12.4) | 24 (22.7-24.6) | 7 (1.6-16.3) | 35 (9.4-72.9) | 27 (10.4-51) | 4 (3.4-3.6) |
| HYDRO-HYGROPHILOUS | 6 (1.1-13.7) | 24 (24.1-24.3) | 22 (11.7-42.1) | 28 (18.8-43) | 28 (12.1-41.1) | 26 (24-27.3) |
| NPPs | 0.2 (0-0.7) | 0.3 (0-0.6) | 0.3 (0-0.8) | 0.4 (0-1.2) | 0 (0-0) | 0.3 (0.2-0.4) |

**Table R.2 -** Summary of the most representative taxa (relative abundance %) identified in the upper part (higher resolution zones) of the Liendo borehole. The single value represents the average and those in parentheses give the range. The percentages of hydro-hygrophilous taxa and NPPs are calculated separately together with the rest of the taxa.

| | **LIE - 7** | **LIE - 8** | **LIE - 9** | **LIE - 10** | **LIE - 11** |
|---|---|---|---|---|---|
| *Abies alba* | 19 (2-64.3) | 1 (0-9.1) | 2 (0-7.4) | 0.1 (0-0.4) | 0.1 (0-0.6) |
| *Alnus* | 4 (1.3-59.7) | 0.5 (0-1.9) | 2 (0-9.1) | 0.5 (0-2.7) | 0.2 (0-1.1) |
| *Betula* | 27 (0-12.5) | 20 (0-47.2) | 18 (0.8-58) | 3 (0-6.8) | 16 (3.9-26.7) |
| *Corylus* | 8 (0.2-22.3) | 4 (0.2-18.1) | 4 (0-16.3) | 2 (0-7.1) | 3 (0-9.2) |
| deciduous *Quercus* | 6 (1-12) | 7 (1.4-36) | 9 (1.1-32.4) | 22 (3.3-42.9) | 12 (6.5-20.9) |
| *Pinus pinaster* | 4 (0-10) | 2 (0-7.3) | 5 (0-17.3) | 2 (0-8) | 4 (0-9.1) |
| *Pinus sylvestris* type | 9 (2.5-16) | 7 (0.7-13.7) | 10 (0.8-33) | 5 (0.6-12.5) | 7 (2.8-11.2) |
| *Erica* type | 2 (0.4-7.4) | 7 (0-24.4) | 3 (0-10.2) | 4 (0.2-11.7) | 5 (1.1-14.4) |
| Apiaceae | 2 (0.6-3.8) | 8 (0-22.5) | 10 (0-35.5) | 9 (0.9-32.9) | 9 (2.8-27.7) |
| *Artemisia* | 2 (0.4-5.9) | 5 (0-29.6) | 2 (0-8.5) | 1 (0.2-3.8) | 2 (0-4.7) |
| Cichorioideae | 1 (0.6-1.9) | 1 (0-2.5) | 2 (0-4.5) | 2 (0-5.6) | 10 (0.9-17.5) |
| Poaceae | 7 (4.8-8.8) | 24 (13.8-60.5) | 23 (8.6-60.7) | 37 (21.5-61.5) | 19 (8.9-27.4) |
| Cyperaceae | 10 (0.6-19.5) | 7 (0-29.6) | 16 (2.8-32) | 10 (1.2-33.5) | 12 (3.4-29.9) |
| Filicales Monolete | 3 (0.2-10.4) | 2 (0-16.8) | 0.5 (0-1.5) | 5 (0-15.3) | 5 (0-9.3) |
| TREES | 82 (69.5-88.9) | 44 (9.4-75.3) | 51 (13.7-82.8) | 37 (12.3-59.5) | 43 (41-50.9) |
| SHRUBS | 3 (0.8-9) | 14 (1-34.7) | 8 (0.6-21.1) | 5 (0.6-11.7) | 9 (1.7-18.1) |
| HERBS | 15 (10.4-21.6) | 42 (20.2-84.3) | 41 (13.2-82.4) | 58 (40.6-89.7) | 48 (45-56.7) |
| HYDRO-HYGROPHILOUS | 16 (12.1-21.8) | 13 (0-22.7) | 24 (11.3-42.8) | 16 (4.7-38.8) | 23 (14.1-31.1) |
| NPPs | 1 (0-3.4) | 6 (0-21.3) | 3 (0-9.7) | 1 (0-2) | 4 (0-23.2) |

### LPAZ LIE-1 (8865-7750 cm)

Starting with the arboreal pollen, in the lowermost LPAZ the abundance of this group makes it also the dominant one (74.9 - 95.4%) (Fig. R.1). Accordingly, there are three taxa with the greatest presence: *Abies alba* (17.3 - 48.6%), *Pinus pinaster* (8.7 - 27.6%) and *Pinus sylvestris* type (5.3 - 26%). Other taxa with a notorious presence have also been identified, such as *Betula* (1 - 22.6%), deciduous *Quercus* (0.7 - 4.4%) and *Fagus sylvatica* (0.4 - 16.8%). With scattered presence, percentages of less than 3.5% have also been identified in several taxa: *Alnus*, *Carpinus betulus* type, *Castaneae* and evergreen *Quercus*.

In the same Figure R.1, we can see that the percentage of shrubs is much lower (2 - 21.9%). The most dominant taxon is *Calluna vulgaris* (0.4 - 10.9%). *Arbutus* type, *Erica* type and *Prunus* type have been identified below 6% individually.

Among herbs (1.9 - 12.4%), the percentages are even lower (Fig. R.2). The taxon with the highest percentage is Poaceae (0.4 - 5.6%), followed by *Polygonum amphibium* (0 - 5%). The remaining taxa identified (Apiaceae, Cardueae, Caryophyllaceae, Chenopodiaceae, Cichorioideae, *Dipsacus fullonum* and *Polygonum aviculare*) do not exceed 2% each.

Regarding hydro-hygrophilous taxa, the percentages of these range from 1.1 to 13.7% (Fig. R.3). Four taxa have been identified, with Filicales Monolete (0.2 - 10.9%) standing out. Cyperaceae, Filicales Monolete and *Myriophyllum* do not exceed 5% each.

To conclude with the first LPAZ at Liendo, non-pollen palynomorphs (NPPs) are hardly present (0 - 0.7%). *Gelanispora* cf. *reticulispora* and *Sordaria* sp. have been identified with percentages below 1% each.

### LPAZ LIE-2 (7750 - 6650 cm)

The arboreal pollen in this LPAZ experiences a considerable decrease (39.2 - 57.4%) (Fig. R.1). In fact, there is also a change in the predominance of individual taxa, with *Alnus* (5.2 - 21.2%) becoming the dominant taxon followed by *Pinus pinaster* (9.7 - 15.3%) and *Betula* (2.4 - 12.3%). Secondarily, we found taxa such as deciduous *Quercus* (5.7 - 8.7%) or *Pinus sylvestris* type (4.2 - 6.2%). *Abies alba*, which was the dominant taxon in LIE-1, now does not exceed 1%.

However, shrubs experienced an increase (18 - 38.2%) (Fig. R.1). This is especially noticeable in the percentages of *Calluna vulgaris* (15.3 - 34.8%), because the rest of the taxa identified, which are the same as in the previous LPAZ, do not exceed 3% individually.

Herbaceous pollen also increases (22.7 - 24.6%) (Fig. R.2). This is reflected in higher percentage values individually, as in the case of the dominant taxon Poaceae (15.9 - 17.2%). The following taxa have also been identified: Apiaceae, *Artemisia*, *Aster* type, Cardueae, *Centaurea nigra* type, Cichorioideae, *Dipsacus fullonum*, *Plantago lanceolata* type and *Polygonum aviculare*. All of them below 4% each.

The presence of aquatic taxa (hydro-hygrophilous) also increases (24.1 - 24.3%) (Fig. R.3). But in this case, it is the taxon Cyperaceae (15.8 - 20.6%) that dominates, followed by Filicales Monolete (1.8 - 5.3%). The taxa Filicales Trilete, *Myriophyllum* and *Pteridium aquilinum* do not exceed 3% each.

Non-pollen palynomorphs (NPPs) (0 - 0.6%) hardly change in overall percentages with regard to the previous LPAZ (Fig. R.3). In terms of taxa, we have identified *Pseudoschizaea circula* and *Sordaria* sp.

### LPAZ LIE-3 (6650 - 5385 cm)

In LIE-3 the arboreal pollen increases again, predominating over the rest of the vegetation with high percentages (73.7 - 95.9%) (Fig. R.1). *Alnus* (0.8 - 50.5%) continues to be the most predominant taxon, although very similar to *Abies alba* (0 - 48.9%), which again reaches high values. *Betula* (4.5 - 37.4%), deciduous *Quercus* (0.4 - 20.6%) and *Pinus pinaster* (3.3 - 29%) also stand out. *Pinus sylvestris* type (0 - 14.6%), *Carpinus betulus* type (0 - 8%) and *Corylus* (0.6 - 4.9%) are also present. The following taxa have also been identified in percentages below 2%: evergreen *Quercus*, *Fagus sylvatica*, *Fraxinus*, *Salix* and *Tilia*.

Shrub pollen experiences a decrease (2.3 - 10%) with respect to LIE-2 (Fig. R.1). The taxon with the highest percentage continues to be *Calluna vulgaris* (1.3 - 4.5%). The remaining taxa are the same as those identified previously but individually these do not exceed 3.5%.

Herbaceous pollen decreases (1.6 - 16.3%) (Fig. R.2). Poaceae continues to be the predominant taxon (0.8 - 11.6%). Except for Apiaceae, which reaches ranges between 0.4 - 4.2%, the remaining taxa (*Artemisia*, *Aster* type, Cardueae, *Centaurea nigra* type, Cichorioideae, *Dipsacus fullonum*, *Plantago lanceolata* type and *Polygonum aviculare*) do not exceed 2% each.

Figure R.3 shows how hydro-hygrophilous vegetation increases (11.7 - 42.1%). In fact, this growth is much more noticeable in the case of Filicales Monolete, which reaches percentages between 1.2 and 35.4%. Cyperaceae (1.2 - 9.8%) and *Myriophyllum* (0.2 - 6.1%) also have a notable presence.

On the same Figure R.3, we can observe the percentages of NPPs (0 - 0.8%), which continue to be very similar to those already noticed in the previous LPAZ at Liendo. Only 2 taxa, *Gelanispora* cf. *reticulispora* and *Sordaria* sp. have been identified, each of them below 1%.

### LPAZ LIE-4 (5385 - 3580 cm)

The tree pollen in LIE-4 shows an increasing trend, where the overall percentage values range from 21.7 to 89.8% (Fig. R.1). Although the maximum values are similar to those observed in the previous pollen zone, a first section of this LPAZ has been identified with values considerably lower than those previously detected. In terms of taxa, *Pinus pinaster* (3.5 - 53.7%) is dominant, followed by *Betula* (0.4 - 45%). In second place we can find: deciduous *Quercus* (3.6 - 17.9%), *Abies alba* (0 - 12.9%) and *Pinus sylvestris* type (1.3 - 12.4%). The rest of the taxa individually barely exceed 2.5%.

The shrub pollen for this LPAZ shows an increase compared with the values observed in LIE-3 (0.8 - 39.6%) (Fig. R.1). The taxon with the highest predominance continues to be *Calluna vulgaris* (0 - 33%). *Arbutus* type would be the taxon with the second highest presence (0 - 4.8%). The rest of the identified taxa (*Cistus* type, *Erica* type, Labiatae and *Prunus* type) do not exceed 2% each.

The increasing trend observed in arboreal pollen is the opposite for herbaceous vegetation, which starts with higher values and ends up decreasing in this LPAZ (9.4 - 72.9%) (Fig. R.2). The dominant herbaceous taxon here is Apiaceae (1.5 - 66.8%). It is followed by Poaceae (2 - 20%) and Cichorioideae (0 - 7.8%). The remaining taxa identified are the same as above and do not surpass 3% in each case.

As for hydro-hygrophilous pollen, the trend is similar to that observed in LIE-3 (18.8 - 43%) (Fig. R.3). The two taxa with the highest abundance are *Myriophyllum* (0.7 - 33.5%) and Cyperaceae (3.8 - 26.4%).

Non-pollen palynomorphs (NPPs) continue with similar values to those observed previously, but this time they exceed 1% in overall percentages for the first time (Fig. R.3). In terms of taxa, the one with the highest presence is *Sordaria* sp. which ranges from 0 to 0.7%.

### LPAZ LIE-5 (3580 - 1790 cm)

Arboreal pollen in this LPAZ continues to reflect the dominant vegetation (43.3 - 83.5%), although there are some moments when herbaceous vegetation seems to slightly outnumber arboreal vegetation (Fig. R.1). *Pinus pinaster* is the most abundant taxon in LPAZ-5 (9 - 59.5%). In second place is deciduous *Quercus* (1 - 31%) and, in third place, *Pinus sylvestris* type (1.1 - 15%).

Figure R.1 shows how shrub pollen is slightly reduced with respect to LIE-4 but, nevertheless, its minimum values are above those previously observed (5.6 - 23.8%). *Calluna vulgaris* is once again the dominant herbaceous species (2.6 - 21.6%).

As mentioned above, herbaceous pollen appears in lower percentages than tree vegetation except in some samples where it slightly exceeds the latter in overall percentages (10.4 - 51%) (Fig. R.2). The two taxa with the highest presence are Cichorioideae (0.4 - 28.5%) and Poaceae (8.3 - 15.9%). The rest of taxa that have been identified correspond to those of previous LPAZ. None of these individually exceeds 2.5%.

The percentages of aquatic pollen (hydro-hygrophilous) are similar to those observed in LIE-4 (12.1 - 41.1%) (Fig. R.3). The presence of Filicales Trilete (0.1 - 36.5%) and Cyperaceae (3.4 - 20.9%) stands out. The following taxa have also been identified: *Myriophyllum* (0.5 - 6.1%) and Filicales Monolete (0.8 - 3.8%).

Non-pollen palynomorphs have not been detected in this LPAZ (Fig. R.3).

### LPAZ LIE-6 (1790 - 690 cm)

The arboreal pollen shows an increase in the overall percentages, especially in its minimum values (94.1 - 96%) (Fig. R.1). Again, the dominant species is *Abies alba* (0.6 - 65.3%). In second place we find deciduous *Quercus* (6.2 - 44.4%). *Pinus pinaster* has also been identified in remarkable percentages (10.6 - 28.1%). *Carpinus betulus* type (0.4 - 8.5%), *Pinus sylvestris* type (4.8 - 7.4%) and *Betula* (2.8 - 5.3%) have also been identified.

The shrub-type vegetation experienced a decrease (0.4 - 2.6%) (Fig. R.1) with *Erica* type as the predominant taxon (0.2 - 1.2%).

Herbaceous pollen also experienced a decrease, in this case quite noticeably (3.4 - 3.6%) (Fig. R.2). The taxa with the greatest presence are Poaceae (1.2 - 1.8%) and *Polygonum aviculare* (0 - 1.8%).

As for hydro-hygrophilous, the overall percentages decrease to between 24 and 27.3% (Fig. R.3). The taxa identified were Filicales Monolete (7.2 - 13.9%), Filicales Trilete (0.1 - 7.1%), *Myriophyllum* (4.8 - 6.6%), *Pteridium aquilinum* (0 - 4.9%) and Cyperaceae (3.2 - 3.6%).

Non-pollen palynomorphs (NPPs) reappear, sparsely, with percentages between 0.2 and 0.4% (Fig. R.3). The only taxon identified was *Sordaria* sp.

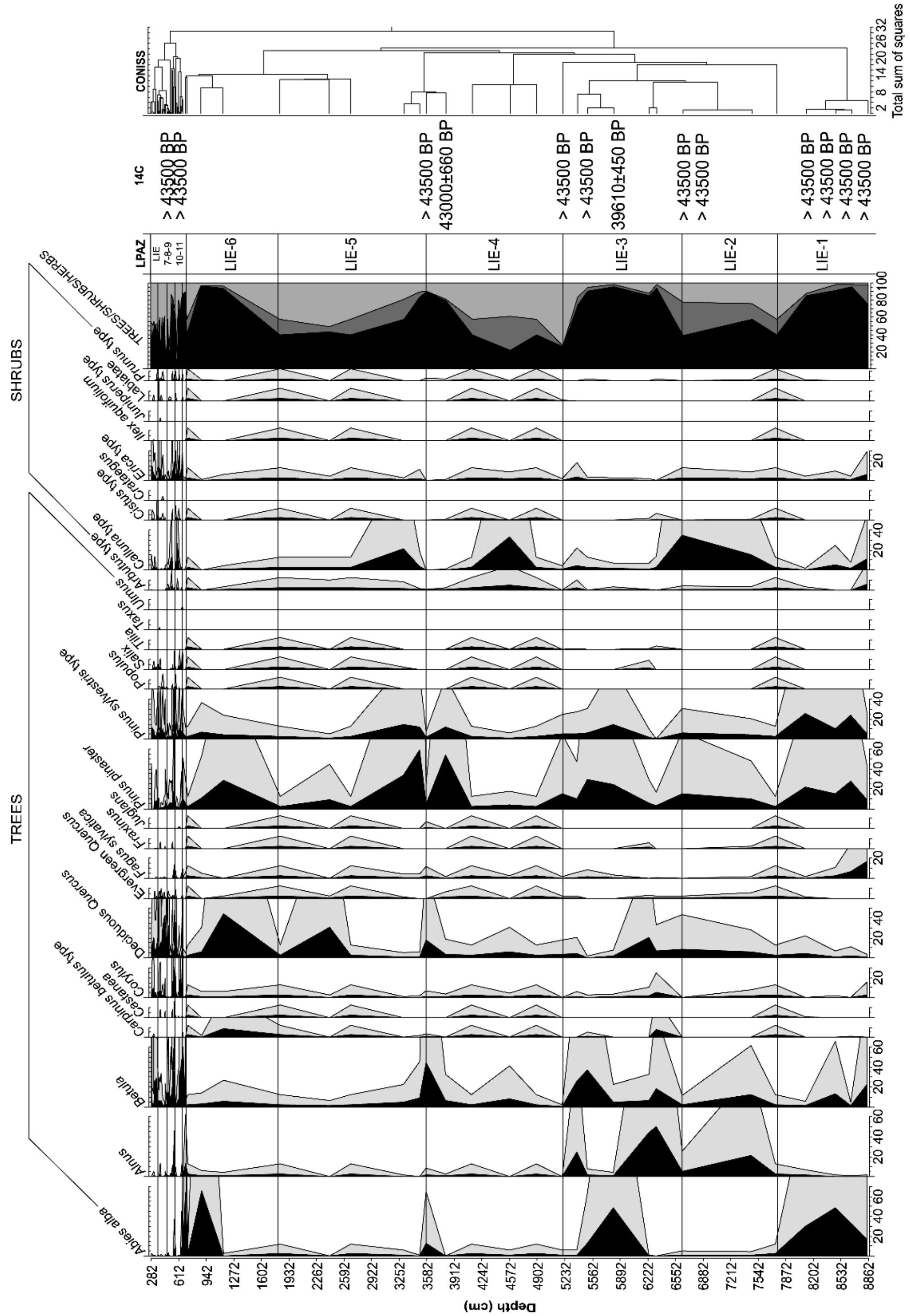


**Figure R.1 -** Pollen diagram corresponding to the arboreal and shrub vegetation along the Liendo borehole. Depth at centimeter scale, the evolution of arboreal and shrub taxa, the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

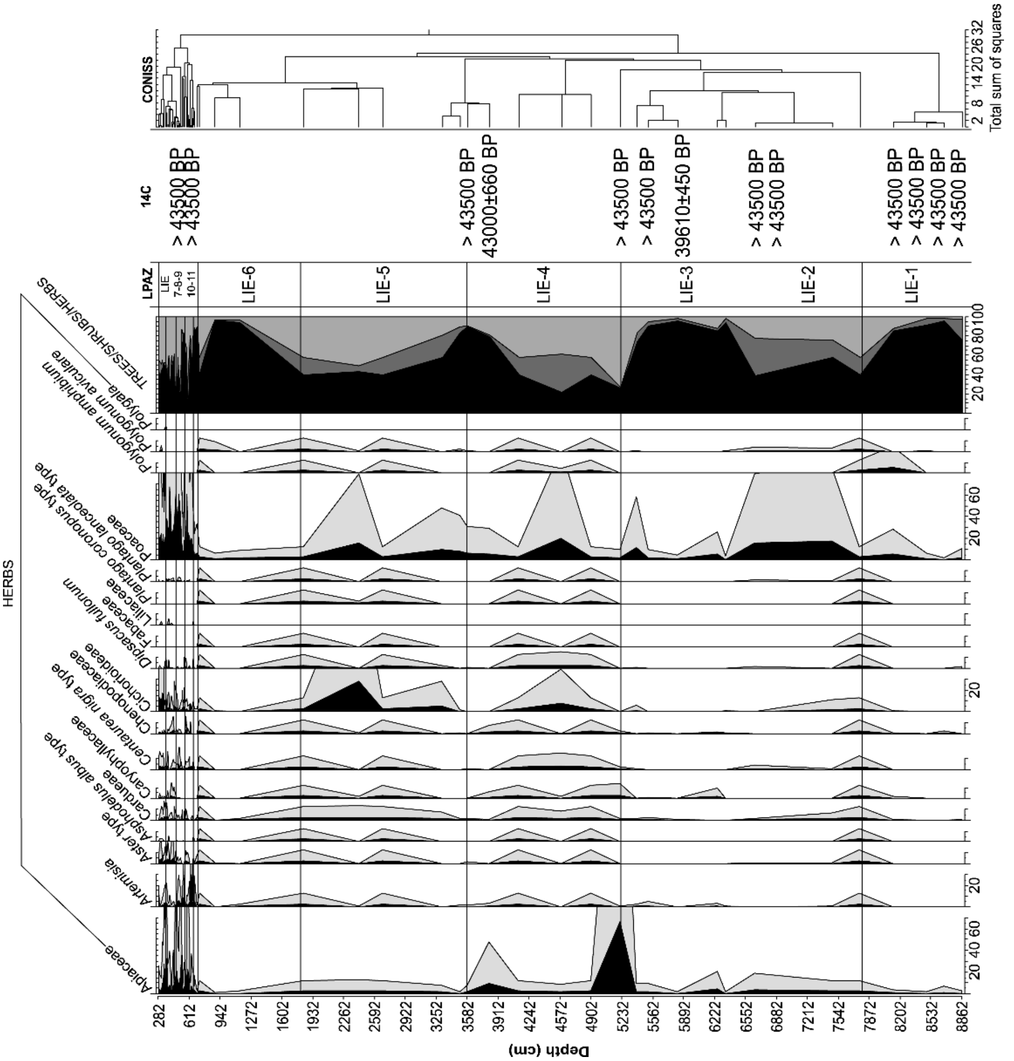


**Figure R.2** - Pollen diagram corresponding to the herbaceous vegetation along the Liendo borehole. Depth at centimeter scale, the evolution of herbaceous taxa, the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

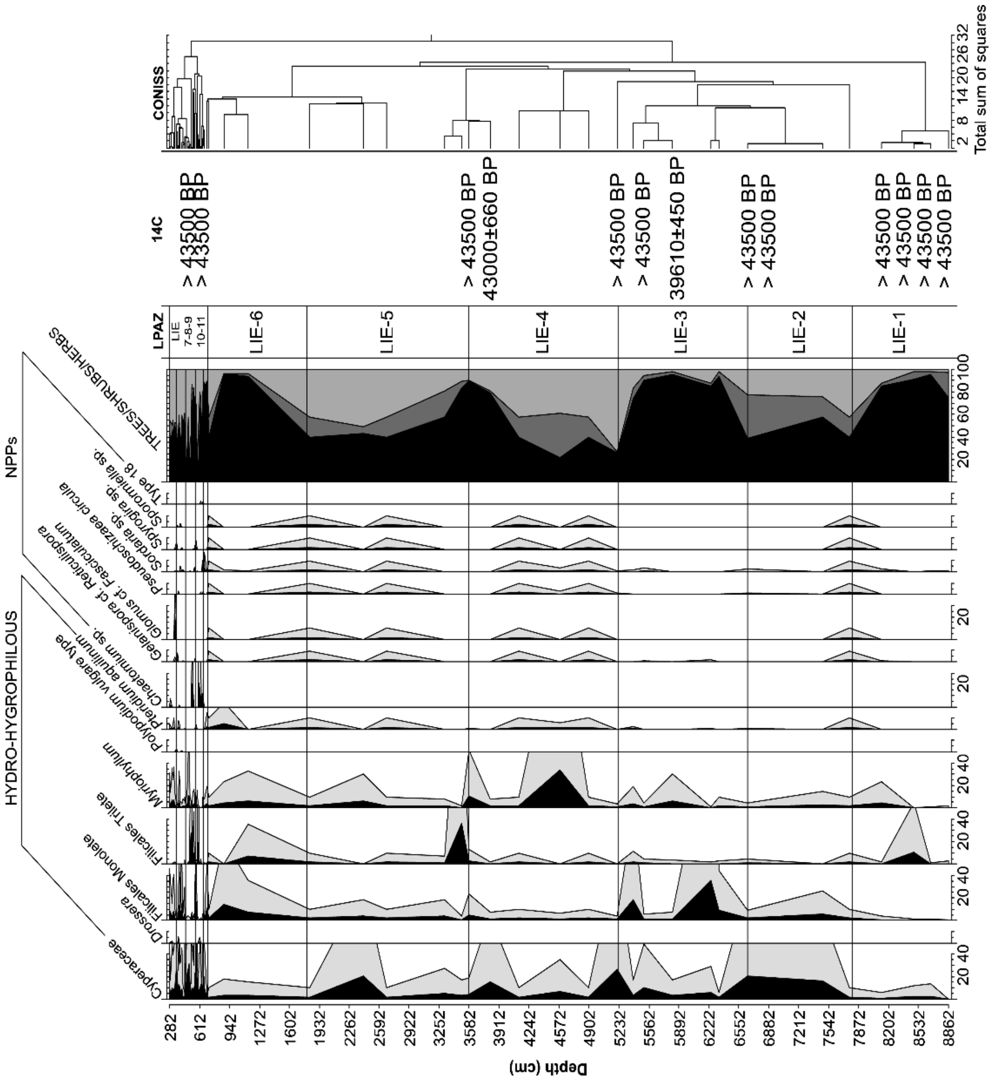


**Figure R.3** - Pollen diagram corresponding to the hydro-hygrophilous vegetation and the non-pollen palynomorphs (NPPs) along the Liendo borehole. Depth at centimeter scale, the evolution of hydro-hygrophilous and NPPs taxa, the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

### LPAZ LIE-7 (690-649 cm)

Regarding arboreal pollen, we can observe in the general percentages (69.5 - 88.9%) that it is the predominant vegetation type (Fig. R.4). This is a LPAZ with alternating dominance between two different taxa: *Abies alba* (2 - 64.3%) and *Betula* (1.3 - 59.7%). Other taxa have also been identified in significant percentages: *Alnus* (0 - 12.5%), *Corylus* (0.2 - 22.3%), deciduous *Quercus* (1 - 12%), *Pinus pinaster* (0 - 10%) and *Pinus sylvestris* type (2.5 - 16%). Other minor taxa, below 4%, are present: *Carpinus betulus* type, *Castanea*, evergreen *Quercus*, *Fagus sylvatica*, *Salix* and *Ulmus*.

Shrub pollen (0.8 - 9%) is much less abundant than tree pollen (Fig. R.4). *Calluna vulgaris*, *Erica* type, *Labiatae* and *Prunus* type taxa have been identified. *Erica* type has the highest presence, with percentages between 0.8 and 7.4%.

Herbaceous taxa are more abundant (10.4 - 21.6%) (Fig. R.5). The presence of Apiaceae (0.6 - 3.8%), *Artemisia* (0.6 - 5.9%) and Poaceae (4.8 - 8.8%) is noteworthy. In percentages below 2%, the following taxa have been identified: *Aster* type, *Asphordelus albus* type, *Centaurea nigra* type, *Cichorioideae*, *Dipsacus fullonum* and Liliaceae.

The presence of hydro-hygrophilous vegetation is also notorious (12.1 -21.8%) (Fig. R.6). Five taxa have been identified: Cyperaceae, Filicales Monolete, Filicales Trilete, *Myriophyllum* and *Pteridium aquilinum*. The presence of Cyperaceae (0.6 - 19.5%) and Filicales Monolete (0.2 - 10.4%) stands out.

Finally, three non-pollen palynomorphs (NPPs) have been identified for this zone: *Chaetomium*, *Pseudoschizaea circula* and *Sordaria* sp. Their overall percentages are between 0 and 3.4% (Fig. R.6).

### LPAZ LIE-8 (649-572 cm)

In general terms, arboreal pollen continues to be dominant (9.4 - 75.3%) (Fig. R.4). Unlike the previous zone, the most predominant taxon is *Betula* (6 - 47.2%) although there is also a significant increase in deciduous *Quercus* (0.2 - 6.5%). *Corylus* (0.2% - 18.1%) and *Pinus sylvestris* type (0.7 - 13.7%) maintain a significant presence. Genera *Juglans* and *Populus* are identified for the first time. *Carpinus betulus* type, evergreen *Quercus* and *Ulmus* taxa are not present in LPAZ LIE-8.

One of the major differences with the previous LPAZ LIE-7 is precisely the increase in the percentage of shrub pollen (1 - 34.7%) (Fig. R.4) which, in some samples, exceed the tree percentages. The taxa with the highest presence are *Calluna vulgaris* (0.3 - 26.1%) and *Erica* type (0 - 24.4%).

A similar pattern occurs with herbaceous pollen, which becomes predominant in some samples of this pollen zone. The total percentages range from 20.2 to 58.3% (Fig. R.5). The distribution of taxa remains similar to the previous one, except that the dominant Apiaceae (2 - 22.5%), *Artemisia* (0 - 29.6%) and Poaceae (13.8 - 25.5%) greatly increase here their values. The family Chenopodiaceae is also identified for the first time.

Figure R.6 shows that the percentages of hydro-hygrophilous pollen are similar to those previously observed (0 - 21%). However, the taxon with the highest presence is now Filicales Trilete (0 - 18.9%), followed by Cyperaceae (0 - 13.1%). *Pteridium aquilinum* appears for the first time.

In the same Figure R.6, the percentages observed for non-pollen palynomorphs are higher (0 - 21.3%). Especially notable is the presence of *Chaetomium* sp. (0 - 21.3%).

### LPAZ LIE-9 (572-475 cm)

The values of tree pollen reach here percentages between 13.7 and 82.8% (Fig. R.4). *Betula* continues to be dominant also in this pollen zone (0.8 - 58%). The presence of *Corylus* (0 - 16.3%), deciduous *Quercus* (2.3 - 32.4%), *Pinus pinaster* (0 - 17.3%) and *Pinus sylvestris* type (0.8 - 28.5%) is also relevant. With smaller percentages, the presence of *Alnus* (0 - 9.1%) and *Abies alba* (0 - 7.4%) is also noteworthy.

Shrub pollen begins to decrease (0.6 - 21%) (Fig. R.4). *Calluna vulgaris*, the predominant taxon, (0 - 13.3%) and *Erica* type (0 - 10.2%) predominate.

Herbaceous pollen experiences a significant increase, with total percentages ranging from 13.2 to 82.4% (Fig. R.5). The dominance of Poaceae (4.3 - 60.7%) is now significantly higher, followed by Apiaceae (0 - 35%). *Artemisia* (0 - 8.5%), meanwhile, would be the taxon with the third highest presence. The remaining taxa (*Aster* type, *Asphodelus albus* type, Cardueae, Caryophyllaceae, *Centaurea nigra* type, Chenopodiaceae, Cichorioideae, *Dipsacus fullonum* and *Plantago lanceolata* type) do not exceed 4%.

The hydro-hygrophilous taxa experienced a noteworthy increase (11.3 - 42.8%) (Fig. R.6). Cyperaceae (6 - 27.2%), Filicales Trilete (0 - 27.9%) and *Myriophyllum* (0% - 10.2%) are the most abundant taxa.

The non-pollen palynomorphs (NPPs), however, maintain the trend observed in the previous pollen zone (0 - 20%) (Fig. R.6). *Chaetomium* sp. remains the most remarkable taxon (0 - 20%).

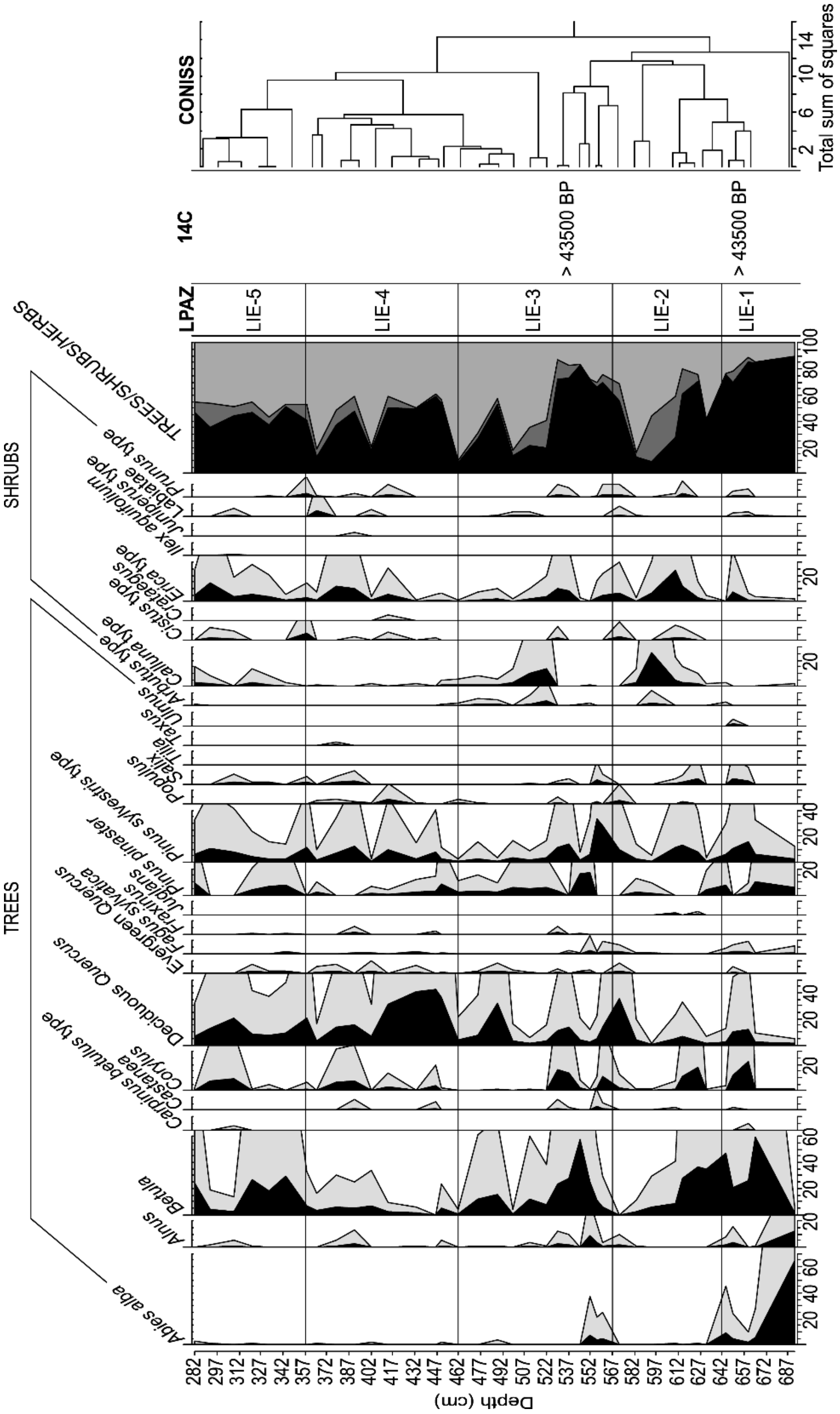


**Figure R.4 -** Pollen diagram corresponding to the arboreal and shrub vegetation along the uppermost section (final 691 cm, higher resolution analysis) of the Liendo borehole. Depth at centimeter scale, the evolution of arboreal and shrub taxa, the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

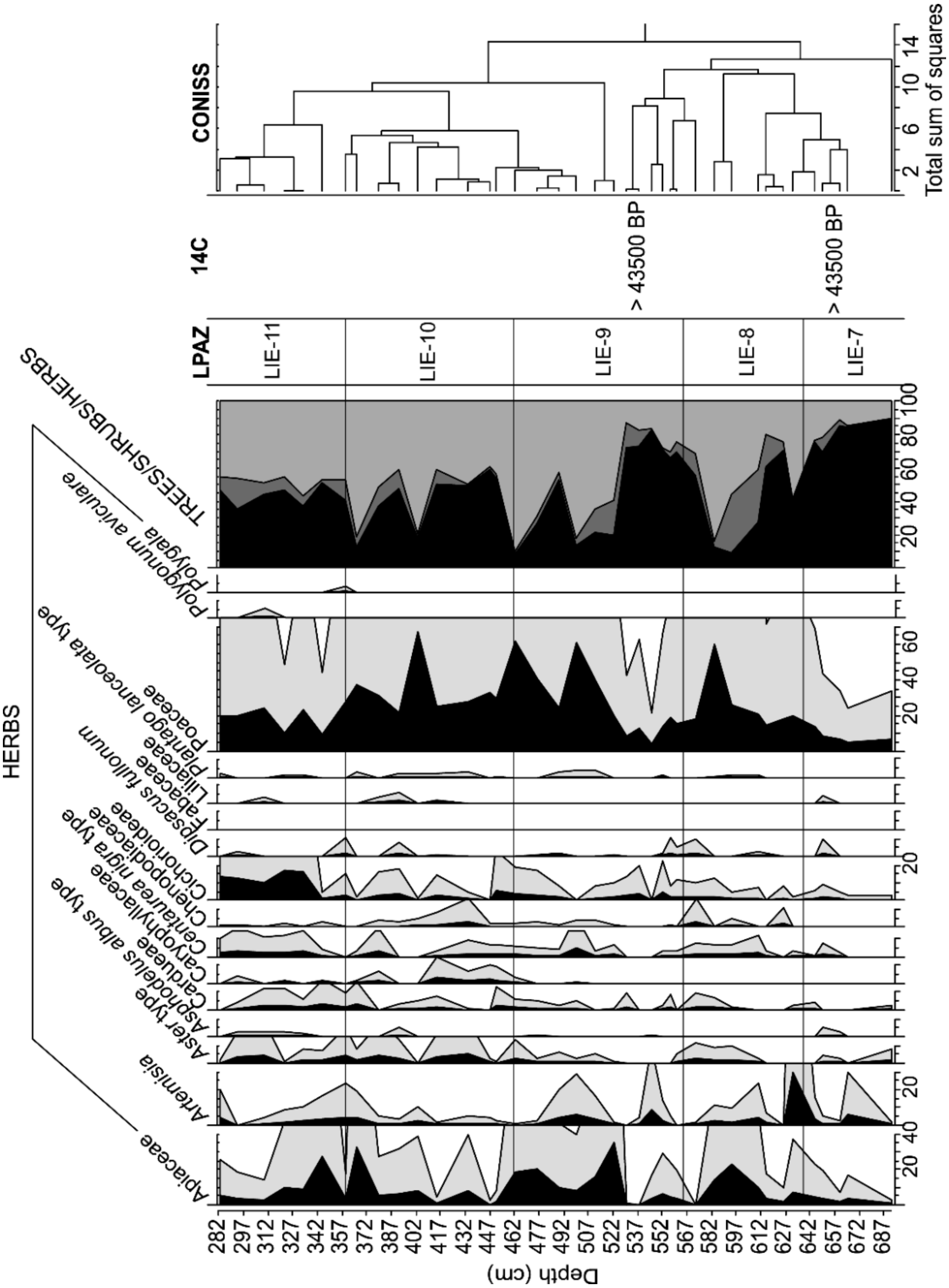


**Figure R.5** - Pollen diagram corresponding to the herbaceous vegetation along the uppermost section (final 691 cm, higher resolution analysis) of the Liendo borehole. Depth at centimeter scale, the evolution of herbaceous taxa, the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

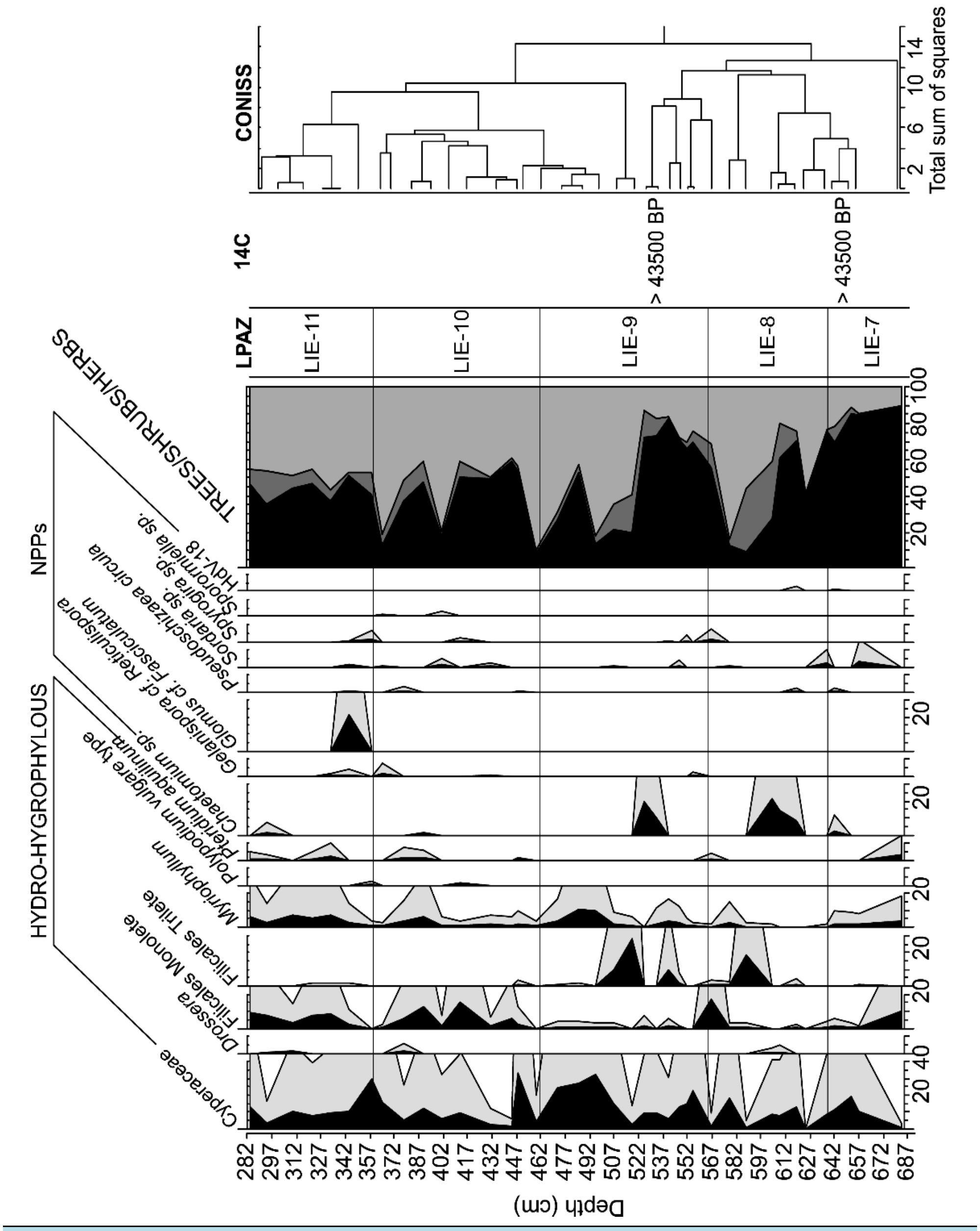


**Figure R.6** - Pollen diagram corresponding to the hydro-hygrophilous vegetation and the non-pollen palynomorphs (NPPs) along the uppermost section (final 691 cm, higher resolution analysis) of the Liendo borehole. Depth at centimeter scale, the evolution of hydro-hygrophilous and NPPs taxa, the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

## LPAZ LIE-10 (475-365 cm)

In general, arboreal pollen decreases (12.3 - 47.9%) in this zone (Fig. R.4). Indeed, deciduous *Quercus* is now the taxon with the highest presence (3.3 - 15%) followed by *Pinus sylvestris* type (1.9 - 12.5%). *Betula* (3.3 - 6%) and *Corylus* (0 - 7%) would be the secondary taxa. In addition, genera *Fraxinus* and *Taxus* are identified for the first time.

The presence of shrub pollen is also reduced (6.7 - 11.7%) (Fig. R.4). *Erica* type still being the dominant taxon (1.5 - 11.7%). Labiatae, which was not identified in the previous pollen zone, reappears and reaches 4.8%. *Crataegus* (0 - 0.9%) has been identified here for the first time.

Herbaceous pollen is, for the first time, predominant throughout this zone. Its percentages range from 40.6 to 89.7% (Fig. R.5). Apiaceae (0.5 - 32.9%) and Poaceae (21.5 - 67.5%) are the families with the highest presence, since the rest of the taxa identified (*Artemisia*, *Aster* type, *Asphodelus albus* type, Cardueae, Caryophyllaceae, *Centaurea nigra* type, Chenopodiaceae, Cichorioideae, *Dipsacus fullonum*, Liliaceae and *Plantago lanceolata* type) do not exceed 4.5% each.

As for hydro-hygrophilous taxa, the percentages in this pollen zone range from 4.7 to 38.3% (Fig. R.6). The presence of Cyperaceae and Filicales Monolete stand out. *Drossera* appears for the first time.

Non-pollen palynomorphs (NPPs) show lower values than those previously observed with percentages between 0 and 2% (Fig. R.6). *Chaetomium* sp., *Gelanispora* cf. *reticulispora*, *Pseudoschizaea circula*, *Sordaria* sp., *Spyrogira* sp. and *Sporormiella* sp. have been identified.

## LPAZ LIE-11 (365-282 cm)

In the final pollen zone of the Liendo borehole, we observe that the arboreal pollen stabilizes, maintaining percentages similar to those observed in LPAZ LIE-10 (35.5 - 50.9%) (Fig. R.4). Again, the dominance is reversed and *Betula* (3.9 - 29.7%) becomes the most abundant genus above deciduous *Quercus* (6.5 - 20.9%) although with relatively even percentages. The presence of *Corylus* (0 - 9.2%), *Pinus pinaster* (0 - 9.1%) and *Pinus sylvestris* type (4.7 - 11.2%) is maintained in significant percentages.

In Figure R.4 a new increase can be observed in the shrub pollen (1.7 - 18%). While this increase is not great, it is enough to highlight that *Erica* type, which stabilizes along this pollen zone, has percentages between 1.1 and 14.4%. The remaining taxa, *Arbutus* type, *Calluna vulgaris*, *Cistus* type, *Erica* type, *Ilex aquifolium*, Labiatae and *Prunus* type barely reach 2.5% each.

As for herbaceous taxa, in this last pollen zone, the analysis shows a decrease in their total percentages, although their presence continues to be quite relevant (45 - 46.7%) (Fig. R.5). Very similar percentages of both Apiaceae (2.8 - 27.7%) and Poaceae (9.8 - 27.4%) have been identified, the latter showing a little more regularity.

The trend of hydro-hygrophilous taxa persists (14 - 31%) (Fig. R.6). Cyperaceae (3.4 - 29.9%), Filicales Monolete (0 - 9.3%) and *Myriophyllum* (0.8 - 7.3%) continue to be the most relevant taxa.

The presence of non-pollen palynomorphs (NPPs) increases with respect to the previous zone (0 - 23.2%) (Fig. R.6). The following taxa have been identified: *Chaetomium* sp., *Gelanispora* cf. *reticulispora*, *Glomus* cf. *fasciculatum*, *Pseudoschizaea circula*, *Sordaria* sp. and *Spyrogira* sp. where *Glomus* cf. *fasciculatum* is the most prominent species (0 - 21.9%).

### 1.1.2. Geochronology

A total of 13 samples (from 8865 to 582 cm) were sent to Beta Analytic for dating by Accelerator Mass Spectrometry (AMS) analysis. All the ages obtained were older than 43,500 cal. years BP, falling outside the resolution of this radiocarbon dating method (Table R.3). Two samples provided more specific dates, 47,679 - 45,015 cal. years BP at 3810 cm and 44,167 - 42,630 cal. years BP at 5820 cm depth. These dates were obtained at 94% probability but are also at the very limit of the temporal resolution of the radiocarbon dating. Therefore, this indicates that we were dealing with a Pleistocene deposit which, in future studies, should be dated using other methodologies (e.g., cosmogenic isotopes or optically stimulated luminescence) that were not available for this study.

**Table R.3** - Radiocarbon results from the Liendo borehole.

| LAB CODE | SAMPLE | MATERIAL | METHOD | DEPTH (cm) | CONVENTIONAL AGE (years BP) | CALIBRATED AGE (cal. years BP) |
|---|---|---|---|---|---|---|
| Beta - 524498 | LIE-545 | Plant | AMS-Standard delivery | 203 | > 43,500 | |
| Beta - 524499 | LIE-650 | Plant | AMS-Standard delivery | 206 | > 43,500 | |
| Beta - 524500 | LIE-3500 | Plant | AMS-Standard delivery | 209 | > 43,500 | |
| Beta - 524501 | LIE-3810 | Plant | AMS-Standard delivery | 3810 | 43,000 ± 660 | 47,679 – 45,015 |
| Beta - 524502 | LIE-5210 | Plant | AMS-Standard delivery | 5210 | > 43,500 | |
| Beta - 524503 | LIE-5510 | Plant | AMS-Standard delivery | 5510 | > 43,500 | |
| Beta - 524504 | LIE-5820 | Plant | AMS-Standard delivery | 5820 | 39,610 ± 450 | 44,167 – 42,630 |
| Beta - 524505 | LIE-6650 | Plant | AMS-Standard delivery | 6650 | > 43,500 | |
| Beta - 524506 | LIE-6950 | Plant | AMS-Standard delivery | 6950 | > 43,500 | |
| Beta - 524507 | LIE-8130 | Plant | AMS-Standard delivery | 8130 | > 43,500 | |
| Beta - 524508 | LIE-8485 | Plant | AMS-Standard delivery | 8485 | > 43,500 | |
| Beta - 524509 | LIE-8670 | Plant | AMS-Standard delivery | 8670 | > 43,500 | |
| Beta - 524510 | LIE-8865 | Plant | AMS-Standard delivery | 8865 | > 43,500 | |

### 1.1.3. Paleoclimate reconstruction

A quantitative paleoclimate reconstruction has been carried out for the Liendo borehole. The reliability of the reconstructions was assessed using the WA-PLS-based transfer function model under cross-validation. A total of 389 harmonized pollen taxa were used in order to perform the quantitative reconstruction. The reconstruction was based on two components, firstly the annual mean temperature (TANN) and secondly the annual mean precipitation (PANN). Both components show an $R^2$ (coefficient of determination) of 0.80 and 0.50 respectively. The root-mean square error of prediction (RMSEP) shows values of 3.24 ºC/yr and 284.47 mm/yr. In addition, the maximum bias present values of 7.58 ºC/yr and 2318.7 mm/yr respectively.

Temperatures range between 2 - 14 ºC/yr and average annual precipitation ranges between 536 - 1213 mm/yr (Fig. R.7) with the greater oscillations in both parameters located below the 500 cm depth. Due to the lack of precise radiocarbon dates, the quantitative model is based on depth.

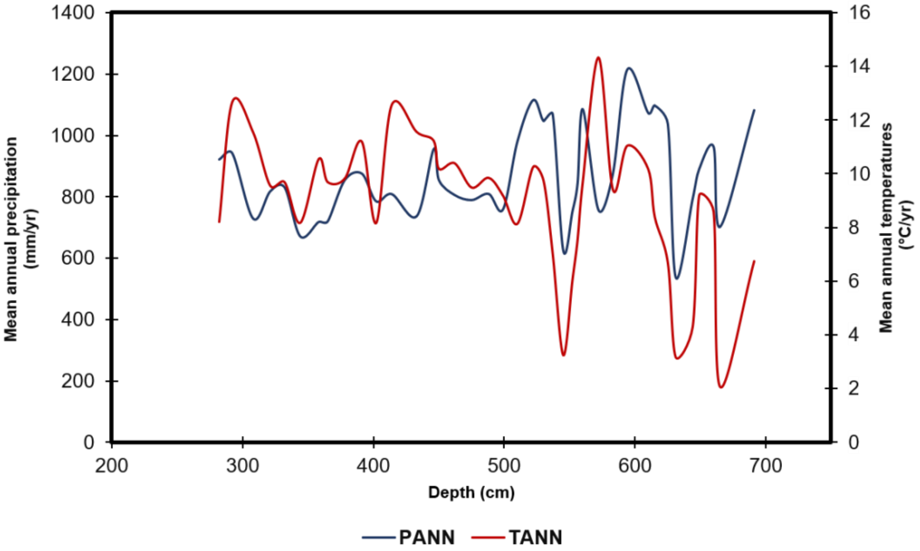


**Figure R.7** - Quantitative paleoclimate reconstruction for the final 700 cm (higher resolution analysis) of the Liendo borehole. In red, the evolution of the mean annual temperature. In blue, the evolution of the mean annual precipitation.

# 2. Holocene

## 2.1. Requejada

### 2.1.1. Pollen analysis

In the Requejada borehole, and thanks to the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) method, four local pollen assemblage zones (LPAZ RE) have been differentiated.

**Table R.4 -** Summary of the most representative taxa identified in Requejada. The single value represents the average and those in parentheses give the range. The percentages of hydro-hygrophilous taxa and NPPs are calculated separately together with the rest of the taxa.

| | RE - 1 | RE - 2 | RE - 3 | RE - 4 |
|---|---|---|---|---|
| *Alnus* | 0 (0 - 0.2) | 0 (0 - 1) | 27 (17,1 - 32,5) | 27 (18,1 - 30,1) |
| *Betula* | 32 (24.7- 45.5) | 29 (18.4 - 40.3) | 11 (7,4 - 16,2) | 7 (3,1 - 11,7) |
| *Corylus* | 17 (13.3 - 24.7) | 18 (12.8 - 24.2) | 8 (5,6 - 14,4) | 5 (0,8 - 10,4) |
| *Eucalyptus* sp. | 0 (0 - 0) | 0 (0 - 0) | 0 (0 - 0,6) | 1 (0 - 5,1) |
| deciduous *Quercus* | 16 (12 - 18.9) | 20 (13.3 - 25.9) | 31 (25 - 42,4) | 26 (15,4 - 37,2) |
| *Pinus pinaster* | 19 (9.6 - 29) | 19 (10.9 - 26.5) | 3 (1,4 - 4,3) | 4 (0,8 - 5,9) |
| *Cerealia* type | 0 (0 - 0) | 0 (0 - 0) | 0.1 (0 - 0,2) | 0.2 (0 - 0,8) |
| Poaceae | 10 (3.2 - 30.7) | 4 (1.4 - 7.6) | 6 (4,6 - 8,7) | 12 (5,4 - 27,6) |
| Cyperaceae | 3 (0.5 - 6.2) | 4 (1.3 - 7.2) | 5 (3,2 - 5,9) | 9 (7,2 - 12,1) |
| Filicales Monolete | 17 (8.8 - 24.4) | 15 (7 - 21.5) | 10 (5,2 - 19,2) | 8 (1,6 - 12,3) |
| *Sordaria* sp. | 2 (1.6 - 4) | 2 (1.2 - 3.9) | 2 (0,9 - 3,9) | 4 (2,5 - 7,2) |
| TREES | 88 (67.6 - 95.2) | 93 (88.6 - 96.7) | 88 (82,2 - 92) | 79 (59,8 - 88,3) |
| SHRUBS | 1 (0.4 - 2.2) | 1 (0.4 - 2) | 2 (0,6 - 3,2) | 1 (0,6 - 2,3) |
| HERBS | 11 (4 - 31.8) | 6 (2.9 - 9.6) | 10 (6 - 14,8) | 20 (9,4 - 39,4) |
| HYDRO-HYGROPHILOUS | 34 (21 - 47.2) | 40 (32.3 - 51) | 30 (23 - 56,6) | 45 (26,8 - 58,4) |
| NPPs | 3 (2.3 - 5.1) | 3 (1.7 - 5.2) | 4 (1,8 - 5,6) | 6 (3,7 - 8,6) |

### LPAZ RE-1 (1542 - 1212 cm) (>7980±30 yr BP)

In this initial pollen zone, 6 samples (at 1592, 1572, 1482, 1452, 1422 and 1302 cm depth) have been found sterile (without pollen content) (Fig. R.4, R.5, R.6).

Arboreal pollen is abundant, a percentage that ranges from 67.7 to 95.2% of the total (Fig. R.8). *Betula* (24.7 - 45.5%), as the dominant taxon, together with *Corylus* (13.3 - 24.7%), deciduous *Quercus* (12 - 18.9%) and *Pinus pinaster* (9.6 - 23.3%) are the most abundant. The other taxa present (*Castanea*, evergreen *Quercus*, *Fagus sylvatica*, *Fraxinus*, *Pinus sylvestris* type, *Salix* and *Tilia*) barely exceed 3% each.

The presence of shrubs oscillates between 0.4 and 1.8% in this pollen zone. The most relevant taxa are *Arbutus* type, *Cistus* type, *Erica* type and *Prunus* type. None of them exceeds 2% throughout this zone (Fig. R.8).

Regarding herbaceous taxa, the relative abundances are between 4 and 31.8% (Fig. R.9). Poaceae (3.2 - 30.7%) is the dominant herbaceous family. The remaining taxa, Apiaceae, *Artemisia*, *Asphodelus albus* type, Cardueae, Chenopodiaceae, Cichorioideae and *Plantago lanceolata* type do not surpass 1% each.

Hydro-hygrophilous plants have an outstanding representation in this zone (Fig. R.10). The total percentages are between 21 - 41.7%. The taxon with the highest abundances is Filicales Monolete (10 - 24.4%). Cyperaceae (0.5 - 6.2%) and Filicales Trilete (0.3 - 4.1%) also have a notable presence.

The presence of non-pollen palynomorphs (NPPs) is scarce (2.3 - 5.1%), with the identification of *Chaetomium* sp. (0 - 0.5%), *Glomus* cf. *fasciculatum* (0 - 0.2%, *Pseudoschizaea circula* (0 - 0.7%), *Sordaria* sp. (1.6 - 4%), *Spirogyra* sp. (0 - 0.8%) and *Sporormiella* sp. (0 - 0,3%) (Fig. R.10).

### LPAZ RE-2 (1212 - 792 cm) (7810±30 - 7290±30 yr BP)

In the second pollen zone the dominance of arboreal pollen continues, increasing both its minimum and maximum percentages (88.6 - 96.7%) (Fig. R.8). Again, *Betula* (18.4 - 40.3%), *Corylus* (12.8 - 24.2%), deciduous *Quercus* (13.3 - 25.8%) and *Pinus pinaster* (10.9 - 26.1%) are the dominant taxa. Among the other tree taxa, *Pinus sylvestris* increased to over 5%, while *Castanea*, evergreen *Quercus*, *Fagus sylvatica*, *Fraxinus*, *Salix* and *Tilia* remained at values below 4% each.

Shrub taxa also maintain a trend similar to that previously observed in LPAZ RE-1 (0.4 - 2%). The taxa present, *Arbutus* type, *Cistus* type, *Erica* type and *Prunus* type still do not represent more than 2% each (Fig. R.8).

Furthermore, herbaceous plants decreased their overall percentages between 2.95 and 9.6% (Fig. R.9). This is due to the significant reduction in the abundance of the previous dominant family, Poaceae, which now has percentages between 1.4 and

7.6%. Apiaceae, *Artemisia*, *Asphodelus albus* type, Cardueae, Chenopodiaceae, Cichorioideae and *Plantago lanceolata* type do not exceed 2%. *Plantago coronopus* type, Caryophyllaceae and *Centaurea nigra* type have also been identified in low percentages.

In general, the presence of hydro-hygrophilous plants increases (33.5 - 51%) (Fig. R.10). The pollen with the highest representation continues to be Filicales Monolete (7 - 21.5%). The percentages of Cyperaceae (1.4 - 7.2%) and Filicales Trilete (0.7 - 5.1%) also increased.

Non-pollen palynomorphs (NPPs) (*Chaetomium* sp., *Glomus* cf. *fasciculatum*, *Pseudoschizaea circula*, *Sordaria* sp., *Spirogyra* sp. and *Sporormiella* sp.) maintain very similar values to the previous pollen zone (1.7 - 5.2%) without exceeding 3% in any of the cases (Fig. R.10).

### LPAZ RE-3 (792 - 312 cm) (1850±30 yr BP - 1980s)

Separated from the previous pollen zone by a sedimentary hiatus, the percentages of arboreal pollen show very similar values to those previously seen (82.2 - 92%) (Fig. R.8). But, in this case, a change in the dominant taxon is observed, with deciduous *Quercus* (25 - 42.4%) as the dominant tree. In addition, after the hiatus, *Alnus* (17.5 - 32.5%) becomes a much more dominant taxon, replacing *Betula* (7.8 - 16.2%). The percentages of *Pinus pinaster* (1.4 - 4.2%) also decrease drastically. *Corylus* (5.6 - 14.4%) also decreases. *Castanea*, evergreen *Quercus*, *Fagus sylvatica*, *Fraxinus*, *Salix* and *Tilia* do not exceed 3% each. It is important to note the appearance of *Eucalyptus* sp. at 582 cm (0 - 0.6%) for the first time.

The slight increase in shrub taxa (0.6 - 3%) in this pollen zone is mainly due to the increase in *Cistus* type, which already exceeds 2% (0 - 2.6%). However, *Erica* type, *Ilex aquifolium* and Labiatae still do not exceed 1% while *Prunus* type has not been identified in this section (Fig. R.8).

In Figure R.6, we can see that the percentage of herbaceous taxa (6 - 13.9%) increases. This is due to a recovery of Poaceae (4.6 - 8.7%) as well as a generalized increase in the rest of herbs, especially Apiaceae (0.4 - 3.3%) and Cichorioideae (0.4 - 2.6%). The remaining taxa (*Artemisia*, *Asphodelus albus* type, Cardueae, Chenopodiaceae, *Plantago lanceolata* type, *Plantago coronopus* type, Caryophyllaceae and *Centaurea nigra* type) do not exceed 1% each. Moreover, *Cerealia* type appears for the first time at 492 cm depth.

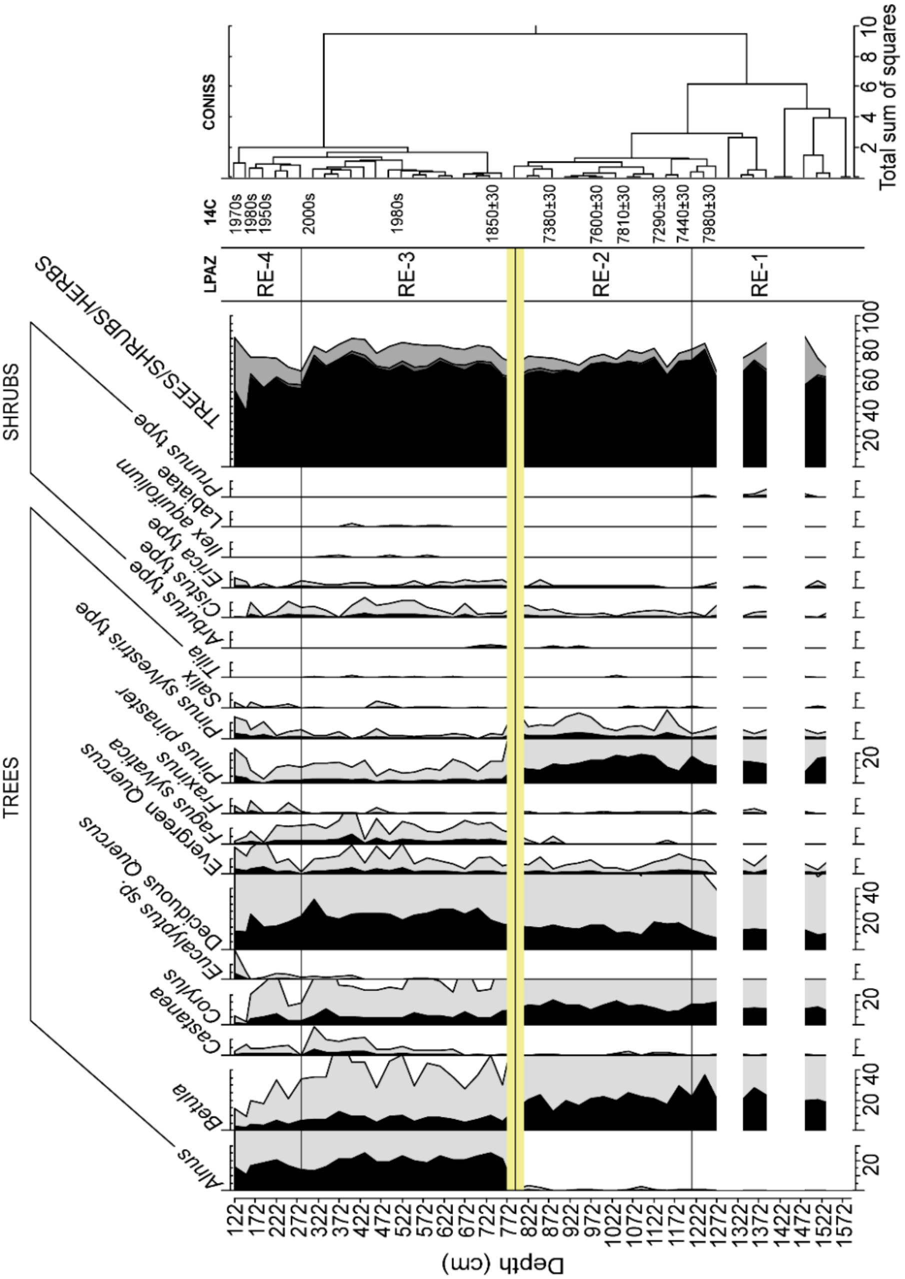


**Figure R.8** - Pollen diagram corresponding to the arboreal and shrub pollen along the Requejada borehole. Depth at centimeter scale, the evolution of arboreal and shrub taxa, the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented. The yellow band indicates the sedimentary hiatus.

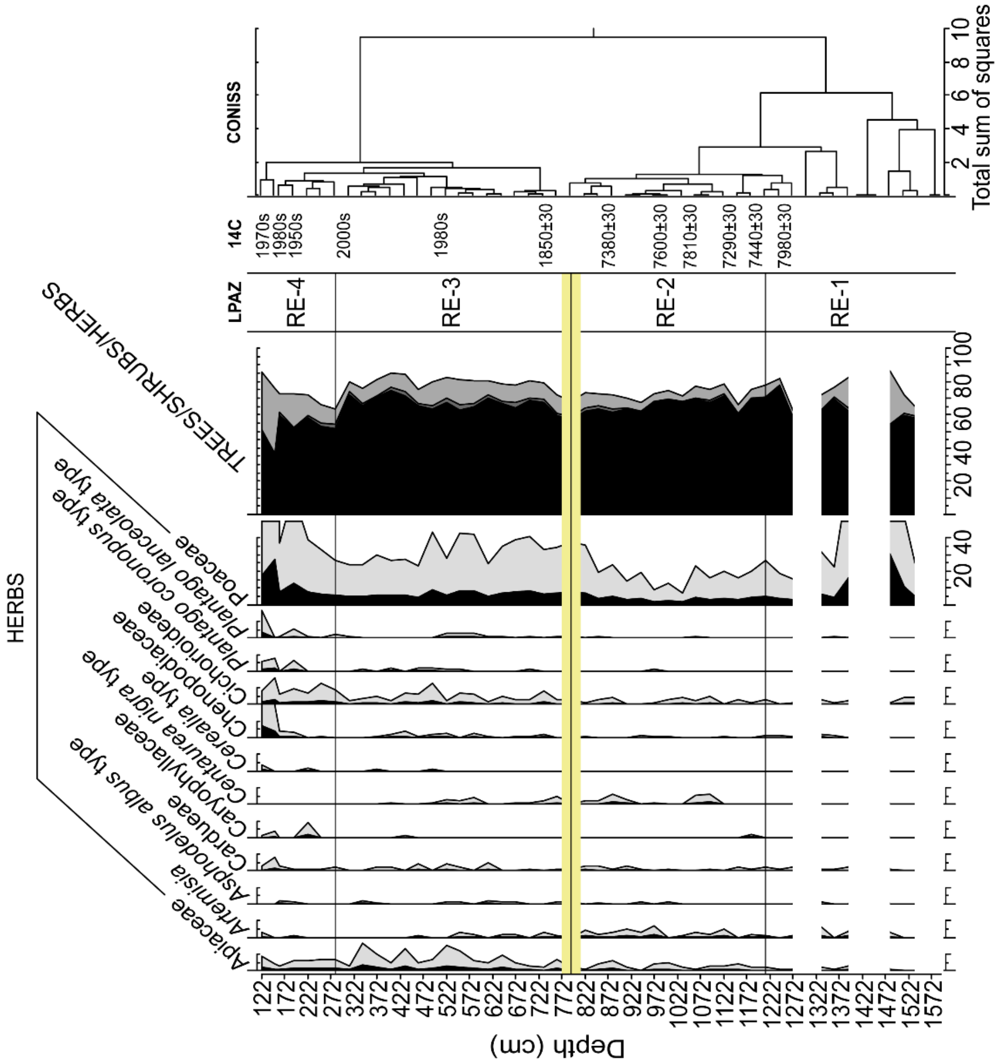


**Figure R.9** - Pollen diagram corresponding to the herbaceous pollen along the Requejada borehole. Depth at centimeter scale, the evolution of herbaceous taxa, the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented. The yellow band indicates the sedimentary hiatus.

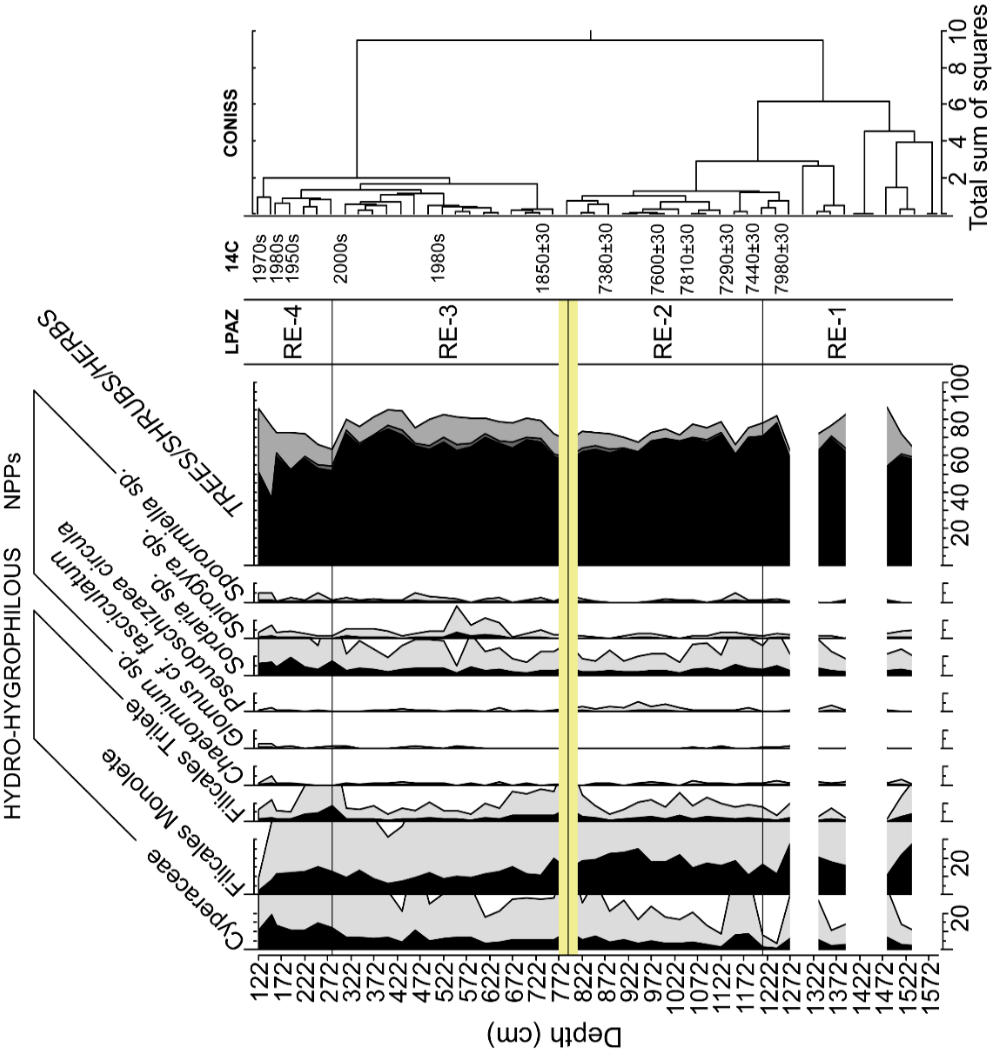


**Figure R.10** - Pollen diagram corresponding to the hydro-hygrophilous pollen and non-pollen palynomorphs (NPPs) along the Requejada borehole. Depth at centimeter scale, the evolution of hydro-hygrophilous and the NPPs taxa, the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented. The yellow band indicates the sedimentary hiatus.

On the left side of Figure R.10, it can be observed that the hydro-hygrophilous taxa (23 - 56.6%) maintain a similar trend to that observed in the previous pollen zone (Cyperaceae 3.2 - 5.9%, Filicales Monolete 5.2 - 19.2% and Filicales Trilete 0.3 - 3.3%).

The non-pollen palynomorphs (NPPs) (*Chaetomium* sp., *Glomus* cf. *fasciculatum*, *Pseudoschizaea circula*, *Spirogyra* sp. and *Sporormiella* sp.) also show a similar trend to the previous zone, with total values between 1.8 and 5.6% and none individually exceeding 4%. A small increase can be observed in the taxon *Sordaria* sp. (1.3 - 3.9%) (Fig. R.10).

### LPAZ RE-4 (312 - 122 cm) (1980s - 2000s)

Arboreal pollen, despite a reduction in its general percentages, continues to be dominant during this final zone of this borehole (56.8 - 88.3%) (Fig. R.8). The dominant taxa continue to be deciduous *Quercus* (15.4 - 37.2%) and *Alnus* (18.1 - 30.1%). *Betula* (3.1 - 11.7%), *Corylus* (0.8 - 10.4%), *Castanea* (0 - 2.7%), evergreen *Quercus* (0.4 - 7.3%), *Fagus sylvatica* (0.4 - 3.7%), *Fraxinus* (0 - 2.4%) and *Salix* (0 - 1.2%) are secondary. *Eucalyptus* sp. increases its percentage values to 5%.

Concerning shrub type pollen, a stabilization in the total percentage values is observed (0.6 - 2.6%) (Fig. R.8). In taxonomic terms, only two shrub taxa have been identified in this pollen zone: *Cistus* type (0 - 2.1%) and *Erica* type (0 - 1.2%).

Continuing with the increasing trend observed in the previous zone, herbaceous plants abundance grows considerably (9.4% - 39.4%) (Fig. R.9) with Poaceae (5.4 - 27.6%), Chenopodiaceae (0 - 7.3%), Cichorioideae (1.3 - 3.1%), *Plantago coronopus* type (0 - 1.6%) and *Plantago* lanceolata type (0 - 3.4%). The remaining identified taxa (Apiaceae, *Artemisia*, *Asphodelus albus* type, Cardueae, Caryophyllaceae and *Cerealia* type) do not exceed 2% each.

The hydro-hygrophilous taxa continue with total values similar to those previously observed (26.8 - 58.4%) (Fig. R.10): Cyperaceae 7.2 - 12.1%, Filicales Monolete 1.6 - 12.3% and Filicales Trilete 0.8 - 5.6%.

Finally, non-pollen palynomorphs (NPPs) increase moderately (3.7 - 8.6%) (Fig. R.10). The presence of *Sordaria* sp. with values between 2.5 and 7.2% represents the difference from the previous pollen zone. Here, *Glomus* cf. *fasciculatum*, *Pseudoschizaea circula*, *Spirogyra* sp. and *Sporormiella* sp. do not exceed 1% each.

### 2.1.2. Geochronology and age-depth model

A total of 12 organic samples were sent to Beta Analytic for radiocarbon dating by Accelerator Mass Spectrometry (AMS). Samples were calibrated using the IntCal20 method (Reimer et al., 2020) (Table R.4).

The oldest age registered (7980±30 yr BP) corresponds to the 1240 cm-depth sample while the most modern sample (1980s) was recorded at 150 cm depth. Therefore, those samples analyzed above 520 cm depth have yielded much younger ages than the preceding ones, all of them belonging to the second half of the 20th century.

**Table R.5** - Radiocarbon results from the Requejada borehole.

| LAB CODE | SAMPLE | MATERIAL | METHOD | DEPTH (cm) | CONVENTIONAL AGE (years BP) | CALIBRATED AGE (cal years BP) |
|---|---|---|---|---|---|---|
| Beta - 490730 | RE-120 | Wood | AMS-Standard delivery | 120 | Post 1950 CE | 1974-1977 CE |
| Beta - 490731 | RE-150 | Wood | AMS-Standard delivery | 150 | Post 1950 CE | 1983-1985 CE |
| Beta - 490732 | RE-160 | Plant | AMS-Standard delivery | 160 | Post 1950 CE | 1955 - 1957 CE |
| Beta - 490733 | RE-280 | Plant | AMS-Standard delivery | 280 | Post 1950 CE | 1956 - 2000 CE |
| Beta - 490734 | RE-520 | Wood | AMS-Standard delivery | 520 | Post 1950 CE | 1956 - 1985 CE |
| Beta - 490735 | RE-760 | Wood | AMS-Standard delivery | 760 | 1850±30 | 1865 - 1715 |
| Beta - 490736 | RE-880 | Shell | AMS-Standard delivery | 880 | 7380±30 | 8322 - 8160 |
| Beta - 490737 | RE-1000 | Shell | AMS-Standard delivery | 1000 | 7600±30 | 8131 - 7864 |
| Beta - 490738 | RE-1060 | Shell | AMS-Standard delivery | 1060 | 7810±30 | 8334 - 8050 |
| Beta - 490739 | RE-1120 | Shell | AMS-Standard delivery | 1120 | 7290±30 | 7807 - 7569 |
| Beta - 490740 | RE-1180 | Shell | AMS-Standard delivery | 1180 | 7440±30 | 7944 - 7692 |
| Beta - 490741 | RE-1240 | Shell | AMS-Standard delivery | 1240 | 7980±30 | 8996 - 8721 |

A depth-age model has also been made using the "R" software and the package Clam 2.2. The best fit was obtained by performing a smoothing spline to the available radiocarbon dates. The confidence intervals of the calibrations and the depth-age model were calculated at 95% (2σ) with 1000 iterations.

The depth-age model indicates the presence of a sedimentary hiatus detected at 792 cm, which marks a chronological gap of about 6000 years (Fig. R.11). In addition, the corresponding LPAZs are also shown for better interpretation.

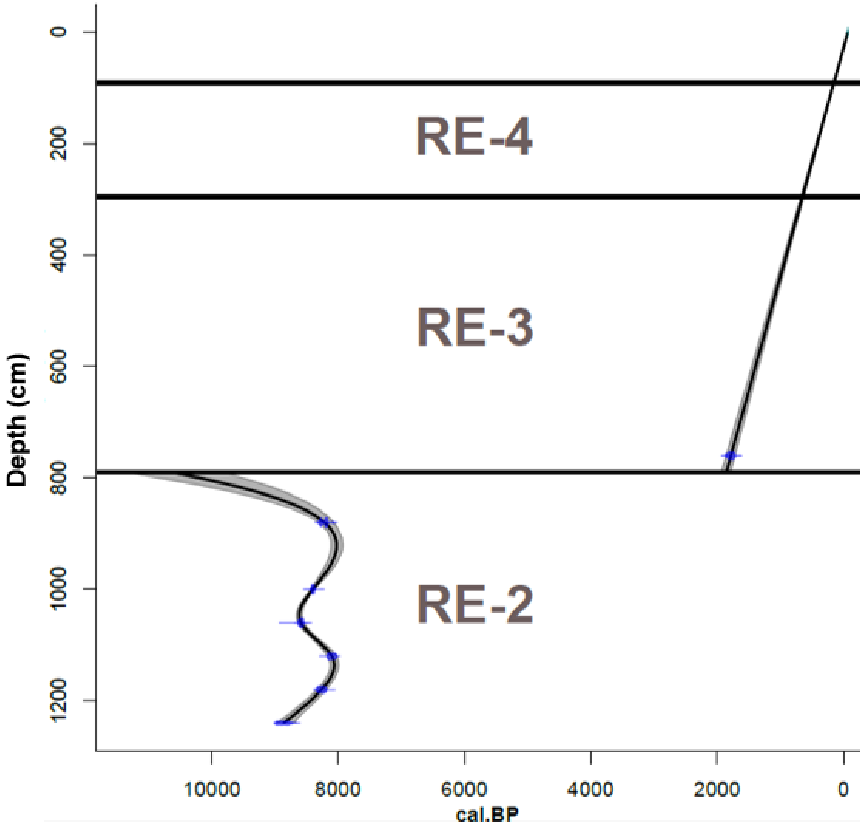


**Figure R.11** - Depth-age model of the Requejada borehole. The defined local pollen assemblage zones (LPAZ) are also represented. The interruption in the model is due to the detection of a hiatus at 792 cm depth.

## 2.2. San Kristobal

### 2.2.1 Pollen analysis

The San Kristobal borehole was divided into four local pollen assemblage zones (LPAZ SK) using the stratigraphically constrained cluster analysis by the method of incremental sum of squares (CONISS).

**Table R.6 -** Summary of the most representative taxa (relative abundance %) identified in the San Kristobal borehole. The single value represents the average and those in parentheses give the range. The percentages of hydro-hygrophilous taxa and NPPs are calculated separately together with the rest of the taxa

| | **SK - 1** | **SK - 2** | **SK - 3** | **SK - 4** |
|---|---|---|---|---|
| *Alnus* | 15 (7.2 - 20.8) | 15 (8.6 - 18.8) | 1 (0 - 2.6) | 10 (6.5 - 14.5) |
| *Betula* | 13 (10.7 - 13.9) | 8 (5.1 - 10) | 1 (0.4 - 3.4) | 10 (8.5 - 11.9) |
| *Eucalyptus* sp. | 0.1 (0 - 0.2) | 0.1 (0 - 0.2) | 0.1 (0 - 0.4) | 0.5 (0.2 - 0.8) |
| deciduous *Quercus* | 42 (26.7 - 53.1) | 25 (12.8 - 34.2) | 3 (1.6 - 4.3) | 9 (5.5 - 11.6) |
| *Fagus sylvatica* | 5 (0.4 - 10.9) | 11 (0.4 - 21.1) | 0.2 (0 - 1.2) | 1 (0.2 - 1.6) |
| *Pinus pinaster* | 11 (3.4 - 14.9) | 14 (2.6 - 36.8) | 12 (6.8 - 17.5) | 37 (30.3 - 47.7) |
| *Erica* type | 0.4 (0 - 1.1) | 3 (0.8 - 6) | 1 (0.4 - 1.2) | 7 (4.6 - 8.6) |
| Apiaceae | 1 (0.5 - 3) | 3 (0.8 - 8.8) | 5 (2.1 - 9.6) | 5 (1.7 - 8.5) |
| *Cerealia* type | 0.1 (0 - 0.2) | 0.2 (0 - 0.4) | 0.1 (0 - 0.2) | 0.1 (0 - 0.2) |
| Chenopodiaceae | 2 (0.6 - 2.6) | 4 (1 - 11) | 8 (1 - 34) | 1 (0.4 - 2) |
| Cichorioideae | 1 (0 - 2.2) | 3 (1.2 - 4.7) | 59 (19 - 79.5) | 3 (2.4 - 3.1) |
| Poaceae | 2 (0.2 - 5.1) | 3 (1.2 - 5.9) | 4 (0.4 - 11.9) | 5 (3.6 - 6.2) |
| Cyperaceae | 2 (0 - 3.4) | 6 (2.7 - 12.2) | 9 (6.3 - 10.3) | 7 (6 - 9) |
| Filicales Monolete | 9 (0 - 11.6) | 10 (8.7 - 13.4) | 6 (2.5 - 9.9) | 10 (7.1 - 12.9) |
| Filicales Trilete | 3 (0 - 9.2) | 6 (3.4 - 7.4) | 3 (1.2 - 6.7) | 4 (2.2 - 4.7) |
| *Sordaria* sp. | 1 (0 - 2.2) | 2 (0.4 - 4.3) | 3 (2.1 - 3.4) | 3 (1.4 - 5.3) |
| TREES | 91 (82.6 - 97.3) | 78 (59.8 - 89.9) | 20 (10.7 - 27.4) | 74 (69.4 - 78.4) |
| SHRUBS | 1 (0.4 - 3) | 6 (2.6 - 10) | 2 (0.6 - 2.6) | 10 (6.7 - 13.2) |
| HERBS | 7 (1.8 - 14.4) | 16 (7.5 - 32.4) | 79 (70 - 88.2) | 16 (14.9 - 17.4) |
| HYDRO-HYGROPHILOUS | 24 (0 - 34) | 35 (27.1 - 42.9) | 25 (18 - 33) | 26 (21.7 - 33.4) |
| NPPs | 2 (0 - 3.5) | 3 (1.5 - 5.8) | 4 (3.3 - 4.5) | 4 (2.8 - 5.7) |

## LPAZ SK-1 (450 - 315 cm)

Due to a sandier nature of this basal zone of the borehole, the resolution in LPAZ SK-1 is lower, but good enough to observe the pollen trend throughout (Fig. R.12, R.13, R.14).

Starting with the arboreal pollen, the dominant taxon is clearly deciduous *Quercus* (26.7 - 53.1%) (Fig. R.12). *Alnus* (7.2 - 20.8%) *Betula* (10.7 - 13.9%), *Fagus sylvatica* (0.4 - 10.9%) and *Pinus pinaster* (3.4 - 14.9%) also have a prominent presence. *Castanea*, *Corylus*, *Eucalyptus* sp., evergreen *Quercus*, *Fraxinus*, *Juglans*, *Pinus sylvestris* type, and *Tilia* do not exceed 4% each.

Shrubby plants, however, account for a much lower percentage (0.4 - 3%) (Fig. R.12). The following taxa have been identified: *Arbutus* type, *Calluna vulgaris*, *Cistus* type, *Erica* type, Labiatae and *Prunus* type. None of these individually exceeds 2%.

The presence of herbaceous plants ranged from 1.8 to 14.4%. The dominant family is Poaceae (0.2 - 5.1%). Apiaceae, *Artemisia*, *Aster* type, Cardueae, *Centaurea nigra* type, *Cerealia* type, Chenopodiaceae, Cichorioideae and *Plantago lanceolata* type have also been identified, but none exceeds 3% (Fig. R.13).

Hydro-hygrophilous plants represent percentages between 0 and 34%. The presence of Filicales Monolete (0 - 11.6%) stands out as the dominant group. Cyperaceae (0 - 3.4%), Filicales Trilete (0 - 9.2%) and *Polypodium vulgare* type (0 - 5.1%) have also been identified (Fig. R.14).

Finally, the non-pollen palynomorphs (NPPs) have percentages between 0 and 3.5% (Fig. R.14). *Chaetomium* sp., *Glomus* cf. *fasciculatum*, *Pseudoschizaea circula*, *Sordaria* sp. and *Spyrogira* sp. have been identified, although they do not exceed 2.5% in any case.

## LPAZ SK-2 (315 - 239 cm)

Arboreal taxa (59.8 - 89.9%) dominate also in this second zone. Deciduous *Quercus* (12.8 - 34.2%) continues to be the taxon with the highest abundance (Fig. R.12). *Alnus* (8.6 - 18.8%) and *Betula* (5.1 - 10%) maintain similar values to those observed in the previous pollen zone. The percentage of *Pinus pinaster* (2.6 - 36.8%) and *Fagus sylvatica* (0.4 - 21.1%) increased considerably. The presence of *Corylus*, *Eucalyptus* sp., evergreen *Quercus*, *Juglans*, *Pinus sylvestris* type, *Salix* and *Tilia* is reduced to no more than 2% each.

Shrub pollen experiences a small growth (2.6 - 7.8%) (Fig. R.12). From all the taxa identified in this section (*Arbutus* type, *Calluna vulgaris*, *Cistus* type, *Erica* type and

*Prunus* type), *Erica* type has the greatest presence (0.8 - 6%). The others do not exceed 2% each.

Herbaceous taxa exhibited a notable growth, with percentages between 7.5 and 32.4% (Fig. R.113). Three families stand out above all: Apiaceae (0.8 - 8.8%), Chenopodiaceae (1 - 11%) and Poaceae (1.2 - 5.9%). Other herbs (*Artemisia*, *Aster* type, Cardueae, *Centaurea nigra* type, *Cerealia* type, Cichorioideae and *Plantago lanceolata* type) do not exceed 5% in any case.

A similar increase is observed in the hydro-hygrophilous plants (27.1 - 42.9%). Their percentages are: Filicales Monolete (8.7 - 13.4%), Cyperaceae (2.7 - 12.2%), Filicales Trilete (6.5 - 7.5%) and *Polypodium vulgare* type (1.9 - 3.7%) (Fig. R.14).

Non-pollen palynomorphs (NPPs) also show a similar increasing trend (1.5 - 5.8%) (Fig. R.14). The same taxa as in the previous zone have been identified (*Chaetomium* sp., *Glomus* cf. *fasciculatum*, *Pseudoschizaea circula*, *Sordaria* sp. and *Spyrogira* sp). The increase of *Sordaria* sp. at the end of this pollen zone is noticeable (0.4 - 4.3%).

### LPAZ SK-3 (239 - 208 cm) (1978 -1980 CE)

The pollen data show a drastic reduction of arboreal pollen with respect to the previous zone (10.7 - 27.4%) (Fig. R.12). *Pinus pinaster* (6.8 - 17.5%) is now the most abundant species among the arboreal taxa. As secondary, deciduous *Quercus* (1.6 - 4.3%), *Alnus* (0 - 2.6%) and *Betula* (0.4 - 3.4%) are noteworthy genera. *Castanea*, *Fagus sylvatica*, *Eucalyptus* sp., evergreen *Quercus*, *Pinus sylvestris* and *Salix* do not exceed 3% each.

The same is also observed for shrub pollen, whose total percentages are reduced between 0.6 and 2.6% (Fig. R.12). The analysis has identified the following taxa: *Arbutus* type, *Calluna vulgaris*, *Erica* type and *Prunus* type. None of them exceeded 2%.

Herbaceous pollen becomes dominant during this pollen zone, obtaining total percentages that range between 70 and 88.2% (Fig. R.13). The dominant subfamily is Cichorioideae (19 - 79.5%). Apiaceae (2.1 - 9.6%), *Aster* type (0 - 3.8%), Chenopodiaceae (1 - 34%) and Poaceae (0.4 - 11.9%) are present. The remaining identified taxa (*Artemisia*, Cardueae, *Cerealia* type and *Plantago lanceolata* type) do not exceed 1% in any case.

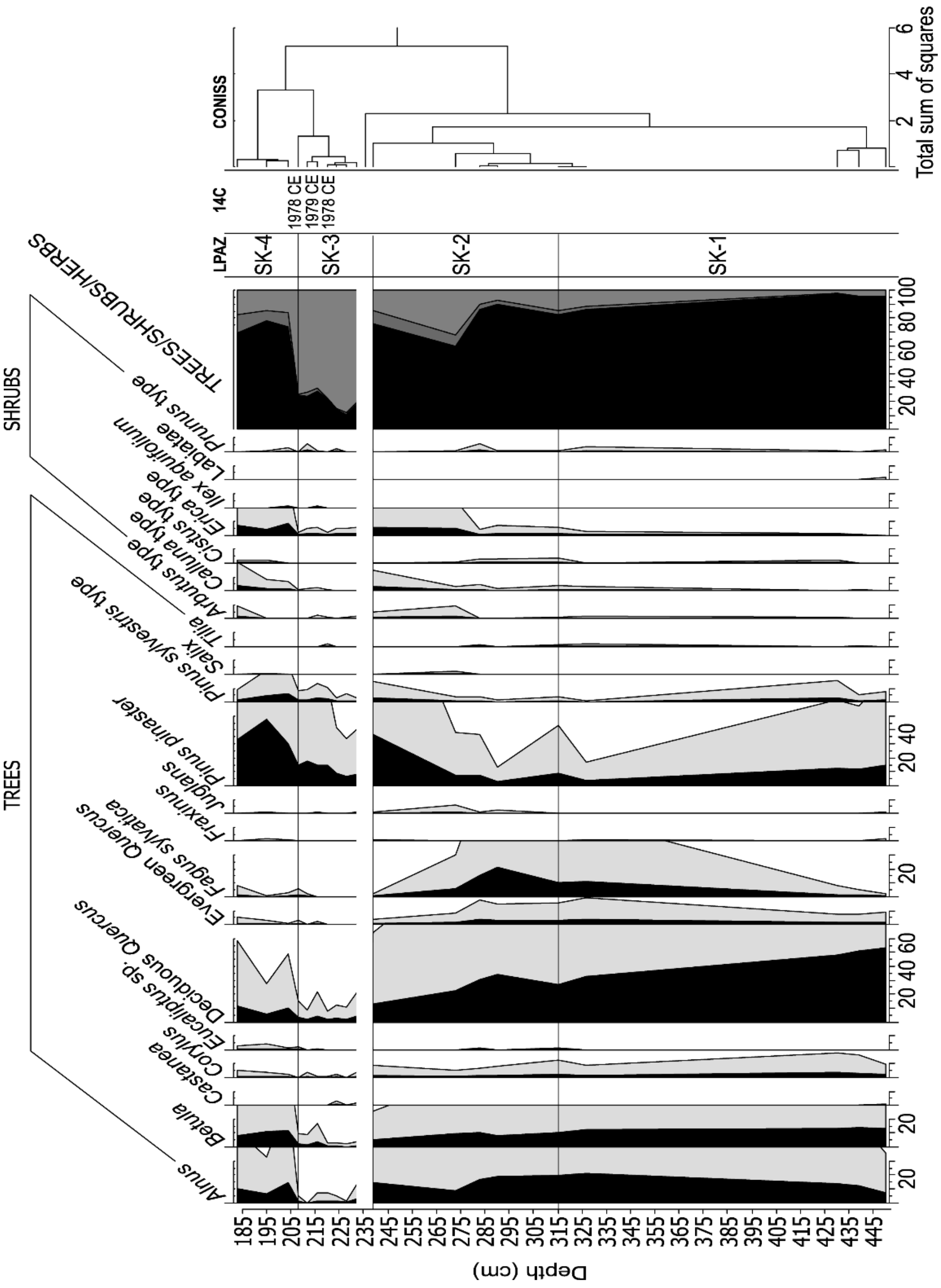


**Figure R.12** - Pollen diagram corresponding to the arboreal and shrub pollen along the San Kristobal borehole. Depth at centimeter scale, the evolution of arboreal and shrub taxa, the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

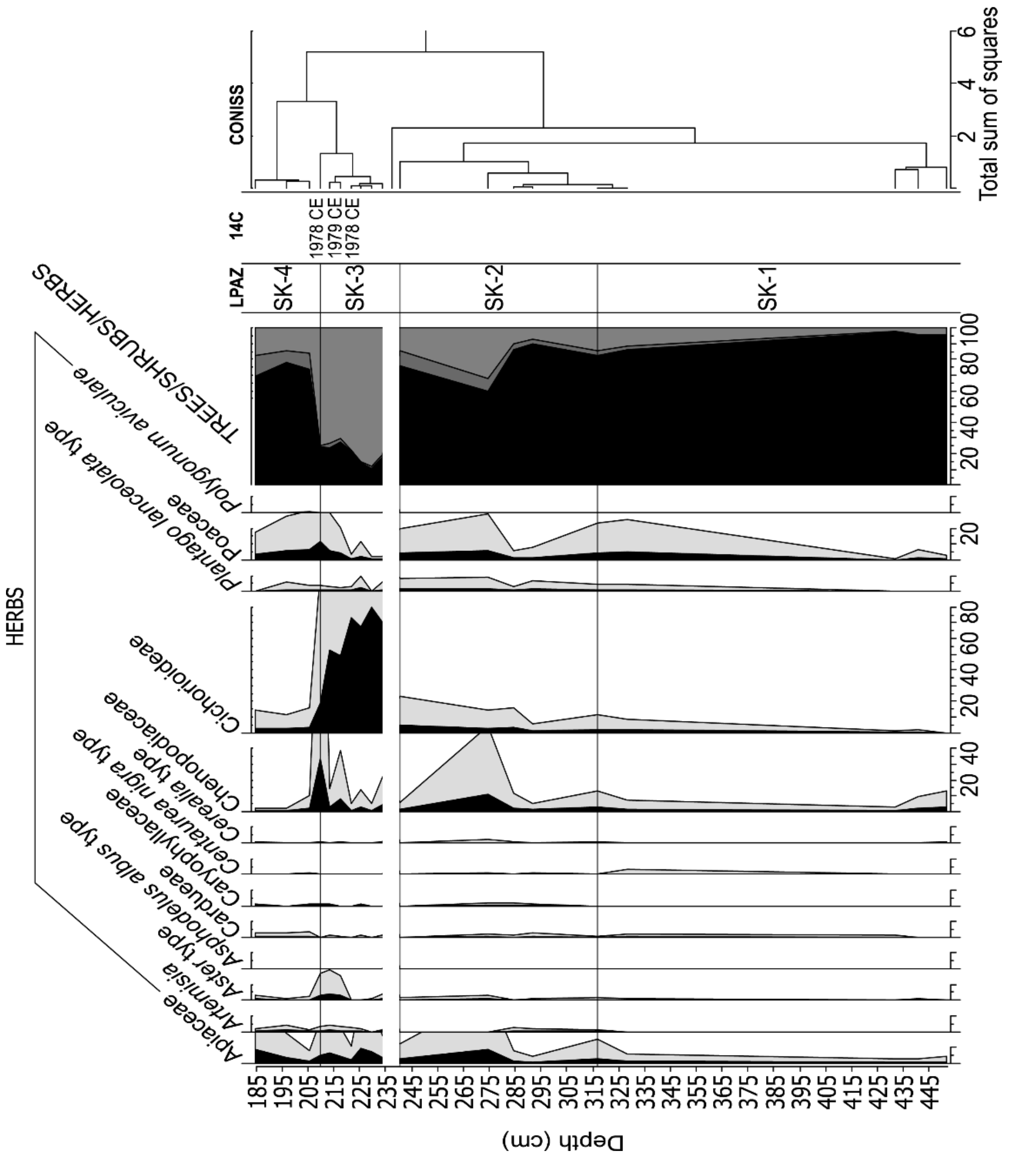


**Figure R.13** - Pollen diagram corresponding to the herbaceous pollen along the San Kristobal borehole. Depth at centimeter scale, the evolution of herbaceous taxa, the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

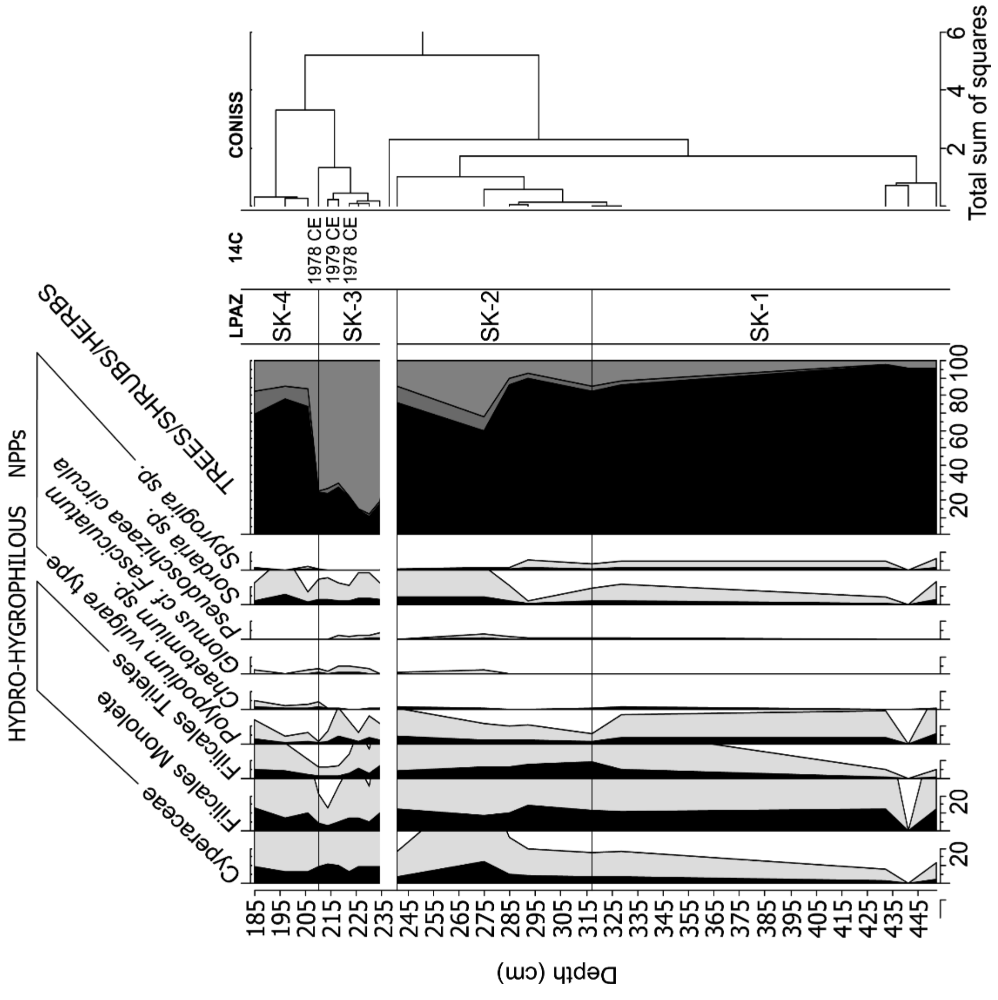


**Figure R.14** - Pollen diagram corresponding to the hydro-hygrophilous pollen and non-pollen palynomorphs (NPPs) along the San Kristobal borehole. Depth at centimeter scale, the evolution of hydro-hygrophilous and the NPPs taxa, the defined local assemblage pollen zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

Regarding the hydro-hygrophilous pollen, there is a slight reduction in its total percentages (18 - 30.7%) (Fig. R.14). The identified taxa also have similar values than the previous zone: Filicales Monolete (2.5 - 9.9%), Cyperaceae (6.3 - 10.3%), Filicales Trilete (1.2 - 6.7%), *Polypodium vulgare* type (0.3 - 4.1%).

Finally, the trend of non-pollen palynomorphs (NPPs) remains similar to the two previous zones (3.3 - 4.5%) (Fig. R.14). The same taxa have been identified: *Chaetomium* sp., *Glomus* cf. *fasciculatum*, *Pseudoschizaea circula*, *Sordaria* sp. and *Spyrogira* sp. In none of them the percentage is higher than 3.5%.

### LPAZ SK-4 (208 - 183 cm) (1978 - 1979 CE)

In this final pollen zone, arboreal pollen recovers its predominance (69.4 - 78.4%) (Fig. R.12). *Pinus pinaster* is the dominant taxon, with percentages that range between 30.3 and 47.7%. *Alnus* (6.6 - 14.5%), *Betula* (8.5 - 11.9%) and deciduous *Quercus* (5.5 - 11.6%) are the main secondary taxa. The following taxa are represented below 6% abundance: *Corylus*, *Eucalyptus* sp., evergreen *Quercus*, *Fagus sylvatica*, *Fraxinus*, *Juglans*, *Pinus pinaster*, *Pinus sylvestris* type and *Salix*.

Shrub pollen also experienced a remarkable growth (6.7 - 13.2%). *Erica* type (4.6 - 8.6%) and *Calluna vulgaris* (1.3 - 4.1%) are the most relevant. *Arbutus* type, *Cistus* type and *Prunus* type do not exceed 2% each (Fig. R.12).

With the increase of shrubs, the reduction of herbaceous pollen returns to the values observed in the basal pollen zone (14.9 - 17.4%) (Fig. R.13). The dominant families are Apiaceae (1.7 - 8.5%) and Poaceae (3.6 - 5.2%). The remaining taxa do not exceed 3% in any case (*Artemisia*, *Aster* type, *Asphodelus albus* type, Cardueae, Caryophyllaceae, *Centaurea nigra* type, *Cerealia* type, Chenopodiaceae, Cichorioideae, *Plantago lanceolata* type and *Polygonum aviculare*).

The hydro-hygrophilous taxa maintained a similar abundance as in the previous zone (21.7 - 33.4%) (Fig. R.14). The taxa identified are Filicales Monolete (7.1 - 12.9%), Cyperaceae (6 - 9%), Filicales Trilete (2.2 - 4.7%) and *Polypodium vulgare* type (0.8 - 2.6%).

Non-pollen palynomorphs (NPPs) identified in this final pollen zone are *Chaetomium* sp., *Glomus* cf. *fasciculatum*, *Sordaria* sp. and *Spyrogira* sp. Their total percentages are similar to those observed in the previous pollen zones (2.8 - 5.7%). It is worth mentioning that only *Sordaria* sp. exceeds 5% abundance (Fig. R.14).

### 2.2.2. Geochronology

For the San Kristobal borehole, three samples were sent for dating (Table R.7). The radiocarbon analyses were performed at Beta Analytic by Accelerator Mass

Spectrometry (AMS). Calibration was performed using the IntCal20 + NHZ1 method (Reimer et al., 2020).

**Table R.7** - Radiocarbon results from the San Kristobal borehole.

| LAB CODE | SAMPLE | MATERIAL | METHOD | DEPTH (cm) | CONVENTIONAL AGE (CE) | CALIBRATED AGE (CE) |
|---|---|---|---|---|---|---|
| Beta - 539167 | SK-203 | Plant | AMS-Standard delivery | 203 | Post 1950 | 1978 - 1979 |
| Beta - 539168 | SK-206 | Plant | AMS-Standard delivery | 206 | Post 1950 | 1979 - 1981 |
| Beta - 539169 | SK-209 | Plant | AMS-Standard delivery | 209 | Post 1950 | 1978 - 1980 |

The ages registered correspond to the decades 1970-1980. The unavailability of more than three dates and the proximity of the ages obtained make the elaboration of the depth-age model not workable. However, the presence of the allochthonous *Eucalyptus* sp. pollen throughout this borehole is a clear indication of its young age.

### 2.2.3. SiZer Analysis

In order to observe the environmental significance of the abundance changes experienced by the taxa Cichoriodideae and *Pinus pinaster*, taxa that are more predominant and show greater changes in their trends, a statistical analysis of significance (SiZer: Significant Zero Crossings) was carried out. The SiZer analysis is able to characterize observed increases and decreases in ecological records over time.

Since we did not have the necessary chronological data to make a depth-age model that would allow SiZer age-based mapping, we used the depth in cm to perform the statistical analysis.

The results show that, indeed, significance is found in percentage variations obtained through pollen analysis.

The initial increase and the subsequent percentage reduction of Cichorioideae between 232 and 212 cm depth have been identified, although not completely (Fig. R.15). This increase can be seen thanks to the red spot that the SiZer map has drawn. It is also able to detect as significant the posterior decriment observed around 212 cm.

However, in the case of the analysis carried out on *Pinus pinaster*, SiZer only shows the increase of this species at the end of the borehole, and not the decrease that takes place when Cichorioideae replaces it as the dominant pollen taxa (Fig. R.16). The fact that the SiZer shows this in purple implies that although the analysis detects the presence of a change it cannot be considered significant. This is something that usually happens when the resolution of the data is not wide enough.

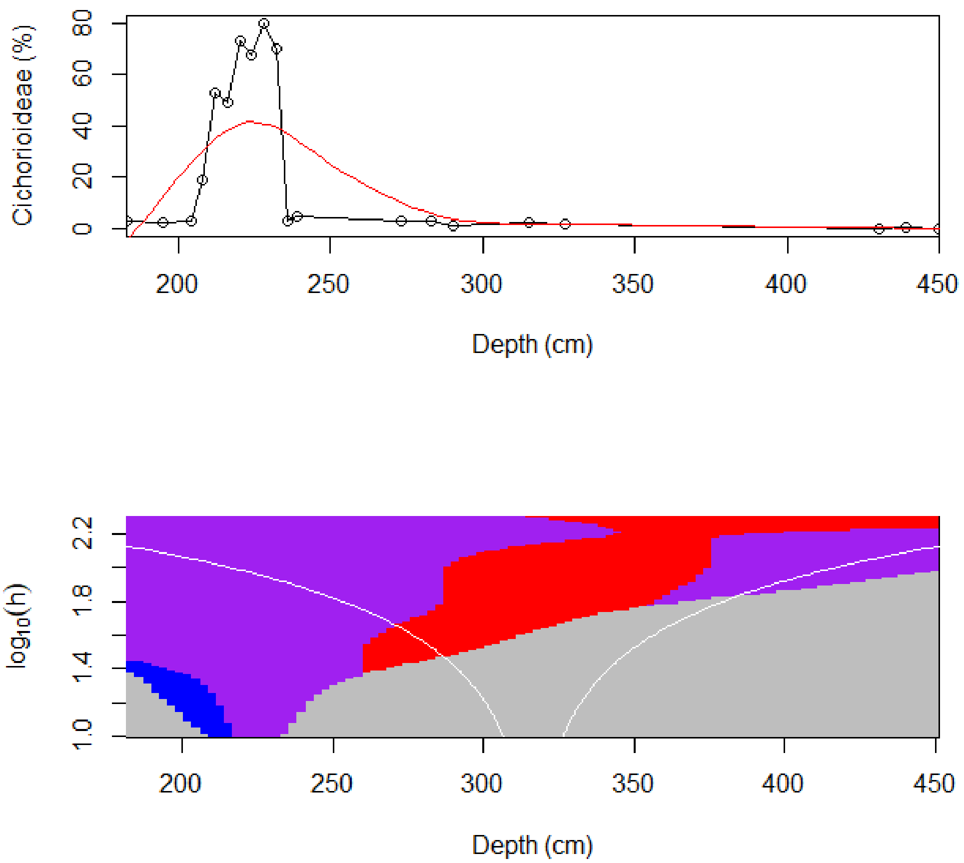


**Figure R.15** - SiZer map of the San Kristobal borehole. The percentage of Cichorioideae pollen is analyzed. The SiZer map categorizes the significance in blue (decreasing), red (increasing) or purple (possibly zero). The bandwidth is h = 30.

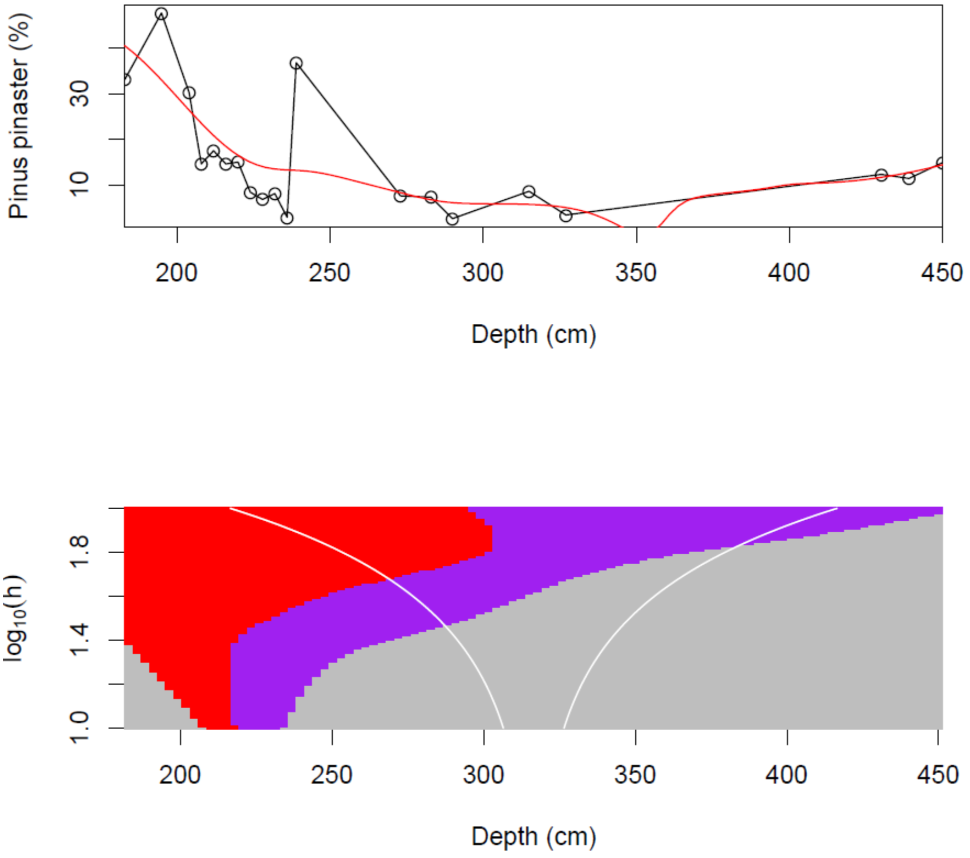


**Figure R.16** - SiZer map of the San Kristobal borehole. The percentage of *Pinus pinaster* pollen is analyzed. The SiZer map categorizes the significance in blue (decreasing), red (increasing) or purple (possibly zero). The bandwidth is h = 30.

## 2.3. Anbeko

### 2.3.1. Pollen analysis

Thanks to the use of stratigraphically constrained cluster analysis by the incremental sum of squares (CONISS) method, four different LPAZ ANB have been identified for the Anbeko borehole.

**Table R.8 -** Summary of the most representative taxa (relative abundance %) identified in the Anbeko borehole. The single value represents the average and those in parentheses give the range. The percentages of hydro-hygrophilous taxa and NPPs are calculated separately together with the rest of the taxa

| | **ANB - 1** | **ANB - 2** | **ANB - 3** | **ANB - 4** |
|---|---|---|---|---|
| *Alnus* | 4 (2.2 - 6) | 7 (5.3 - 7.8) | 5 (1.6 - 10.5) | 7 (3.1 - 13.2) |
| *Betula* | 16 (4.5 - 29.4) | 11 (5.5 - 18.1) | 19 (3.6 - 34) | 10 (6 - 21.7) |
| deciduous *Quercus* | 29 (23.8 - 34.9) | 26 (25.9 - 26.5) | 29 (3.1 - 40) | 29 (20.3 - 43.9) |
| *Pinus pinaster* | 29 (10.4 - 44.9) | 20 (15 - 24.2) | 22 (10.5 - 53) | 16 (7 - 32) |
| *Pinus sylvestris* type | 8 (5.2 - 10.7) | 10 (5.1 - 17.6) | 5 (1.6 - 23.4) | 3 (1.6 - 6) |
| *Tilia* | 0.2 (0 - 0.6) | 2 (0.6 - 2.8) | 2 (0.2 - 3.7) | 7 (0.2 - 44.9) |
| *Cerealia* type | 0 (0 - 0) | 0.1 (0 - 0.4) | 0.1 (0 - 0.4) | 0.1 (0 - 0.2) |
| Chenopodiaceae | 3 (2.8 - 4.5) | 7 (4.7 - 9.7) | 7 (0.5 - 11.1) | 11 (4.1 - 18.5) |
| Filicales Monolete | 9 (5.7 - 14) | 7 (4.9 - 8.6) | 8 (2.7 - 13.1) | 5 (3.3 - 10.7) |
| *Polypodium vulgare* type | 4 (2.1 - 4.9) | 4 (2 - 4.9) | 5 (1.6 - 11.1) | 3 (0.8 - 4.1) |
| *Sordaria* sp. | 2 (1.4 - 2) | 1 (0.4 - 3.4) | 1 (0 - 1.1) | 1 (0.2 - 1.7) |
| TREES | 89 (87.5 - 92) | 83 (77 - 87.5) | 87 (73.3 - 95.2) | 79 (67.3 - 93.2) |
| SHRUBS | 2 (0.2 - 4.5) | 1 (0 - 2.1) | 1 (0 - 2.7) | 1 (0 - 2.9) |
| HERBS | 9 (7.9 - 10.8) | 16 (11.9 - 20.8) | 13 (4.6 - 25.5) | 19 (6.4 - 30.1) |
| HYDRO-HYGROPHILOUS | 35 (30.3 - 39.6) | 33 (24.1 - 44.2) | 29 (10.6 - 46.9) | 19 (15.3 - 39.3) |
| NPPs | 2 (1.9 - 3.1) | 2 (0.8 - 4.2) | 1 (0 - 2) | 1 (0.2 - 4) |

## LPAZ ANB-1 (850 - 650 cm)

There are no dates for this basal pollen zone and the palynological resolution obtained is not optimal as sampling efforts were concentrated on the upper part of the borehole, where a more detailed analysis was carried out (Fig. R.17, R.18, R.19). However, as with the previous San Kristobal borehole, the resolution is sufficient to give a general idea of the vegetation trend in this pollen zone.

In addition, no specific dates for this pollen zone are available although, because of the dates obtained in the upper part of the borehole, this pollen zone must have been deposited before 4000 years BP.

Starting with the arboreal pollen (Fig. R.17), we can observe that trees are undoubtedly the dominant pollen (85.5 - 92%). The predominant taxon is *Pinus pinaster* (10.4 - 44.9%). It is followed by deciduous *Quercus* (23.8 - 34.9%), *Betula* (4.5 - 29.4%) and *Pinus sylvestris* (5.2 - 10,7%) as secondary taxa. *Alnus*, *Corylus*, evergreen *Quercus*, *Fagus sylvatica* and *Tilia* are also present but do not exceed 4% in any case.

Continuing with shrubs, these appear in very low percentages (0.2 - 4.7%) (Fig. R.17). Three different taxa have been identified in this pollen zone: *Arbutus* type, *Erica* type and Labiatae, all of them below 1% abundance, except *Erica* type that occasionally exceeds 4%.

The presence of herbaceous plants is relatively higher (7.9 - 10.8%) (Fig. R.18). Chenopodiaceae is the most dominant herbaceous family with percentages between 2.8 - 4.5%. Poaceae also has a relevant presence (1.1 - 3.7%). Other taxa identified are *Artemisia*, Cardueae, Caryophyllaceae, *Centaurea nigra*, Cichorioideae and *Plantago lanceolata* type, all below 2% each.

Hydro-hygrophilous pollen identified has a much higher presence (30.3 - 39.6%). Filicales Monolete (5.7 - 14%) is the predominant taxon while *Polypodium vulgare* type is the second most represented taxon in this pollen zone (0.8 - 2.6%). Cyperaceae and Filicales Trilete have also been identified, but never above 2% in any case (Fig. R.19).

Regarding the non-pollen palynomorphs (NPPs), *Chaetomium*, *Sordaria* sp. and *Spyrogira* sp. have been identified, although none of them exceeds 2% (Fig. R.19).

## LPAZ ANB-2 (650 - 439 cm)

In this second pollen zone radiocarbon dates are not available to accurately date this section of the borehole. Therefore, this pollen zone is also assumed to have accumulated prior to 4000 years BP.

Arboreal pollen continues to be the predominant pollen in LPAZ ANB-2, although with a lower percentage than before (77 - 87.5%). A change in the dominant taxon is observed in this zone, with deciduous *Quercus* now having the highest abundance (25.9 - 26.5%). Even so, the difference with *Pinus pinaster* is small (15 - 24.2%). *Betula* (5.5 - 18.1%) and *Pinus sylvestris* (5.1 - 17.6%) remain as secondary taxa. Other representative taxa are *Alnus* (5.3 - 7.5%), *Corylus* (1 - 2.5%), evergreen *Quercus* (1.5 - 3.5%), *Fagus sylvatica* (0 - 8%) and *Tilia* (0.6 - 2.8%). *Salix* and *Populus* have been identified, appearing here for the first time in this borehole, although they do not exceed 1% each (Fig. R.17).

Shrubs also see their overall percentage reduced (0 - 2.1%) in this zone (Fig. R.17). Some new taxa have been identified along with *Arbutus* type and *Erica* type: *Calluna vulgaris*, *Cistus* type and *Prunus*. Still, none of these reaches 2%. Labiatae disappears in this second zone.

Herbaceous pollen does increase in LPAZ ANB-2 (11.9 - 20.8%) (Fig. R.18). The dominant family continues to be Chenopodiaceae (4.7 - 9.7%). Apiaceae (1.4 - 3.8%), Cichorioideae (0.4 - 3.5%) and Poaceae (0 - 2.8%) are the secondary herbs. Other taxa, like *Artemisia* and Cardueae, do not exceed 1% each, while *Plantago lanceolata* shows a spike at the end of this zone and reaches 5% abundance. The appearance of *Cerealia* type for the first time in this sedimentary record, although in very low percentages (0.4%), is noteworthy.

In terms of hydro-hygrophilous taxa (Fig. R.19), there is a stabilization, maintaining overall values similar to those observed in the previous zone (24.1 - 44.2%). Filicales Monolete (4.9 - 8.6%), *Polypodium vulgare* (2 - 4.9%), Cyperaceae (0.7 - 1.3%) and Filicales Trilete (2.2 - 5%) represent this type of pollen.

To conclude with this zone, the non-pollen microfossil taxa (NPPs) exhibit an increase in the percentages of *Sordaria* sp. (0.6 - 3.4%) (Fig. R.19). Nevertheless, *Chaetomium* sp., *Spyrogira* sp. and the new species *Pseudoschizaea circula* have values below 1% in each case.

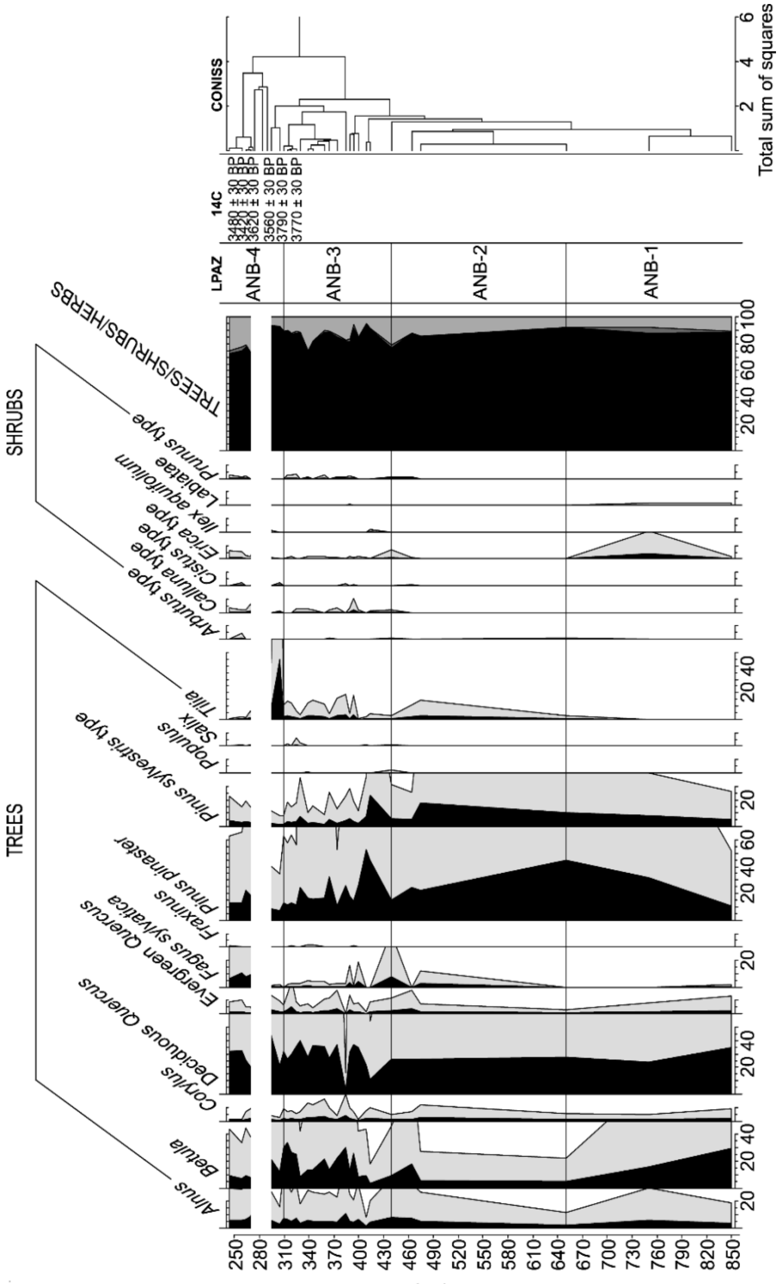


**Figure R.17** - Pollen diagram corresponding to the arboreal and shrub pollen along the Anbeko borehole. Depth at centimeter scale, the evolution of arboreal and shrub taxa, the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

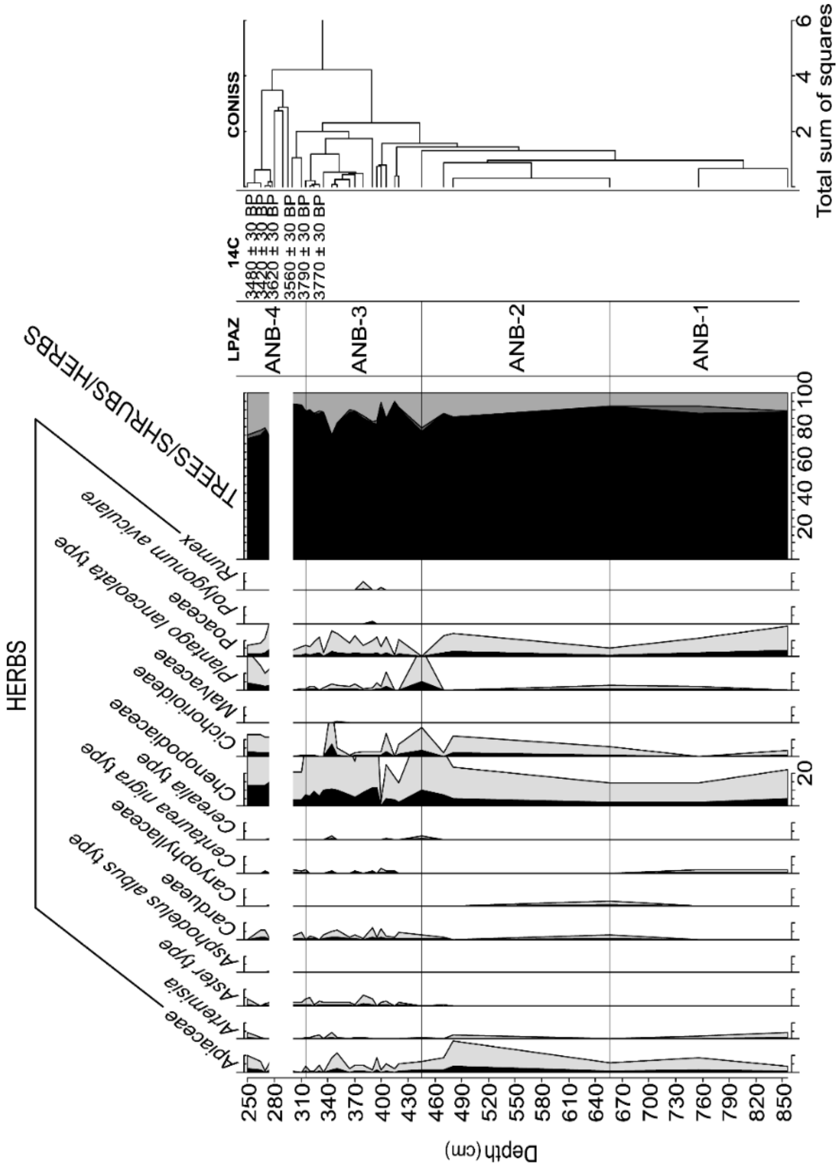


**Figure R.18** - Pollen diagram corresponding to the herbaceous pollen along the Anbeko borehole. Depth at centimeter scale, the evolution of herbaceous taxa, the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

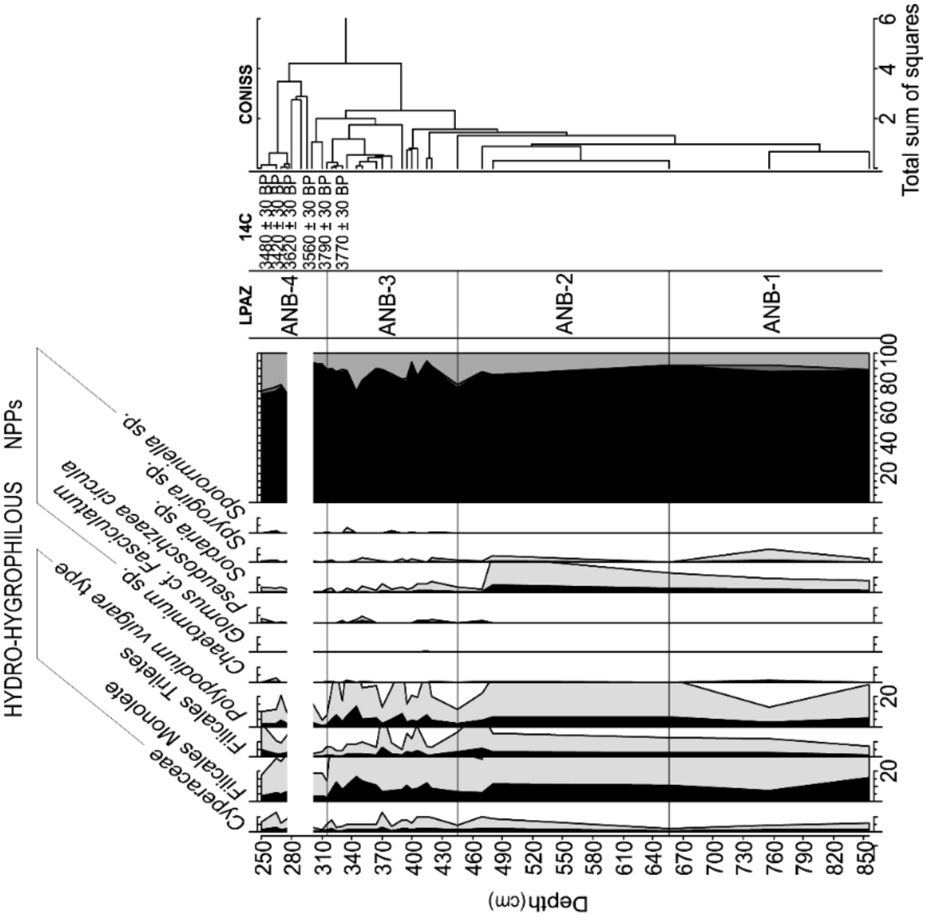


**Figure R.19** - Pollen diagram corresponding to the hydro-hygrophilous pollen and non-pollen palynomorphs (NPPs) along the Anbeko borehole. Depth at centimeter scale, the evolution of hydro-hygrophilous and the NPPs taxa, the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

### LPAZ ANB-3 (439 - 308 cm) (3770 ± 30 yr BP)

Unlike the two previous pollen zones, we have here the first radiocarbon dating. The date provided by the radiocarbon analysis is 3770 ± 30 yr BP in the upper part of this zone (Fig. R.17, R.18, R.19).

Arboreal pollen abundance is again increasing (73.3 - 95.2%) (Fig. R.17). Thus, it continues to be the dominant pollen type. The high presence of taxa such as deciduous *Quercus* (3.1 - 40%) and *Pinus pinaster* (10.5 - 53%) and the increase in the rate of occurrence of other taxa such as *Betula* (3.6 - 30.2%) are characteristic of this third zone. *Alnus* begins to have a notable presence, with percentages between 1.6 and 10.5%. Abundances below 4% have been identified for *Corylus*, evergreen *Quercus*, *Fagus sylvatica*, *Pinus sylvestris* type and *Tilia*, whereas *Fraxinus*, *Populus* and *Salix* do not exceed 1% each.

This is not the case of the shrub pollen, which maintains a certain regularity with respect to the previous zones (0 - 2.8%) (Fig. R.17). In fact, all the taxa identified in this section of the borehole (*Arbutus* type, *Calluna vulgaris*, *Cistus* type, *Erica* type, *Ilex aquifolium*, Labiatae and *Prunus* type) are below 2.5% abundance.

All this determines the reduced presence of herbaceous plants (5.6 - 25.5%). As in previous LPAZ ANB-1 and ANB-2, Chenopodiaceae (2.8 - 11.1%) is the herbaceous family most representative of this zone. Apiaceae, Cichorioideae, Poaceae, *Artemisia*, Cardueae, *Rumex*, *Plantago lanceolata* and *Cerealia* type do not surpass 3% each (Fig. R.18).

Continuing with the hydro-hygrophilous pollen, in this third pollen zone at Anbeko, values similar to those found in the previous two zones are observed (10.6 - 46.9%) (Fig. R.19). Indeed, Filicales Monolete (2.7 - 13.1%) continues to be the dominant taxon, followed by *Polypodium vulgare* (1.6 - 11.1%), Cyperaceae (0.4 - 2.1%) and Filicales Trilete (0.7 - 5.1%).

The overall values of non-pollen palynomorphs (NPPs) decrease in LPAZ ANB-3 (0 - 1.3%). All taxa identified in this pollen zone (*Sordaria* sp., *Chaetomium* sp., *Spyrogira* sp., *Pseudoschizaea circula*, *Glomus* cf. *fasciculatum* and *Sporormiella* sp.) are under 1% each (Fig. R.19).

### LPAZ ANB-4 (308 - 244 cm) (3790± 30 - 3420± 30 yr BP)

Pollen dynamics remains similar in this final zone (Fig. R.17) with a clear predominance of arboreal pollen (71.7 - 93.2%). Deciduous *Quercus* (20.3 - 43.9%) is the main taxon and *Pinus pinaster* (7 - 32%) is also highly represented. The values of *Betula* (6 - 21.7%) and *Alnus* (3.1 - 13.2%) are also maintained. The observed increase of *Tilia*, which can reach 45% abundance, is remarkable although only in one sample at 304 cm depth. The rest of the taxa identified (*Corylus*, evergreen *Quercus*, *Fagus sylvatica*, *Pinus sylvestris* and *Salix*) do not exceed 3% in any case.

The shrub type pollen is practically equivalent to the previous zone (0 - 2.9%) (Fig. R.17). The following pollen taxa have been identified below 2% abundance: *Arbutus* type, *Calluna vulgaris*, *Cistus* type, *Erica* type, *Ilex aquifolium* and *Prunus* type.

Herbaceous pollen has percentages between 6.4 - 30.1%, which is an increase with respect to LPAZ ANB-3 (Fig. R.18). This increase can be clearly observed in the dominant family Chenopodiaceae (4.1 - 18.5%). Other taxa that slightly increase their percentages here are *Plantago lanceolata* (0 - 2.9%) and Poaceae (0.8 - 4.6%). Apiaceae, Cichorioideae, *Artemisia*, Cardueae and *Cerealia* type do not exceed 3% each.

Hydro-hygrophilous pollen (15.3 - 39.3%) decreases slightly in this zone, with Filicales Monolete (3.4 - 10.7%), *Polypodium vulgare* (0.8 - 2.1%), Cyperaceae (0.2 - 2.4%) and Filicales Trilete (0.3 - 3.4%) as most representative (Fig. R.19).

Lastly, non-pollen palynomorphs (NPPs) maintain similar percentages (0.2 - 1.6%) to those of LPAZ ANB-3, with all identified taxa (*Sordaria* sp., *Chaetomium* sp., *Spyrogira* sp., *Pseudoschizaea circula*, *Glomus* cf. *fasciculatum* and *Sporormiella* sp.) exhibiting less than 1% abundance in any case (Fig. R.19).

### 2.3.2. Geochronology and depth-age model

A total of 6 samples were sent to Beta Analytic laboratories for radiocarbon dating (Table R.9). Calibration was performed using the IntCal20 method (Reimer et al., 2020). All calibrations were performed with Calib 8.20 software (Reimer et al., 2020; Stuiver et al., 2020).

The oldest recorded age corresponds to the sample at 304 cm depth that has an age of 3790±30 yr BP. On the other hand, at 274 cm depth the most recent date has been obtained: 3420±30 yr BP. This implies that all the dates were obtained in LPAZ ANB-4 and are located between 4300 and 3700 cal. yr BP.

The depth-age model presented here (Fig. R.20) has been performed with the R Clam 2.2 software package. The best fit was obtained by performing a smoothing spline to the available radiocarbon dates. The confidence intervals of the calibrations and of the depth-age model were calculated at 95% (2σ) with 1000 iterations. A representation of the pollen zones affected by the dates obtained as depth function and the cluster analysis performed through the pollen analysis have also been included.

According to the calibration of the dates, the oldest date obtained would be 4257 cal. yr BP. That is why, observing the evolution of the depth-age model, we can say that, for the lower undated pollen zones, it is probable that ages are older than 4000 years BP.

**Table R.9** - Radiocarbon results from the Anbeko borehole.

| LAB CODE | SAMPLE | MATERIAL | METHOD | DEPTH (cm) | CONVENTIONAL AGE (years BP) | CALIBRATED AGE (cal. years BP) |
|---|---|---|---|---|---|---|
| Beta - 562898 | ANB-272 | Plant | AMS-Standard delivery | 272 | 3480 ± 30 | 3838 - 3686 |
| Beta - 562899 | ANB-274 | Plant | AMS-Standard delivery | 274 | 3420 ± 30 | 3725 - 3584 |
| Beta - 562900 | ANB-279 | Plant | AMS-Standard delivery | 279 | 3620 ± 30 | 3988 - 3843 |
| Beta - 562901 | ANB-289 | Plant | AMS-Standard delivery | 289 | 3560 ± 30 | 3929 - 3817 |
| Beta - 562902 | ANB-304 | Plant | AMS-Standard delivery | 304 | 3790 ± 30 | 4257 - 4084 |
| Beta - 562903 | ANB-319 | Plant | AMS-Standard delivery | 319 | 3770 ± 30 | 4239 - 4080 |

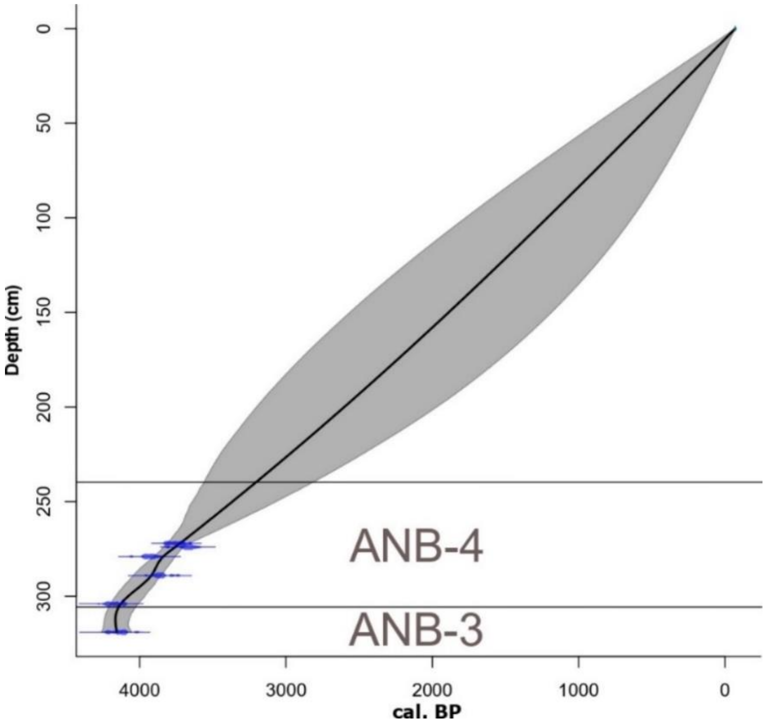


**Figure R.20** - Depth-age model of the Anbeko borehole. The defined local pollen assemblage zones (LPAZ ANB) that could be directly dated are also represented.

## 2.4. Ozollo

### 2.4.1. Pollen analysis

The stratigraphically constrained cluster analysis by the incremental sum of squares (CONISS) method performed for the Ozollo borehole has enabled us to identify four local pollen assemblage zones (LPAZ OZO).

**Table R.10 -** Summary of the most representative taxa (relative abundance %) identified in the Ozollo borehole. The single value represents the average and those in parentheses give the range. The percentages of hydro-hygrophilous taxa and NPPs are calculated separately together with the rest of the taxa.

| | **OZO - 1** | **OZO - 2** | **OZO - 3** | **OZO - 4** |
|---|---|---|---|---|
| *Alnus* | 18 (8.7 - 25.3) | 20 (15.1 - 25.1) | 21 (11.9 - 35.6) | 12 (5.9 - 23.3) |
| *Betula* | 12 (4.2 - 18.2) | 12 (6.5 - 18.3) | 13 (9.1 - 24.4) | 7 (2.7 - 12.2) |
| deciduous *Quercus* | 27 (22.7 - 32.6) | 28 (20.8 - 35.8) | 26 (19.6 - 34.8) | 23 (12.6 - 35.4) |
| *Fagus sylvatica* | 6 (3.5 - 7.9) | 7 (2.8 - 13.6) | 8 (2 - 29.1) | 5 (2 - 7.6) |
| *Pinus pinaster* | 9 (3.7 - 18.5) | 8 (2.6 - 10.1) | 7 (1.9 - 11) | 17 (8.1 - 41.7) |
| *Cerealia* type | 0.1 (0 - 0.2) | 0.1 (0 - 0.4) | 0.1 (0 - 0.4) | 0.1 (0 - 0.4) |
| Chenopodiaceae | 9 (3.1 - 16.8) | 8 (5.6 - 12.3) | 8 (2.7 - 12.8) | 18 (7.4 - 45.8) |
| Filicales Monolete | 5 (0 - 7.9) | 6 (1.9 - 7.6) | 5 (3 - 8.2) | 11 (5.9 - 24.9) |
| *Sordaria* sp. | 1 (0 - 2.8) | 2 (0.1 - 5.4) | 1 (0.3 - 3.2) | 1 (0 - 1.7) |
| TREES | 78 (65.1 - 83.5) | 79 (72.7 - 83.9) | 80 (75.4 - 89.5) | 70 (48.7 - 81.5) |
| SHRUBS | 2 (0.8 - 2.9) | 1 (0.4 - 3.6) | 2 (0.4 - 3.1) | 2 (0.4 - 2.5) |
| HERBS | 20 (15.6 - 33.5) | 20 (15.2 - 25.5) | 18 (8.6 - 21.9) | 28 (16 - 51) |
| HYDRO-HYGROPHILOUS | 29 (0 - 45.6) | 29 (23.2 - 36.3) | 27 (15.2 - 37.9) | 40 (22.9 - 59.7) |
| NPPs | 2 (0 - 6.7) | 3 (1 - 7.4) | 2 (0.5 - 4.3) | 2 (0.8 - 5.6) |

### LPAZ OZO-1 (524 - 430 cm) (2470±30 yr BP)

The percentages of arboreal pollen (65.1 - 83.5%) for this basal pollen zone in the borehole make this type of pollen the predominant one (Fig. R.21). Deciduous

*Quercus* (22.7 - 32.6%) is the most dominant taxon among the identified trees. Other taxa also have a notable presence, such as *Alnus* (8.7 - 25.3%), *Betula* (4.2 - 18.2%), *Fagus sylvatica* (3.5 - 7.9%) and *Pinus sylvestris* type (0.8 - 5.2%). *Corylus*, evergreen *Quercus* and *Tilia* have also been identified, but in percentages of less than 4% each of them.

On the right side of Figure R.21, we can see that shrub pollen has low percentage values (0.8 - 2.4%) compared to tree pollen. Various taxa have been identified (*Arbutus* type, *Calluna vulgaris*, *Erica* type, Labiatae, *Prunus* type) but all of them have values below 2% in any case.

Herbaceous pollen (Fig. R.22) appears in higher percentages than those observed for shrubs. Their abundances range from 15.6 to 35.5%. The most dominant herb is Chenopodiaceae, which ranges from 3.6 to 16.8%. Secondarily, the taxa with more presence are Apiaceae (0.6 - 14.1%), Cichorioideae (0 - 7.1%) and Poaceae (3 - 6.6%). Other herbs identified, although in percentages less than 1% abundance, are *Artemisia*, *Aster* type, Cardueae, Caryophyllaceae, *Centaurea nigra* type, *Cerealia* type and *Plantago lanceolata* type.

Regarding the hydro-hygrophilous pollen (Fig. R.23), its percentages are quite high (22.2 - 45.6%). Among the taxa identified, Filicales Monolete is the most dominant (0 - 7.9%). Other taxa, such as Cyperaceae (0 - 1.9%), Filicales Trilete (0 - 5.1%) and *Polypodium vulgare* type (0 - 2.8%), have also been identified.

In the same Figure R.23, on the right side, we can see that the percentage of non-pollen palynomorphs (NPPs) is between 0 and 6.7%. The taxa *Chaetomium* sp., *Glomus* cf. *fasciculatum*, *Pseudoschizaea circula*, *Sordaria* sp., *Spyrogira* sp. and *Sporormiella* sp. have been found. None of these taxa individually exceeds 3% in percentage values. Only *Sordaria* sp. exhibits a certain regularity (0 - 2.8%).

### LPAZ OZO-2 (430 - 272 cm) (3670±30 - 1860±30 yr BP)

In Figure R.21, on the left side, we can observe that the assemblage of arboreal pollen is similar to that in the previous pollen zone. The overall percentages are high (72.4 - 83.9%) and, therefore, the predominance of arboreal pollen seems clear. The small increase in the minimum values results in minor generalized increases, such as those observed for the predominant taxon, deciduous *Quercus* (20.8 - 35.8%). Species such as *Fagus sylvatica* (2.8 - 13.6%) and *Pinus pinaster* (2.6 - 10.1%) also experience these small percentage increases. Despite this, the taxa with the secondary presence continue to be *Alnus* (15.1 - 23.8%) and *Betula* (6.5 - 18.3%). *Abies alba*, *Corylus*, *Fraxinus* and *Tilia* have also been identified in this pollen zone, although with percentages lower than 3% in any case.

Shrub pollen also shows the same regular trend (0.4 - 3.6%) (Fig R.21). The most significant taxa are also the same as in the previous basal zone: *Arbutus* type, *Calluna vulgaris*, *Erica* type, Labiatae and *Prunus* type. Individually, the percentages do not exceed 1%.

Herbaceous plants, meanwhile, see their percentages reduced in some samples during LPAZ OZO-2 (15.2 - 25.5%) as can be observed for the taxon with the highest presence, Chenopodiaceae (5.6 - 12.3%) (Fig. R.22). The secondary taxa continue to be Apiaceae (1.2 - 4.1%), Cichorioideae (0.8 - 10.1%) and Poaceae (2 - 9.1%), while the rest of the identified herbs (*Artemisia*, *Aster* type, Cardueae, Caryophyllaceae, *Centaurea nigra* type, *Cerealia* type and *Plantago lanceolata* type) barely exceed 1% each.

In Figure R.23, on the left side, we can observe the presence of the hydro-hygrophilous plants in this zone. Their general percentages are between 23.2 and 36.3%. This represents a small reduction in the presence of this pollen type as compared with the previous basal zone. The percentage values for the most representative taxa are: Filicales Monolete (1.9 - 7.4%), Cyperaceae (0.4 - 2.1%), Filicales Trilete (1.3 - 4.8%) and *Polypodium vulgare* (0.4 - 2.9%).

On the right side of Figure R.23, we can observe that the non-pollen palynomorphs (NPPs) experience a general increase (1 - 7.4%). This can be verified in the abundance of the dominant taxon, *Sordaria* sp., which now has a percentage range between 0.5 and 5.4%. *Chaetomium* sp., *Glomus* cf. *fasciculatum*, *Pseudoschizaea circula*, *Spyrogira* sp. and *Sporormiella* sp. never reach 2% individually.

### LPAZ OZO-3 (272 - 175 cm) (1150 ± 30 yr BP)

Arboreal pollen also predominates in this pollen zone and its percentages (75.4 - 89.5%) continue to be very high, even higher than in the previous zone (Fig. R.21). The dominant taxon is deciduous *Quercus* (19.6 - 34.8%), but *Alnus* is experiencing a slight growth in this zone, reaching percentages between 11.9 and 35.6%. In some samples, the values of *Alnus* are even higher than those observed for deciduous *Quercus*. *Betula* (9.4 - 24.5%) and *Fagus sylvatica* (2 - 29.1%) are also experiencing an increase, which is not synchronous but is close in temporal terms. Other taxa identified include *Pinus pinaster* (1.9 - 11%), *Pinus sylvestris* (0.4 - 3.1%), *Abies alba* (0 - 0.2%), *Corylus* (0.4 - 2.7%) and *Tilia* (0.2 - 2.9%).

On the right side of Figure R.21, we can observe that the percentage of shrub taxa (0.4 - 3.1%) remains practically unchanged with respect to the previous zone. This similarity can also be seen in the identified taxa themselves (*Arbutus* type, *Calluna* *vulgaris*, *Erica* type, Labiatae and *Prunus* type), all of them below 1.5% abundance. The only novelty is the identification of scarce *Ilex aquifolium*.

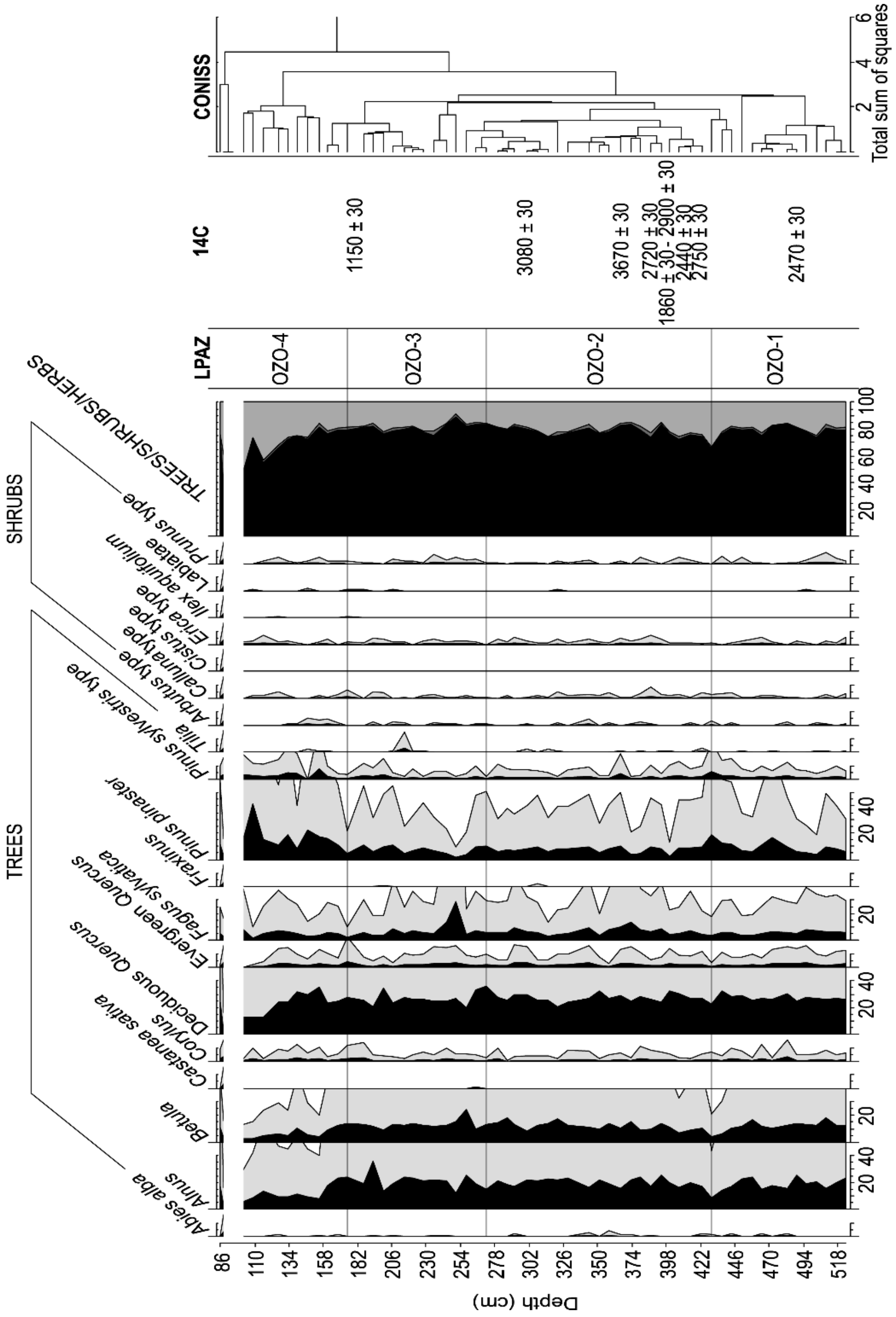


**Figure R.21** - Pollen diagram corresponding to the arboreal and shrub pollen along the Ozollo borehole. Depth at centimeter scale, the evolution of arboreal and shrub taxa, the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

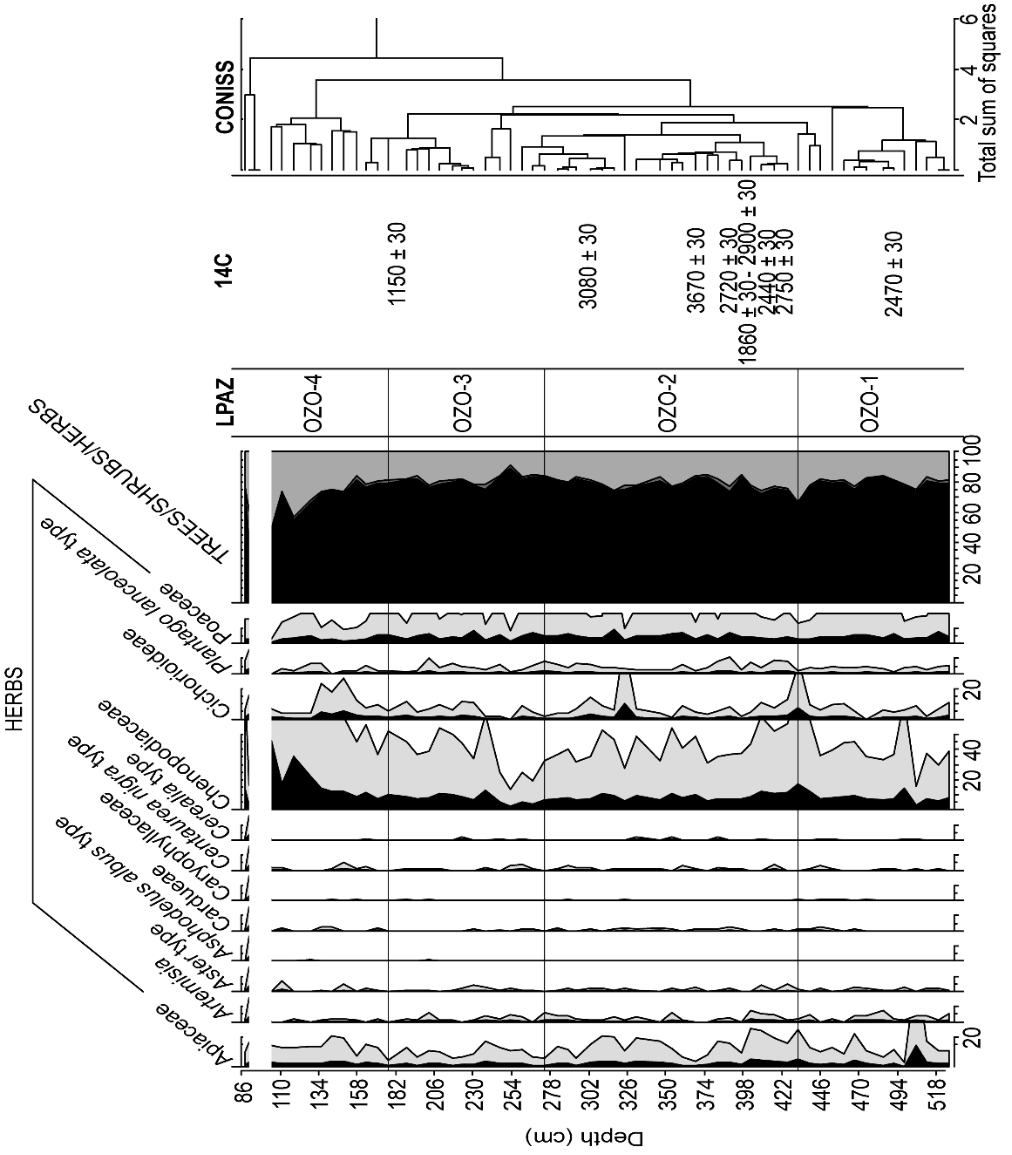


**Figure R.22** - Pollen diagram corresponding to the herbaceous pollen along the Ozollo borehole. Depth at centimeter scale, the evolution of herbaceous taxa, the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

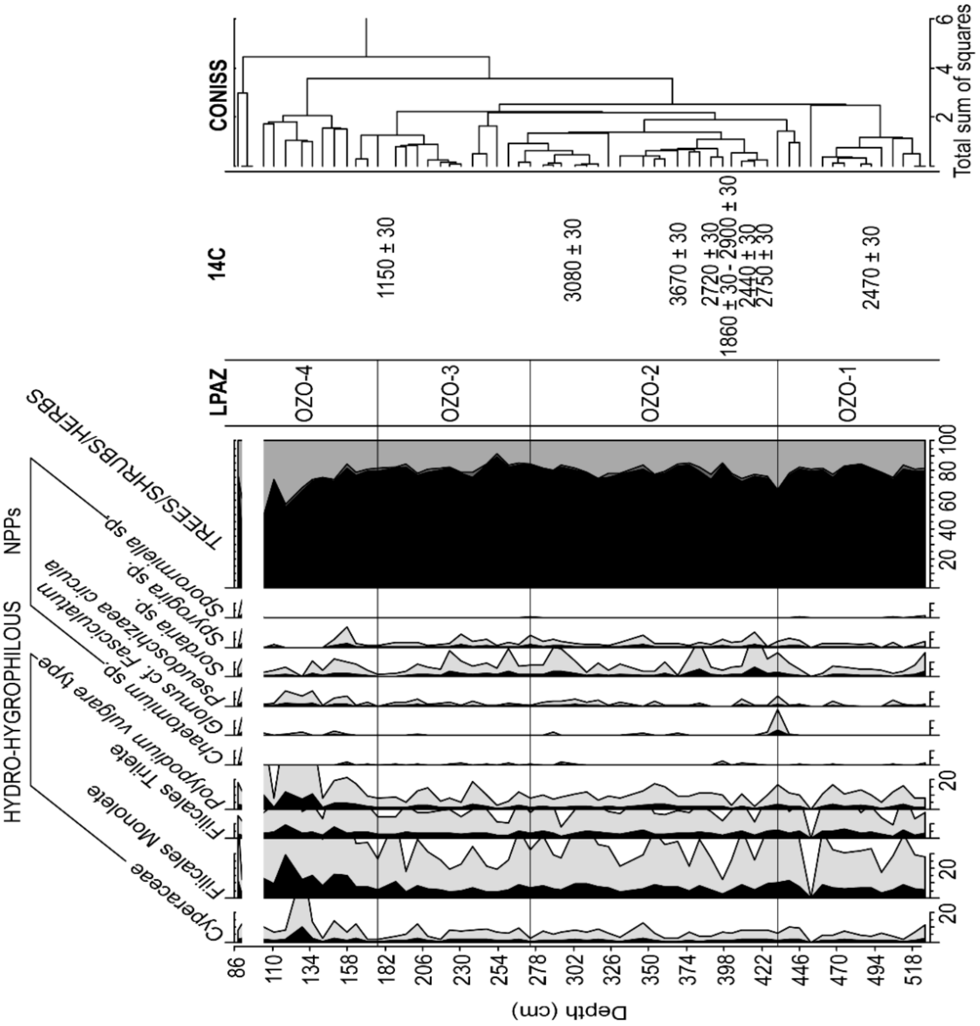


**Figure R.23** - Pollen diagram corresponding to the hydro-hygrophilous pollen and non-pollen palynomorphs (NPPs) along the Ozollo borehole. Depth at centimeter scale, the evolution of hydro-hygrophilous and the NPPs taxa, the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

The situation is similar as regards the herbaceous pollen, whose abundance shows a regularity with respect to the previous pollen zones (8.9 - 21.6%) (Fig. R.22). In fact, the same structure is maintained in terms of taxon dominance. The most dominant is Chenopodiaceae, with percentages between 4.9 and 10.8%. Poaceae (1.7 - 8.7%), Apiaceae (0.9 - 3.5%) and Cichorioideae (0 - 2.4%) are secondary in LPAZ OZO-3. The remaining taxa (*Artemisia*, *Aster* type, Cardueae, Caryophyllaceae, *Centaurea nigra* type, *Cerealia* type and *Plantago lanceolata* type) reach a maximum of 2% in any case. The presence of a new taxon, *Asphodelus albus* type (0 - 0.2%), has been identified.

Hydro-hydrophyte pollen is also present with the same levels of abundance as in the previous zone (15.2 - 37.9%) (Fig. R.23). The identified taxa are Filicales Monolete (3 - 8.2%), Filicales Trilete (1.8 - 3.8%), *Polypodium vulgare* (0.5 - 2.2%) and Cyperaceae (0.3 - 2.1%).

To conclude with this pollen zone, to the right side of Figure R.23, we can observe that the abundance of the non-pollen palynomorphs (NPPs) (0.5 - 4.3%) is reduced, as occurs with the pollen of minor predominance. However, these lower values can be better observed in the individual percentages, with *Sordaria* sp. barely exceeding 3% in some samples. Meanwhile, the rest of the taxa (*Chaetomium* sp., *Glomus* cf. *fasciculatum*, *Pseudoschizaea circula*, *Spyrogira* sp. and *Sporormiella* sp.) rarely reach 1% in each case.

### LPAZ OZO-4 (175 - 86 cm)

There are no precise dates available for this uppermost section of the borehole, so we cannot determine the age of this pollen zone. The most recent dating is at 176 cm depth, which may indicate that temporally this zone should be younger than 1150±30 yr BP. Moreover, and regarding the pollen analysis, two sterile samples have been found, which correspond to 88 and 95 cm depth (Figs. R.21, R.22, R.23).

Figure R.21 shows that in this final zone the dynamics of arboreal pollen undergoes a general decrease (48.7 - 81.5%). Although it is not a very pronounced decrease, it is sufficient to detect changes when the taxa are analyzed individually. For example, the percentages of deciduous *Quercus* (12.6 - 31.5%), *Alnus* (8 - 23.3%), *Betula* (3 - 12.2%) and *Fagus sylvatica* (2 - 7.6%) decline compared with the previous zones. Another taxon experiencing a small decrease is *Pinus sylvestris* type (0 - 7.8%). *Abies alba*, *Corylus* and *Tilia* are below 3% each.

The shrub pollen scarcely varies compared to the previous zone (Fig. R.21). It follows the same trend throughout the borehole, with total percentages for LPAZ

OZO-4 between 0.4 and 2.5%. The taxa found here are *Arbutus* type, *Calluna vulgaris*, *Erica* type, Labiatae, *Prunus* type and *Ilex aquifolium*. These taxa never exceeded 1.5% individually.

We can observe a notorious difference in the evolution of the herbaceous pollen. Throughout LPAZ OZO-4, herbaceous pollen increases (16 - 51%) compared with the previous pollen zones (Fig. R.22). If we focus the analysis on the individual taxa, we can see that the predominant family, Chenopodiaceae, considerably increases its percentages from around 127 cm depth to the top. This means that, despite not being regular, this taxon ends up reaching a percentage range between 7.4 and 45.8%. Other forms, such as Cichorioideae (0.8 - 5.4) and Apiaceae (1.5 - 4.2%), are also increasing but not so abruptly. Poaceae percentages decrease slightly (0.6 - 5.8%). The rest of the identified taxa (*Artemisia* type, *Aster* type, Cardueae, Caryophyllaceae, *Centaurea nigra* type, *Cerealia* type and *Plantago lanceolata* type) maintain values very similar to those already detected in other zones of this Ozollo borehole.

Hydro-hygrophilous pollen also shows an increasing trend with respect to the previous zone (22.9 - 59.7%) (Fig. R.23). The dominant taxon Filicales Monolete now displays values between 9.6 and 24.9%. Filicales Trilete (2.4 - 8.3%), *Polypodium vulgare* (1.3 - 9.7%) and Cyperaceae (0.3 - 9.4%) also increase in this zone.

Finally, the non-pollen palynomorphs (NPPs) abundance, 0.8 - 5.3%, continues the same trend observed previously in LPAZ OZO-3. All taxa identified (*Sordaria* sp., *Chaetomium* sp., *Glomus* cf. *fasciculatum*, *Pseudoschizaea circula* and *Spyrogira* sp.) have individual percentages lower than 2.5% (Fig. R.23).

### 2.4.2. Geochronology and age-depth model

A total of nine samples (seven marine and two terrestrial) (Table R.11) were selected for radiometric analysis from the Ozollo borehole. The IntCal20 calibration curve was used for the terrestrial samples, while the Marine 20 curve was used for the marine samples where the corresponding local reservoir effect (ΔR = -7 ± 50 years) was applied to the calibration. All calibrations were performed with Calib 8.20 software (Tisnérat et al., 2010; Heaton et al., 2020; Reimer et al., 2020; Stuiver et al., 2020).

As shown in Table R.11, the dates obtained from the marine remains (shells) present older ages than those dates obtained from the terrestrial remains (plants). A time-reversal in the ages from the shells can also be observed. These two issues will be treated in more detail in the Discussion section.

The oldest age corresponds to 386 cm depth (3670±30 yr BP) while the most recent one comes from 176 cm depth (1159±30 yr BP). Therefore, the temporal lapse covered by the radiocarbon dated section of this borehole is between 3720 cal. yr BP and 967 cal. yr BP (Table R.11).

**Table R.11** - Radiocarbon results from the Ozollo borehole.

| LAB CODE | SAMPLE | MATERIAL | METHOD | DEPTH (cm) | CONVENTIONAL AGE (years BP) | CALIBRATED AGE (cal. years BP) |
|---|---|---|---|---|---|---|
| Beta-590121 | OZO-176 | Plant | AMS-Standard delivery | 176 | 1150 ±30 | 967 - 961 |
| Beta-590124 | OZO-289 | Shell | AMS-Standard delivery | 289 | 3080 ±30 | 3004 - 2624 |
| Beta-590125 | OZO-386 | Shell | AMS-Standard delivery | 386 | 3670 ± 30 | 3720 - 3329 |
| Beta-590126 | OZO-396 | Shell | AMS-Standard delivery | 396 | 2720 ± 30 | 2608 - 2152 |
| Beta-590127 | OZO-398 | Plant | AMS-Standard delivery | 398 | 1860 ±30 | 1831 - 1707 |
| Beta-590128 | OZO-398B | Shell | AMS-Standard delivery | 398 | 2900 ± 30 | 2753 - 2370 |
| Beta-590129 | OZO-401 | Shell | AMS-Standard delivery | 401 | 2440 ± 30 | 2244 - 1812 |
| Beta-590130 | OZO-402 | Shell | AMS-Standard delivery | 402 | 2750 ± 30 | 2655 - 2205 |
| Beta-590135 | OZO-519 | Shell | AMS-Standard delivery | 519 | 2470 ± 30 | 2281 - 1861 |

As in previous cases, a depth-age model was performed using the "R" software and the Clam 2.2 package. In the case of this Ozollo borehole, the best fit (inverted dates included) was obtained by performing a linear interpolation (Fig. R.24). The confidence intervals of both the calibrations and depth-age model were calculated at 95% (2σ) with 1000 iterations. A representation of the pollen zones involved has also been included.

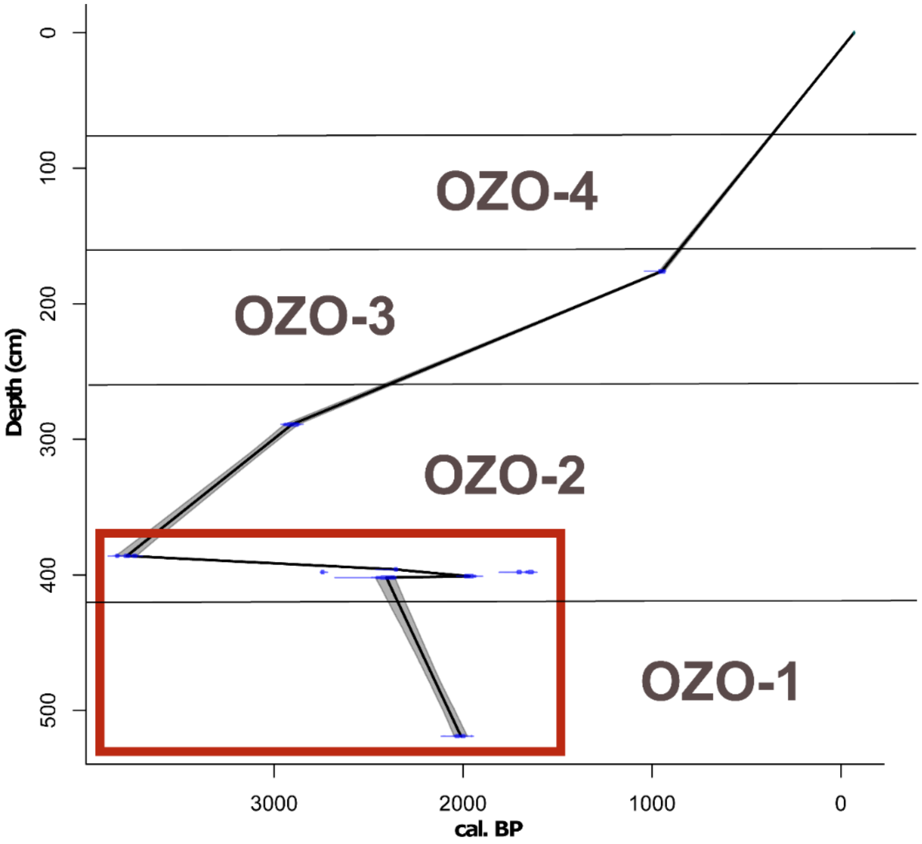


**Figure R.24** - Depth-age model of the Ozollo borehole. The defined local pollen assemblage zones (LPAZ OZO) are also represented. The red frame indicates radiocarbon samples with inverted ages.

### 2.4.3. Paleoclimate reconstruction

The quantitative paleoclimate reconstruction of the Ozollo borehole has been carried out by means of a WA-PLS-based transfer function model under cross-validation. A total of 389 harmonized pollen taxa were used in order to perform the quantitative reconstruction.

The reconstruction was again carried out on two components, mean annual temperature (TANN) and mean annual precipitation (PANN). The coefficient of determination $R^2$ resulted in 0.80 for TANN and 0.50 for PANN. Regarding the root-mean square error of prediction (RMSEP), the values were 3.24 ºC/yr and 284.47 mm/yr respectively. Finally, the maximum bias has shown a value of 7.58 ºC/yr for temperatures and 2318.7 mm/yr for precipitation.

The range of mean annual temperatures observed after the paleoclimate reconstruction is 8 - 11 ºC/yr and mean annual precipitation ranges from 670 - 943 mm/yr (Fig. R.25).

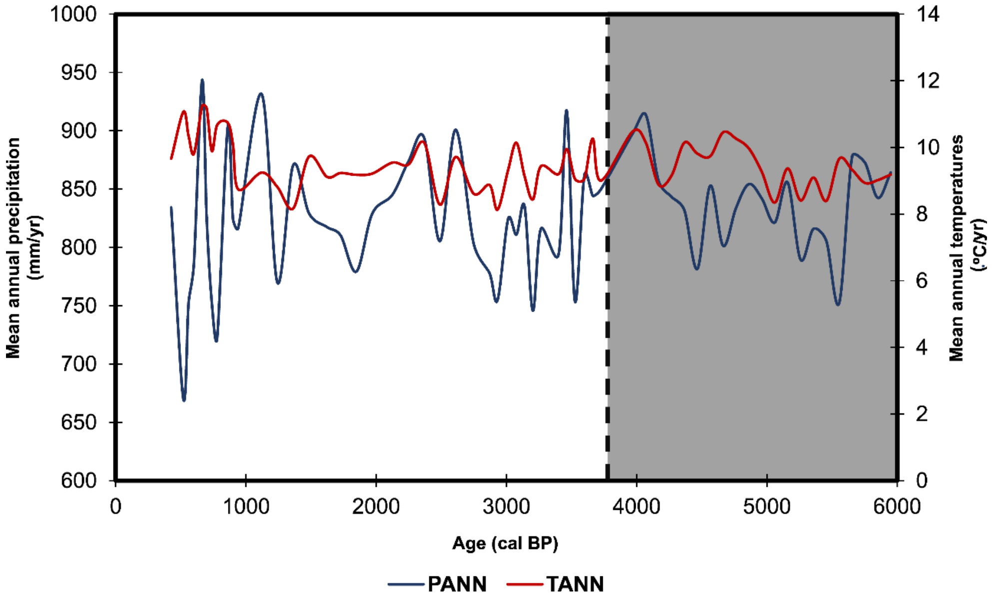


**Figure R.25** - Quantitative paleoclimate reconstruction results from the Ozollo borehole (6000 - ~ 400 cal. yr BP). In red, the evolution of the mean annual temperature. In blue, the evolution of the mean annual precipitation. The gray background area represents the inverted radiocarbon samples and therefore the dates are not precise.

### 2.4.4. SiZer analysis

At the end of the borehole (corresponding to LPAZ OZO-4) a notable increase in Chenopodiaceae pollen is detected (Fig. R.22). This increase also coincides with the abundance decreases of arboreal taxa such as *Alnus*, *Betula* and deciduous *Quercus* (Fig. R.21). Therefore, we decided to submit these data to a significance analysis to see if these changes in the pollen record are statistically significant and to characterize the observed increases and decreases in ecological records over time.

The depth-age model shows that this increase appears to be temporally framed around 700 cal. yr BP. In turn, the beginning of this increase would correspond to 127 cm depth. Consequently, in order to verify the significance of these changes, the different taxa involved were subjected to a SiZer (Significant Zero Crossings) analysis.

The results obtained are interesting, since the resolution of the pollen analysis and the dates obtained are sufficient to perform a reliable SiZer analysis. As can be observed in the different mappings obtained (Figs. R.26, R.27, R.28, R.29), both for the increase in Chenopodiaceae and for the decreases in tree taxa, SiZer detects significance.

Regarding Chenopodiaceae (Fig. R.26), SiZer has not only detected the increase of this taxon at 700 cal. yr BP, but it has also identified a small reduction around 2800 cal. yr BP.

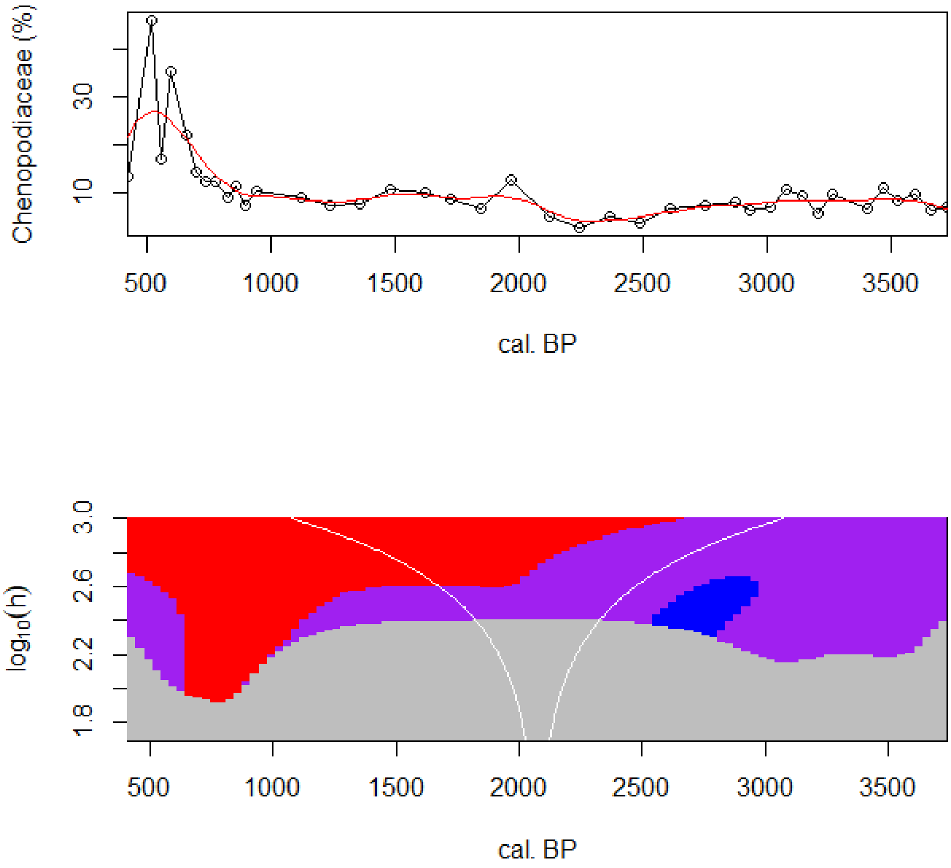


**Figure R.26** - SiZer map of the Ozollo borehole with the analysis of Chenopodiaceae abundance. The SiZer map categorizes the significance in blue (decreasing), red (increasing) or purple (possibly zero). The bandwidth is h = 30.

In the case of *Alnus* and *Betula* (Fig. R.27, R.28), the SiZer analysis and the depth-age model indicate the start of their decrease earlier (900 cal. yr BP) than the beginning of the Chenopodiaceae increase.

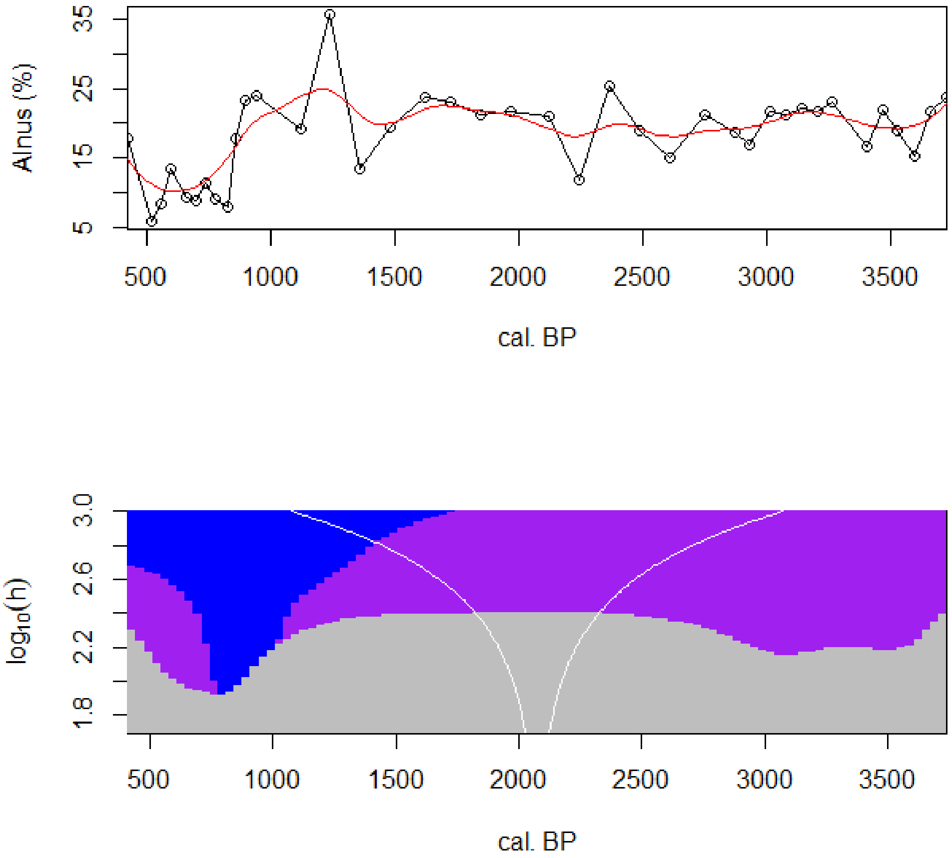


**Figure R.27** - SiZer map of the Ozollo borehole with the analysis of the *Alnus* abundance. The SiZer map categorizes the significance in blue (decreasing), red (increasing) or purple (possibly zero). The bandwidth is h = 30.

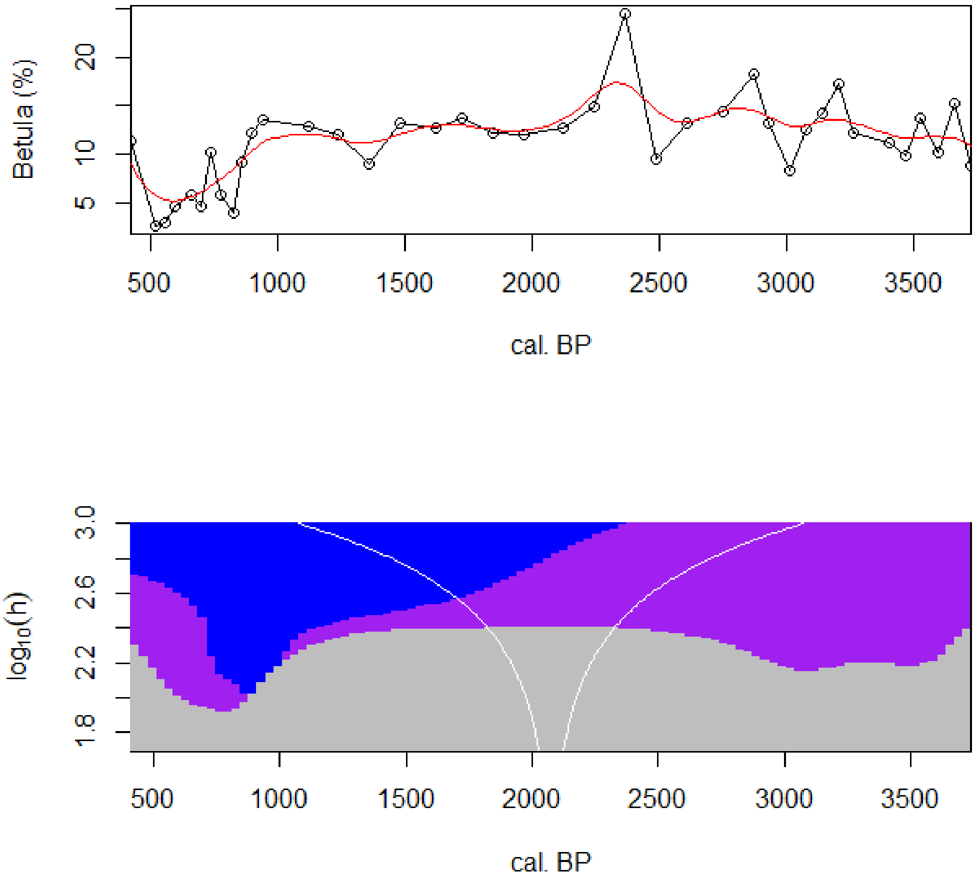


**Figure R.28** - SiZer map of the Ozollo borehole with the analysis of the *Betula* abundance. The SiZer map categorizes the significance in blue (decreasing), red (increasing) or purple (possibly zero). The bandwidth is h = 30.

However, the SiZer analysis detects also that the temporal reduction of deciduous *Quercus* takes place later in time (600 cal. yr BP) than the decrease observed for *Alnus* and *Betula*. Therefore, this reduction in deciduous *Quercus* abundance is closer in time to the increase in Chenopodiaceae (Fig. R.29).

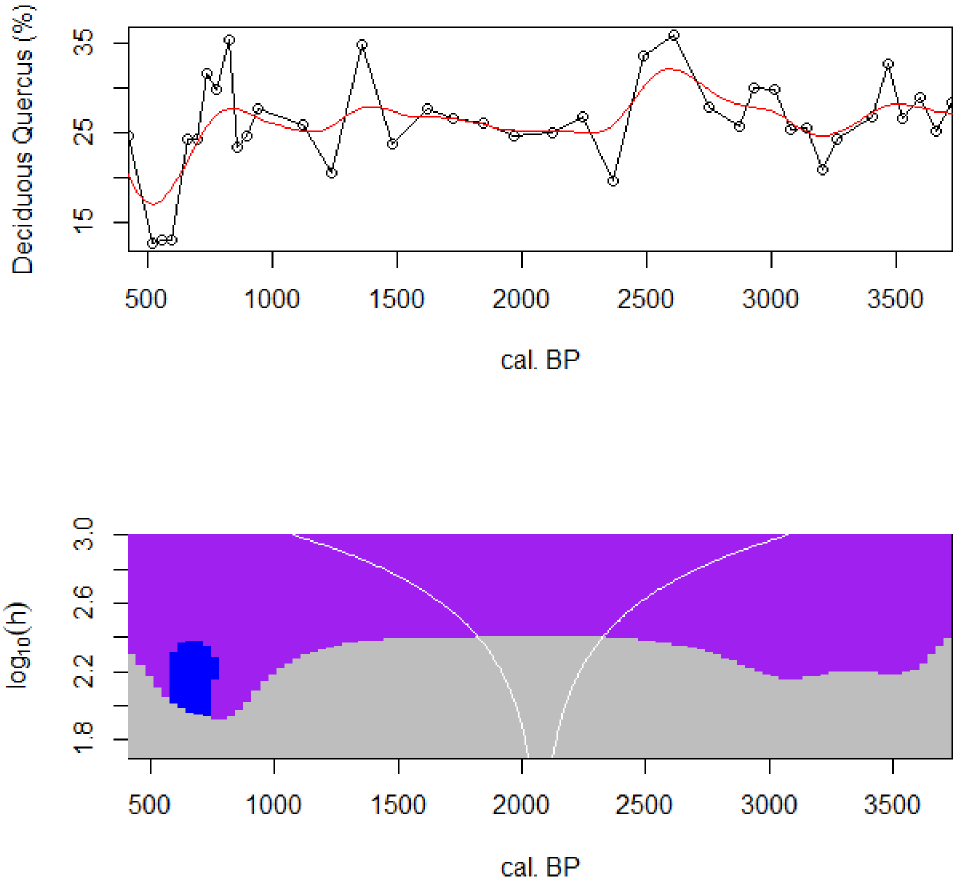


**Figure R.29** - SiZer map of the Ozollo borehole with the analysis of the deciduous *Quercus* abundance. The SiZer map categorizes the significance in blue (decreasing), red (increasing) or purple (possibly zero). The bandwidth is h = 30.

# 3. Anthropocene

## 3.1. Miengo

### 3.1.1. Pollen analysis

The Miengo core has been divided into three LPAZ MIE through stratigraphically constrained cluster analysis by the method of incremental sum of squares (CONISS).

**Table R.12 -** Summary of the most representative taxa identified (relative abundance %) in the Miengo core. The single value represents the average and those in parentheses give the range. The percentages of hydro-hygrophilous taxa and NPPs are calculated separately together with the rest of the taxa.

| | **MIE - 1** | **MIE - 2** | **MIE - 3** |
|---|---|---|---|
| *Alnus* | 14 (10.8 - 17.8) | 14 (8.3 - 19.1) | 20 (18.7 - 21) |
| *Betula* | 19 (17.3 - 20.4) | 19 (16.6 - 21.4) | 22 (19.9 - 24.2) |
| *Eucalyptus* sp. | 0.2 (0 - 0.7) | 0.3 (0.2 - 0.5) | 1 (0.4 - 1.1) |
| deciduous *Quercus* | 11 (8.6 - 13.7) | 10 (7.6 - 13.3) | 9 (7.2 - 9.8) |
| *Pinus pinaster* | 6 (2.9 - 6.6) | 9 (5 - 12.7) | 14 (8.2 - 19.1) |
| *Cerealia* type | 0.4 (0.2 - 0.7) | 0.2 (0 - 0.5) | 0.2 (0 - 0.8) |
| Cichorioideae | 5 (3.9 - 8.4) | 3 (1.3 - 6.3) | 1 (0.5 - 1.2) |
| Poaceae | 20 (16.1 - 25.3) | 23 (20.3 - 26.5) | 13 (9.1 - 16) |
| Cyperaceae | 3 (2.7 - 5.8) | 4 (1.6 - 5.8) | 2 (1.3 - 3.5) |
| Filicales Monolete | 7 (6 - 9.7) | 5 (4.4 - 8.4) | 5 (4.1 - 7.6) |
| *Sordaria* sp. | 4 (2.8 - 7.1) | 1 (0.8 - 2.5) | 1 (0.5 - 1.7) |
| TREES | 59 (55.9 - 63.5) | 61 (54.4 - 67.5) | 77 (71.5 - 82.1) |
| SHRUBS | 5 (2.3 - 6.9) | 3 (1.6 - 5.2) | 2 (0.4 - 2.4) |
| HERBS | 36 (32.1 - 38.7) | 35 (29.9 - 40.4) | 21 (15.5 - 27) |
| HYDRO-HYGROPHILOUS | 26 (22.3 - 29.8) | 23 (16.5 - 29.9) | 16 (13 - 17.9) |
| NPPs | 5 (3.1 - 7.5) | 2 (1.3 - 3.2) | 1 (0.9 - 2) |

### LPAZ MIE-1 (49 - 27 cm) (1830 - 1914 CE)

Starting with the arboreal pollen, the total percentages observed in Figure R.30 oscillate between 55.9 and 63.5. This makes this type of pollen the predominant one in this zone. The dominant taxon is *Betula* (17.3 - 20.4%). *Alnus* (10.8 - 17.8%) and deciduous *Quercus* (8.6 - 13.7%) are also found in significant abundance together with *Pinus pinaster* (2.9 - 6.6%). Other taxa (*Castanea*, *Corylus*, *Eucalyptus* sp., evergreen *Quercus*, *Fagus sylvatica*, *Fraxinus*, *Pinus sylvestris* type and *Salix*) have also been identified, each one below 5% abundance.

In the same Figure R.30, on the right, we can see how shrub taxa are concentrated in percentages between 2.3 and 6.9%. Three forms were identified: *Arbustus* type (0 - 1.6%), *Erica* type (1.4 - 4.1%) and *Prunus* type (0.6 - 2.1%).

The most represented pollen type after trees is herbaceous plants. Their total percentages range from 32.1 to 38.7% (Fig. R.31). Poaceae is the most dominant family among the herbs (16.1 - 25.3%) followed by Cichorioideae (3.9 - 8.4%). The remaining taxa identified are Apiaceae, Artemisia, *Aster* type, Cardueae, Caryophyllaceae, *Centaurea nigra* type, *Cerealia* type, Chenopodiaceae, Fabaceae, *Plantago coronopus* type, *Plantago lanceolata* type and *Polygonum aviculare*. None of these taxa individually exceeds 5% abundance. In any case, the most remarkable of these is *Plantago lanceolata* (1.1 - 4.4%).

In the case of the hydro-hygrophilous plants, the percentages are also significant (22.3 - 29.8%) (Fig. R.32). Among the three taxa identified, Filicales Monolete is the one with the highest representation (6 - 9.7%). The other two are Filicales Trilete (3 - 6.1%) and Cyperaceae (2.7 - 5.8%).

To conclude with LPAZ MIE-1, the non-pollen palynomorphs (NPPs) show percentage values of abundance between 3.1 and 7.5% (Fig. R.32). The presence of *Sordaria* sp. stands out (2.8 - 7.1%) while *Chaetomium* sp., *Globus* cf. *fasciculatum, Pseudochizaea circula* sp. and *Spyrogira* sp. do not exceed 1% in any case.

### LPAZ MIE-2 (27 - 10 cm) (1914 - 1983 CE)

Arboreal pollen increased in this pollen zone (54.4 - 67.5%) (Fig. R.30). Although the dominant taxon is still *Betula* (16.6 - 21.4%), the percentages of *Alnus* (8.3 - 19.1%) and *Pinus pinaster* (5 - 12.7%) are those that really increase here. Deciduous *Quercus* also has a relevant presence (7.6 - 13.3%). *Castanea*, *Corylus*, *Eucalyptus* sp., evergreen *Quercus*, *Fagus sylvatica*, *Fraxinus*, *Pinus sylvestris* type and *Salix* are found in values below 6% individually. It is interesting to note that the presence of *Eucalyptus* sp. stabilized for the first time in this zone of the core, appearing in all its samples.

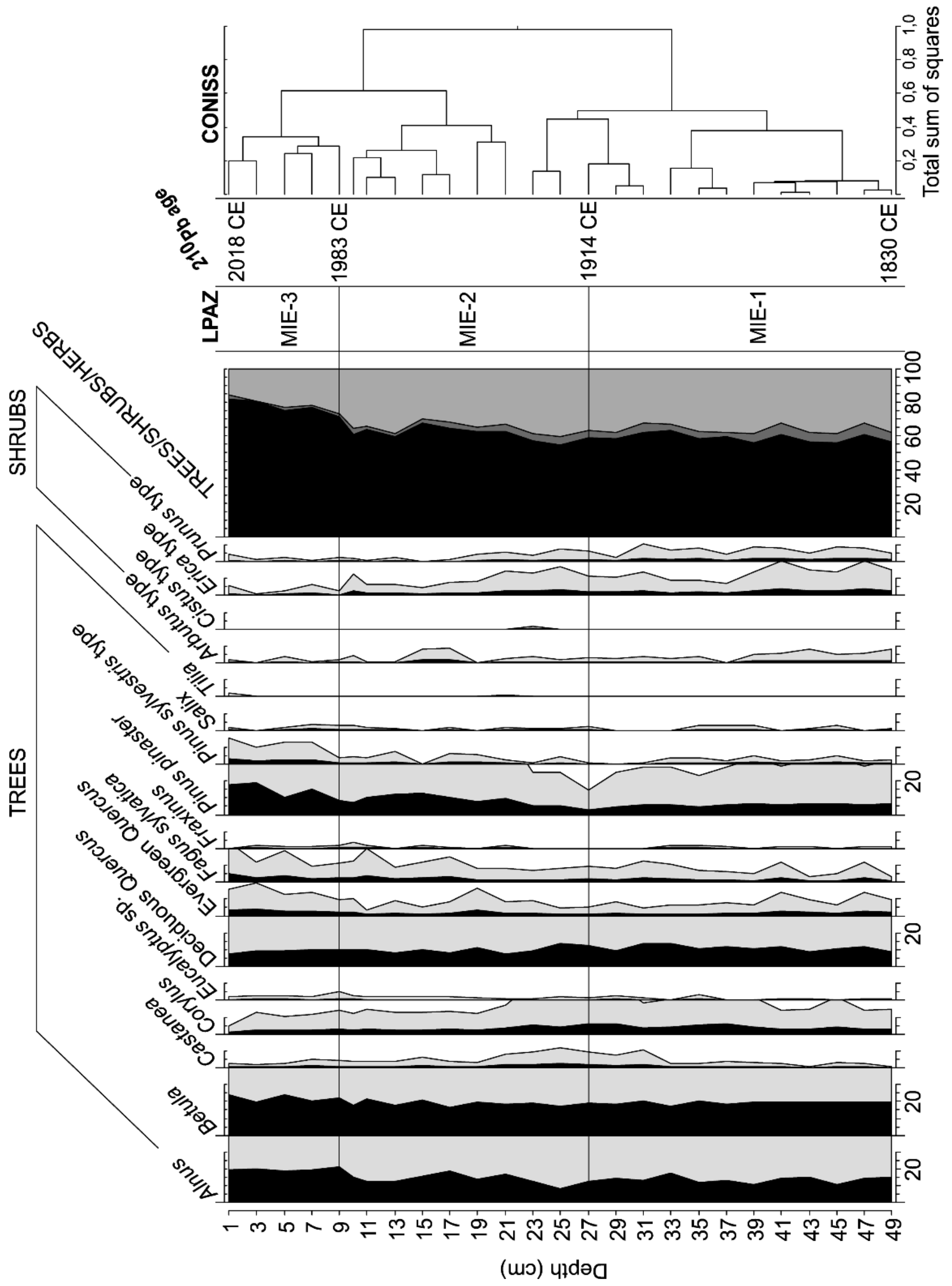


**Figure R.30** - Pollen diagram corresponding to the arboreal and shrub pollen along the Miengo core. Depth at centimeter scale, the evolution of arboreal and shrub taxa, the defined local pollen assemblage zones (LPAZ), the $^{210}$Pb dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

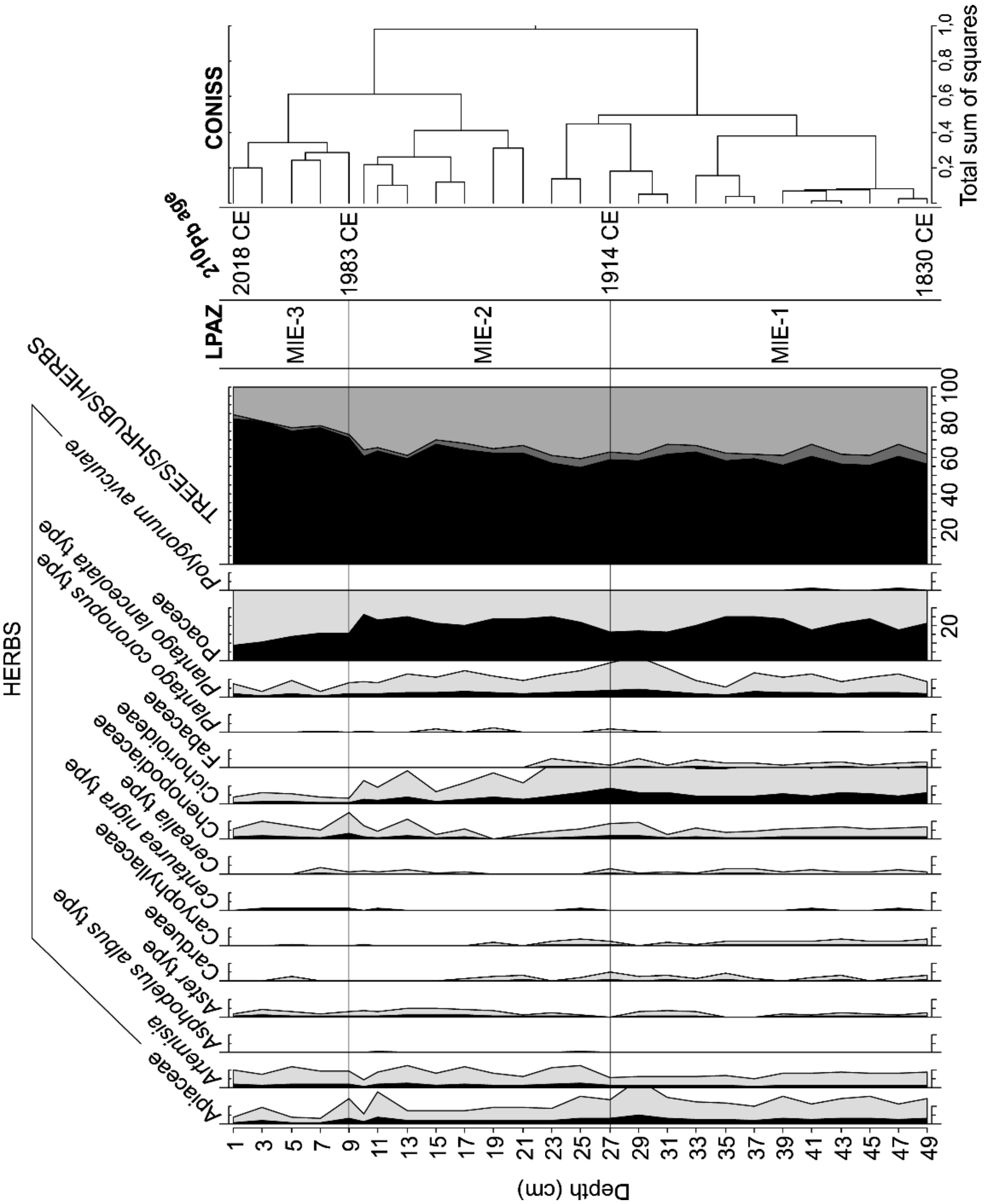


**Figure R.31** - Pollen diagram corresponding to the herbaceous pollen along the Miengo core. Depth at centimeter scale, the evolution of herbaceous taxa, the defined local pollen assemblage zones (LPAZ), the $^{210}$Pb dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) re represented.

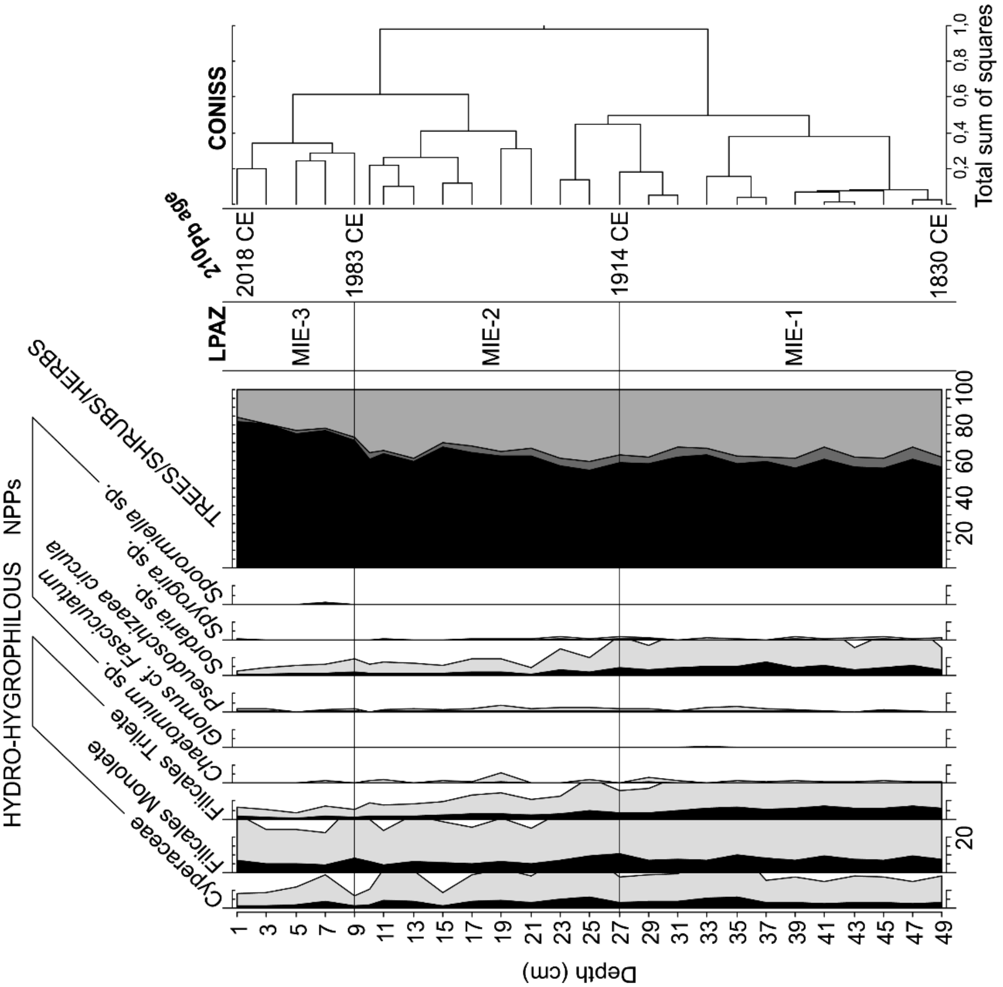


**Figure R.32** - Pollen diagram corresponding to the hydro-hygrophilous pollen and non-pollen palynomorphs (NPPs) along the Miengo borehole. Depth at centimeter scale, the evolution of hydro-hygrophilous and the NPPs taxa, the defined local pollen assemblage zones (LPAZ), the $^{210}$Pb dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

On the right in Figure R.30, the percentages of shrub pollen (1.6 - 5.2%) remain similar to those found in the previous zone. The same shrub species have been identified: *Erica* type (0.9 - 3.4%), *Arbutus* type (0 - 1.7%) and *Prunus* type (0 - 1.4%).

The overall percentages of the herbaceous taxa are relatively similar to the previous zone (29.9 - 40.4%) (Fig. R.31). However, in the case of the Poaceae form, an increase in its presence is observed, raising its range between 20.3 and 26.5%. Nevertheless, other herbs, such as Cichorioideae, decreased (1.3 - 6.3%). The abundance of the other herbaceous taxa (Apiaceae, *Artemisia*, *Asphodelus albus* type, *Aster* type, Cardueae, Caryophyllaceae, *Centaurea nigra* type, *Cerealia* type, Chenopodiaceae, Fabaceae, *Plantago coronopus* type and *Plantago lanceolata* type) hardly ever reaches 3% individually.

The presence of hydro-hygrophilous pollen maintains a regular abundance (16.1 - 29.9%). Filicales Monolete (4.4 - 8.4%), Filicales Trilete (1.5 - 2.4%) and Cyperaceae (1.6 - 5.8%) (Fig. R.32).

At the same time, the presence of non-pollen palynomorphs (NPPs) slightly decreases (1.3 - 3.2%) (Fig. R.32). The following taxa have been identified: *Chaetomium* sp., *Pseudoschizaea circula*, *Sordaria* sp. and *Spyrogira* sp. with an individual abundance less than 2.5%.

### LPAZ MIE-3 (10 - 0 cm) (1983 - 2018 CE)

In Figure R.30, on the left, we can observe how arboreal pollen increases considerably its total percentages (71.5 - 82.2%). *Betula* (19.9 - 24.2%) continues to be the dominant taxon. Deciduous *Quercus* maintains its abundance as in the previous pollen zone (7.2 - 9.8%). *Alnus*, in contrast, experiences a certain increase in its total values (18.7 - 21%). *Pinus pinaster* is the taxon that shows the greatest increase, which now has a percentage range between 8.2 and 19.1%. Moreover, *Eucalyptus* sp. not only appears regularly but it even reaches 1% of representativeness. The remaining taxa identified are *Castanea*, *Corylus*, evergreen *Quercus*, *Fagus sylvatica*, *Fraxinus*, *Pinus sylvestris* type, *Salix* and *Tilia*. Each of these taxa remains below 5% abundance.

Shrub pollen experienced a generalized reduction (0.4% - 2.4%) in this zone (Fig. R.30). *Arbutus* type, *Erica* type and *Prunus* type do not exceed 1.5% individually.

A more evident reduction is observed in herbaceous pollen (Figure R.31). The percentages decrease to 15.5 and 23.1%. At individual level, the reduction in Poaceae (9.1 - 16%) is noteworthy. In addition, *Asphodelus albus* type and Fabaceae disappear in this final zone. The percentages of the other herbaceous plants that had a greater presence (Cichorioideae, Apiaceae and *Plantago lanceolata* type) are now reduced, and together with the remaining taxa (*Artemisia*, *Aster* type, Cardueae, Caryophyllaceae, *Centaurea nigra* type, *Cerealia* type, Chenopodiaceae and *Plantago coronopus* type) exhibit percentages below 2.5% each.

Hydro-hygrophilous taxa also experience a reduction (13 - 17.9%) (Fig. R.32). Although it is less appreciable than for herbaceous plants, the percentages of identified taxa become: Filicales Monolete (4.1 - 7.6%), Filicales Trilete (0.6 - 1.4%) and Cyperaceae (1.3 - 3.5%).

To conclude with the Miengo core, the trend of non-pollen palynomorphs (NPPs) also shows a decline, although small. There have been identified, below 1.5% abundance, the taxa: *Chaetomium* sp., *Pseudoschizaea circula*, *Sordaria* sp., *Spyrogira* sp. and *Sporormiella* sp. (Fig. R.32).

### 3.1.2. Geochronology

In contrast to the boreholes, which have been dated by radiocarbon analysis, short-lived radioisotopes analysis of $^{210}$Pb and $^{137}$Cs and sedimentation rate have been used for the short cores due to their younger age. Through gamma spectrometry, the samples from Miengo were studied at the Department of Medical and Surgical Sciences in the University of Cantabria (UC).

In Figure R.33, we can see how the $^{210}$Pb$_{ex}$ activity ranges in this core between 32.6 - 109.2 Bq kg$^{-1}$. It is at 32 cm depth when the concentration of this radioisotope disappears.

Small concentrations of $^{137}$Cs (0.47 - 4.05 Bq kg$^{-1}$) have also been measured (Fig. R.34). In this case, concentrations disappear at 34 cm with a relative constancy up to 4 cm where a small rebound is observed.

Using the CIC (Constant Initial Concentration) model (Appleby & Oldfield, 1978; Robbins, 1978), it was possible to calculate the sedimentation accumulation rate (SAR) (0.30 ± 0.02 cm yr$^{-1}$) and a mass accumulation rate (MAR) of 0.54 ± 0.03 g cm$^{-2}$ yr$^{-1}$ for this core.

Therefore, the estimated dates that have been calculated for the Miengo core range from 1830 CE at the base to 2018 CE, the year of collection of this core.

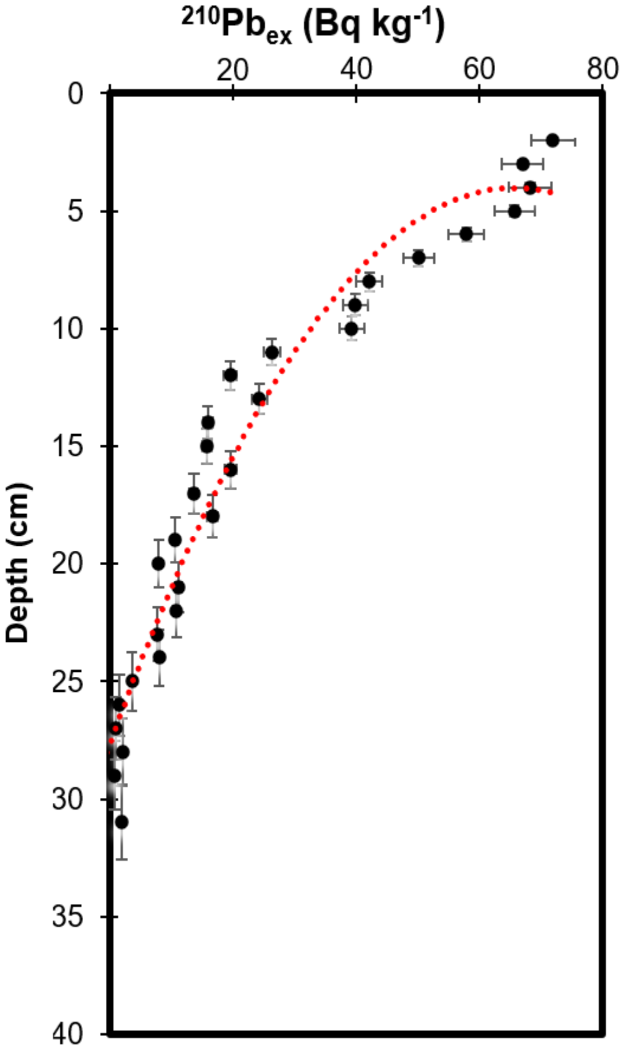


**Figure R.33** - Distribution of $^{210}Pb_{ex}$ (Bq kg$^{-1}$) with depth along the Miengo core.

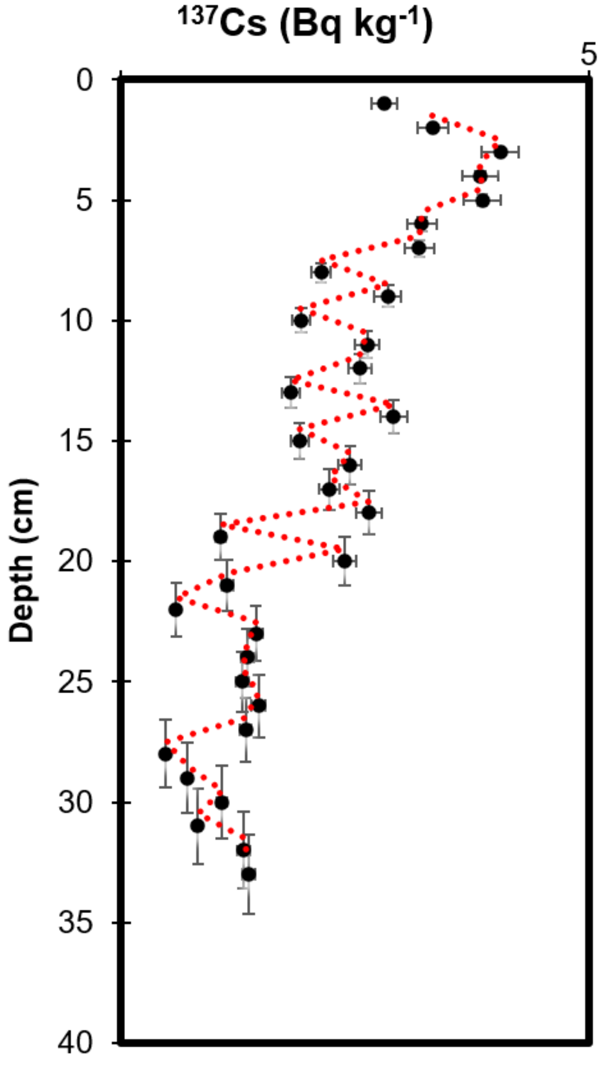


**Figure R.34** - Distribution of $^{137}$Cs (Bq kg$^{-1}$) with depth along the Miengo core.

## 3.2. Axpe

### 3.2.1. Pollen analysis

**Table R.13 -** Summary of the most representative taxa (relative abundance %) identified in the Axpe core. The single value represents the average and those in parentheses give the range. The percentages of hydro-hygrophilous taxa and NPPs are calculated separately together with the rest of the taxa.

| | **AXP - 1** | **AXP - 2** |
|---|---|---|
| deciduous *Quercus* | 3 (1.2 - 3.2) | 1 (0.9 - 1.1) |
| *Pinus pinaster* | 5 (2.2 - 13.4) | 28 (15.8 - 36.5) |
| *Erica* type | 2 (0.3 - 3.8) | 0.3 (0 - 0.7) |
| Apiaceae | 7 (2.2 - 12.7) | 2 (0.6 - 4.5) |
| *Cerealia* type | 1 (0.2 - 1.3) | 0 (0 - 0) |
| Chenopodiaceae | 33 (18.9 - 44.2) | 34 (23.2 - 40.5) |
| Cichorioideae | 2 (0.7 - 5.3) | 3 (0.6 - 9) |
| Poaceae | 3 (0.9 - 4.8) | 1 (0.5 - 1.1) |
| Cyperaceae | 12 (5.6 - 20.4) | 9 (2.6 - 17.2) |
| Filicales Monolete | 11 (6.2 - 23.3) | 8 (1.4 - 13.4) |
| Filicales Trilete | 11 (5.8 - 14.3) | 3 (0.6 - 6.4) |
| *Sordaria* sp. | 2 (0 - 15.2) | 2 (0.8 - 4) |
| TREES | 23 (12.1 - 35) | 40 (32.5 - 44.8) |
| SHRUBS | 4 (1.2 - 8.2) | 1 (0.6 - 1) |
| HERBS | 73 (63.8 - 81.9) | 59 (50.6 – 66.9) |
| HYDRO-HYGROPHILOUS | 49 (31.3 - 98.2) | 33 (6.4 - 68.3) |
| NPPs | 4 (1.4 - 21.9) | 5 (2.2 - 8.4) |

The Axpe core is a replica of the Axpe Norte core extracted in 2009 and studied by Ane García-Artola for her doctoral thesis, and whose data were published by Irabien et al. (2015). Their chronology of the core, based on the $^{210}Pb_{ex}$ and $^{137}Cs$

radioisotope analyses, has been included here in order to present our results of all sedimentary sequences in a more coherent way.

The pollen analysis of the Axpe core is characterized by a large number of samples without pollen content (sterile). In spite of this, some trends can be deduced thanks to the samples that have given results. As in the case of the other cores and boreholes, a stratigraphically constrained cluster analysis by the incremental sum of squares (CONISS) has been performed to divide this core into local pollen assemblage zones (LPAZ AXP). Consequently, Axpe has been divided into two LPAZs.

### LPAZ AXP-1 (49 - 15 cm) (1773 - 1936 CE)

For this basal zone, a total of nine samples resulted sterile (no pollen content) (Fig. R.35, R.36, R.37).

Beginning with the arboreal pollen, the range of total percentages goes from 9.1 to 15.9% (Fig. R.35). Among all the taxa observed, the only one with a clearly notorious presence is *Pinus pinaster* (2.2 - 13.4%). Deciduous *Quercus* would be the secondary taxon (1.2 - 3.1%). The rest of the identified taxa (*Alnus*, *Betula*, *Castanea*, *Corylus*, evergreen *Quercus*, *Fagus sylvatica*, *Fraxinus*, *Juglans*, *Pinus sylvestris* type, *Salix* and *Tilia*) do not exceed 2% in any case. Shrub pollen has an even smaller abundance (0.5 - 5.6%) (Fig. R.35). Four taxa were identified: *Erica* type (0.3 - 2.9%) and *Arbutus* type (0.1 - 2.1%) with the highest percentage of occurrence, and *Cistus* type and *Prunus* type that barely exceed 1% each.

In Figure R.36, we can see that herbaceous pollen clearly dominates this basal pollen zone of Axpe. The percentage range of herbs goes from 28 to 61%. The most abundant taxon is Chenopodiaceae (18.9 - 44.4%), and Poaceae (0.9 - 4.8%) and Apiaceae (2.2 - 12.7%) are secondary. Below 1.5% individual abundance the following forms have been identified: *Artemisia*, *Aster* type, Cardueae, Caryophyllaceae, *Centaurea nigra* type, *Cerealia* type, Cichorioideae, Fabaceae, *Plantago coronopus* type, *Plantago lanceolata* type and *Polygonum aviculare*. High percentages of hydro-hygrophilous taxa were also identified (31.3 - 98.2%) (Fig. R.37). Filicales Monolete is the taxon with the highest presence (7.1 - 23.3%), followed closely by Cyperaceae (5.6 - 20.4%) and Filicales Trilete (5.8% - 14.3%).

To conclude with LPAZ AXP-1, non-pollen palynomorphs (NPPs) have been identified in a percentage range between 1.4 and 21.9% abundance (Fig. R.37). Among all taxa, the one with the highest presence is *Sordaria* sp. (0 - 15.2%). The remaining taxa identified (*Chaetomium* sp., *Glomus* cf. *fasciculatum*, *Pseudoschizaea circula*, *Spyrogira* sp. and *Sporormiella* sp.) do not represent individually more than 3%.

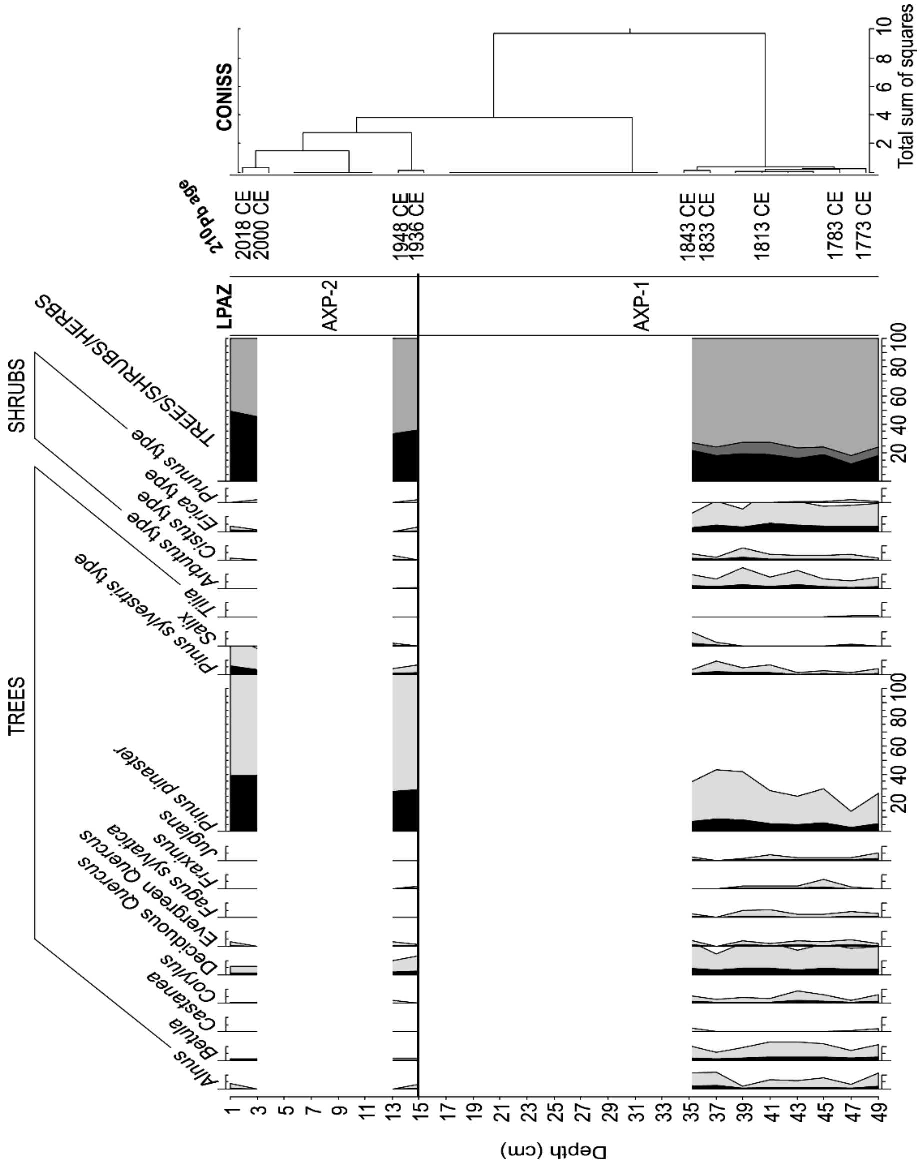


**Figure R.35** - Pollen diagram corresponding to the arboreal and shrub pollen along the Axpe core. Depth at centimeter scale, the evolution of arboreal and shrub taxa, the defined local pollen assemblage zones (LPAZ), the $^{210}$Pb dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

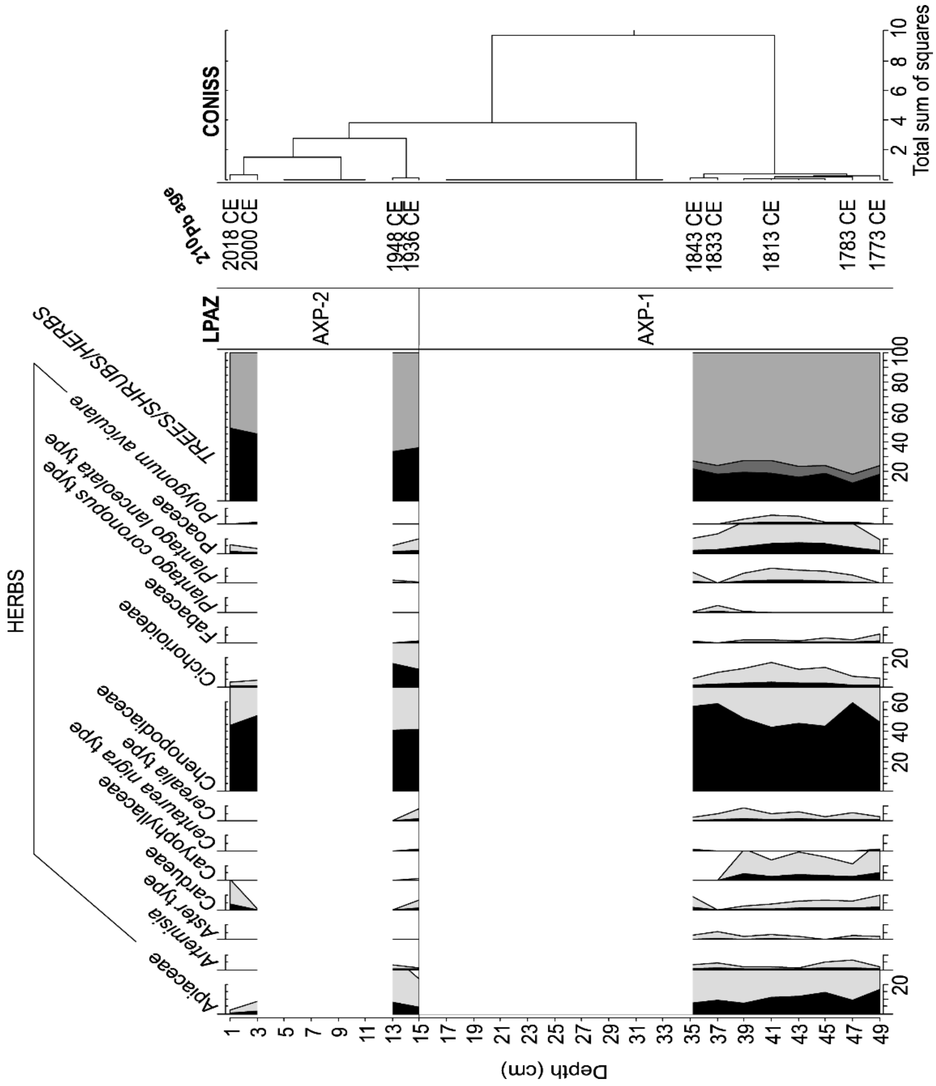


**Figure R.36** - Pollen diagram corresponding to the herbaceous pollen along the Axpe core. Depth at centimeter scale, the evolution of herbaceous taxa, the defined local pollen assemblage zones (LPAZ), the $^{210}$Pb dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

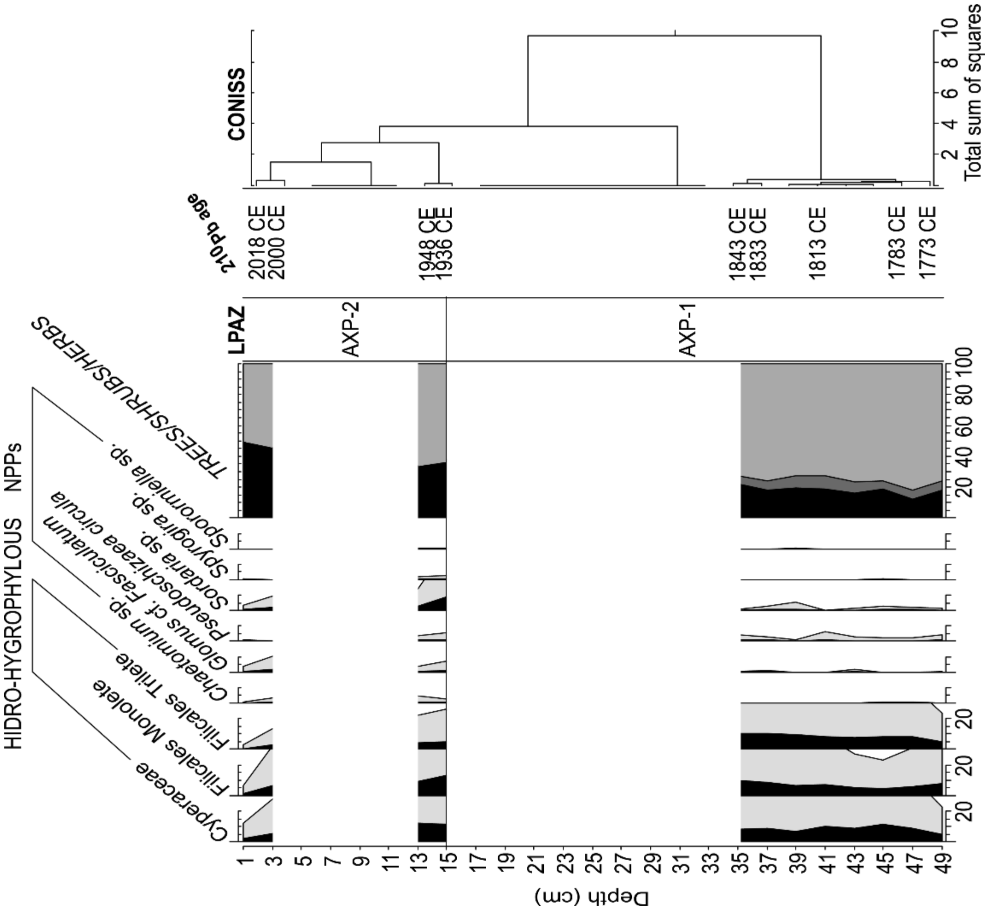


**Figure R.37** - Pollen diagram corresponding to the hydro-hygrophilous pollen and non-pollen palynomorphs (NPPs) along the Axpe core. Depth at centimeter scale, the evolution of hydro-hygrophilous and the NPPs taxa, the defined local pollen assemblage zones (LPAZ), the $^{210}$Pb dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

### LPAZ AXP-2 (15 - 0 cm) (1936 - 2018 CE)

A total of four sterile samples were found in this pollen zone (Fig. R.35, R.36, R.37).

As can be seen on the left side of Figure R.35, the arboreal pollen (18.4 - 44.6%) experiences a considerable growth in this zone. The most dominant taxon is *Pinus pinaster* (15.8 - 36.5%), followed by *Pinus sylvestris* type (0.5 - 5.3%). The rest of the tree species identified in this zone (*Alnus*, *Betula*, *Corylus*, deciduous *Quercus*, evergreen *Quercus* and *Salix*) remain individually below 1%.

In Figure R.35, on the right side, we can see that shrub pollen (0.3 - 0.9%) decreases compared to the abundance values observed in the previous zone. The taxa identified are *Cistus* type, *Erica* type and *Prunus* type.

Despite the increase in arboreal pollen, herbaceous pollen (37.9 - 46.6%) continues to be dominant in this zone (Fig. R.36). Chenopodiaceae is still the taxon with the highest presence (23.2 - 40.5%). The major change observed in this zone is the disappearance of several taxa that had previously been identified in the lower zone (*Aster* type, Caryophyllaceae, *Centaurea nigra* type, *Cerealia* type, Fabaceae and *Plantago coronopus* type).

A significant decrease (6.4 - 68.6%) is observed in the hydro-hygrophilous taxa (Fig. R.37). Cyperaceae is now the family with the highest abundance, between 17.2 and 2.6%. Both Filicales Monolete (1.4 - 13.4%) and Filicales Trilete (0.6 - 6.4%) decreased their percentages in this upper zone.

Finally, the analysis also shows a decrease in the percentages of non-pollen palynomorphs (NPPs) (2.2 - 8.4%) (Fig. R.37). The taxa with the highest abundance are *Glomus* cf. *fasciculatum* (0.8 - 2.6%) and *Sordaria* sp. (0.8 - 4%). *Chaetomium* sp., *Pseudoschizaea circula*, *Spyrogira* sp. and *Sporormiella* sp. have been identified but account for less than 1% each.

### 3.2.2. Geochronology

As mentioned above, the Axpe core is a replica of the so-called Axpe Norte core (Irabien et al., 2015).

The analyses showed that the $^{210}Pb_{ex}$ activity ranges from 26.9 - 232.5 Bq kg$^{-1}$ (Fig. R.38). The observed activity is not stable and regular up to 26 cm, increasing exponentially from 13 cm.

As for the $^{137}$Cs concentrations, a range between 3.6 - 13.2 Bq kg$^{-1}$ was obtained (Fig. R.39). In addition, it was possible to identify the peak between 9 and 5 cm that allows us to date it around 1963 CE.

Using the CIC (Constant Initial Concentration) model (Appleby & Oldfield, 1978; Robbins, 1978), it was possible to estimate the age of the Axpe core ranging from the year 1773 CE (extrapolated age) to 2018 CE, year in which the replica of the original Axpe Norte core was collected.

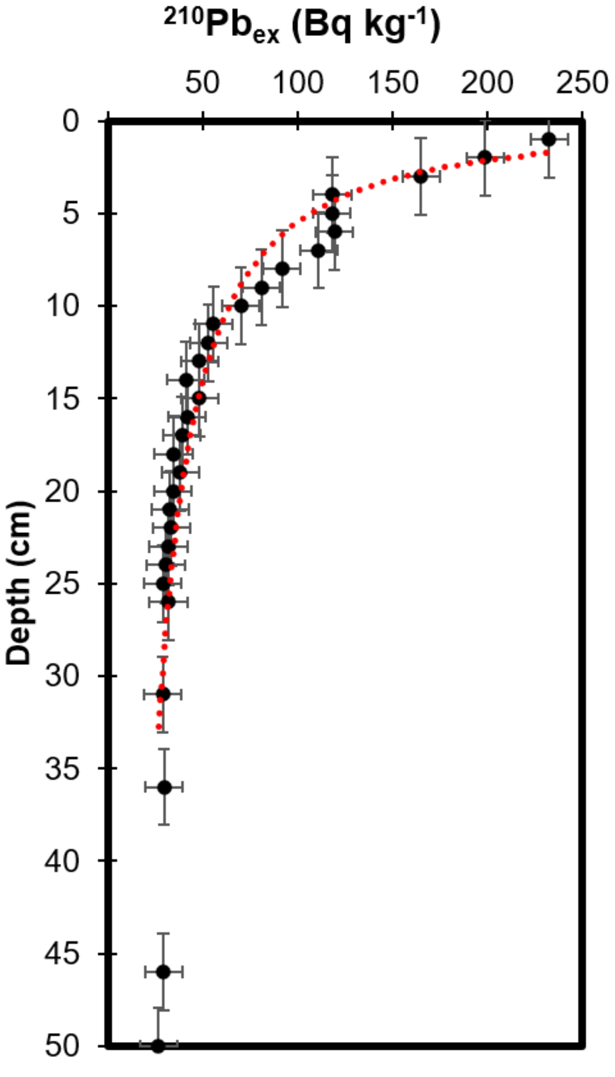


**Figure R.38** - Distribution of $^{210}$Pb$_{ex}$ (Bq kg$^{-1}$) with depth along the Axpe Norte core. Readapted from Irabien et al. (2015).

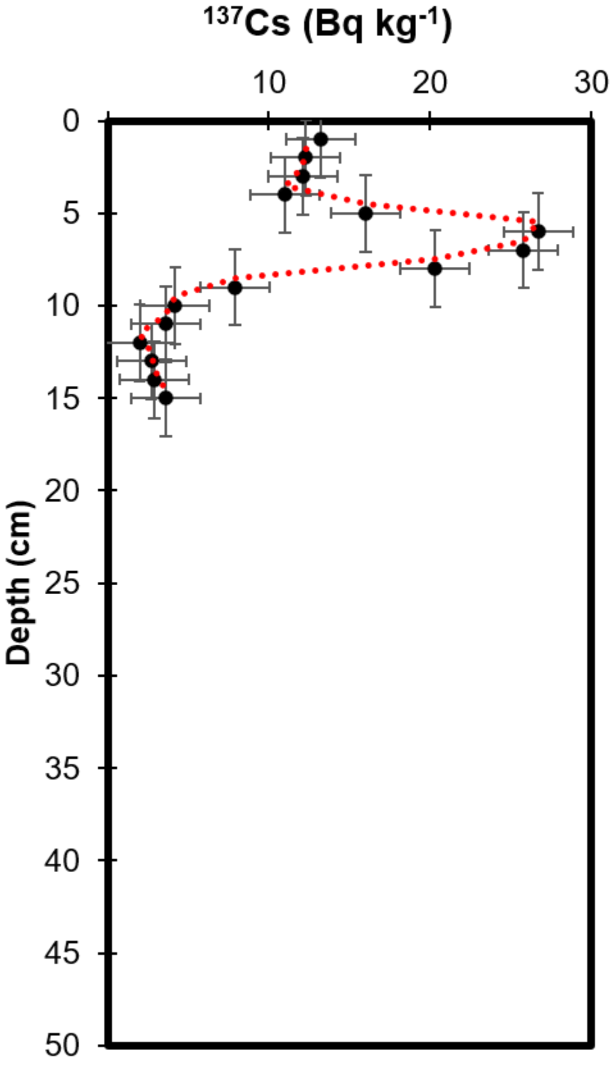


**Figure R.39** - Distribution of $^{137}$Cs (Bq kg$^{-1}$) with depth along the Axpe Norte core. Readapted from Irabien et al. (2015).

## 3.3. Zumaia

### 3.3.1. Pollen analysis

The pollen analysis of the Zumaia core was carried out on one of the replicates extracted in 2018. The chronology of the core based on short-lived radioisotopes was recently published in Cearreta et al. (2021). These published dates ($^{210}Pb_{ex}$ and $^{137}Cs$ analysis) have been included here in order to present our results in a coherent way.

A stratigraphically constrained cluster analysis by the incremental sum of squares (CONISS) has been performed to divide the core into local pollen assemblage zones (LPAZ ZUM). Based on this analysis, the core has been divided into five LPAZs.

### LPAZ ZUM-1 (45 - 33 cm) (1828 - 1878 CE)

Arboreal pollen in this basal zone ranges from 14.5 to 23% (Fig. R.40). Five tree taxa with very similar percentages dominate this pollen assemblage: *Betula* (1.6 - 7.1%), deciduous *Quercus* (2.9 - 6.8%), *Castanea* (2 - 6.2%), *Pinus pinaster* (2.2 - 5.6%) and *Alnus* (1.2 - 4.7%). Other taxa such as *Corylus*, evergreen *Quercus*, *Fagus sylvatica*, *Fraxinus*, *Pinus sylvestris* type, *Salix* and *Tilia* have also been identified but these do not exceed 3% individually.

The presence of shrub pollen (6.6 - 11%) is notorious (Fig. R.40). The identified taxa are *Arbutus* type (0.6 - 2.6%), *Cistus* type (0 - 2%), *Erica* type (2.4 - 5.8%) and *Prunus* type (0 - 1%).

Herbaceous pollen (63.5 - 77.3%) is the predominant pollen in this zone (Figure R.41). Apiaceae is clearly the dominant taxon with percentages between 30.1 and 44.6%. *Cerealia* type (4.3 - 7.6%), Cichorioideae (7.4 - 16.4%) and Poaceae (6.4 - 11.1%) also have a remarkable abundance. The remaining taxa identified (*Artemisia*, *Asphodelus albus* type, *Aster* type, Cardueae, Caryophyllaceae, *Centaurea nigra* type, Chenopodiaceae, Fabaceae and *Plantago lanceolata* type) do not exceed 4% each.

A high percentage of hydro-hygrophilous pollen has also been identified (35 - 43.4%) (Fig. R.42). The following taxa are present in this zone: Cyperaceae (6.5 - 11.6%), Filicales Monolete (7.8 - 10.8%) and Filicales Trilete (7.4 - 16.7%).

The percentages of non-pollen palynomorphs (NPPs) range from 4.7 to 7.6% (Fig. R.42) and the identified taxa are *Chaetomium* sp. (0.1 - 0.9%), *Glomus* cf. *fasciculatum* (0 - 0.4%), *Pseudoschizaea circula* (0.2 - 1.4%), *Sordaria* sp. (3.7 - 5.1%), *Spyrogira* sp. (0.3 - 1%) and *Sporormiella* sp. (0 - 0,3%).

**Table R.14 -** Summary of the most representative taxa (relative abundance %) identified in the Zumaia core. The single value represents the average and those in parentheses give the range. The percentages of hydro-hygrophilous taxa and NPPs are calculated separately together with the rest of the taxa.

| | ZUM - 1 | ZUM - 2 | ZUM - 3 | ZUM - 4 | ZUM - 5 |
|---|---|---|---|---|---|
| *Alnus* | 3 (1.2 - 4.7) | 6 (1.6 - 8.9) | 13 (6.2 - 20) | 26 (20.7 - 28.2) | 21 (20.4 - 21.9) |
| *Betula* | 4 (1.6 - 7.1) | 6 (3 - 8.8) | 13 (7.1 - 22.3) | 17 (13.1 - 19.7) | 17 (12.5 - 22.8) |
| *Eucalyptus* sp. | 0 (0 - 0) | 0.1 (0 - 0.2) | 0 (0 - 0) | 0.1 (0 - 0.2) | 0.1 (0 - 0.2) |
| deciduous *Quercus* | 5 (2.9 - 6.8) | 5 (4.3 - 5.6) | 6 (4.7 - 8.3) | 5 (4.7 - 5.6) | 5 (3 - 6.4) |
| *Pinus pinaster* | 3 (2 - 5.6) | 6 (3.2 - 10.1) | 15 (11.1 - 20.5) | 26 (20.8 - 34.6) | 31 (25.3 - 34.2) |
| Apiaceae | 37 (30.1 - 44.6) | 26 (18 - 33.1) | 7 (3.7- 10.1) | 1 (0.4 - 1) | 1 (0.8 - 1.2) |
| *Cerealia* type | 6 (4.3 - 7.6) | 5 (3 - 7.9) | 4 (1.6 - 7.5) | 0.5 (0.2 - 0.6) | 0.1 (0 - 0.2) |
| Cichorioideae | 11 (7.4 - 16.4) | 10 (6.2 - 13.8) | 9 (3.4 - 16.1) | 1 (0.6 - 1) | 1 (0.4 - 1.4) |
| Poaceae | 8 (6.4 - 11.1) | 18 (15.5 - 23.2) | 17 (15.4 - 18) | 11 (9.4 - 12.1) | 8 (6.8 - 9.9) |
| Cyperaceae | 9 (6.5 - 11.6) | 8 (6.1 - 11.3) | 7 (4.4 - 12) | 2 (0.9 - 2.6) | 1 (1.1 - 1.9) |
| Filicales Monolete | 9 (7.8 - 10.8) | 8 (6.2 - 9.7) | 6 (4.9 - 7.7) | 3 (1.6 - 4.2) | 2 (1.6 - 2.5) |
| Filicales Trilete | 13 (7.4 - 16.7) | 11 (7.6 - 12.5) | 9 (4.8 - 11.7) | 2 (0.4 - 3.2) | 1 (0.9 - 1.8) |
| *Sordaria* sp. | 4 (3.7 - 5.1) | 3 (1.8 - 3.8) | 4 (2.6 - 5.5) | 2 (1.3 - 2.6) | 1 (0.7 - 1.6) |
| TREES | 22 (14.5 - 32) | 28 (19.1 - 39.1) | 53 (40.1 - 67.1) | 82 (79.2 - 82.9) | 85 (83.8 - 86.4) |
| SHRUBS | 8 (4.5 - 11) | 7 (5 - 8.5) | 4 (2.5 - 5.4) | 2 (1.6 - 3.6) | 1 (0.4 - 2.4) |
| HERBS | 70 (63.5 - 77.3) | 66 (55.2 - 73.9) | 42 (30.4 - 54.7) | 16 (15.4 - 17.3) | 14 (12 - 15.8) |
| HYDRO-HYGROPHILOUS | 40 (35 - 43.4) | 36 (28.9 - 41.9) | 31 (23.3 - 40.7) | 13 (8.1 - 15.7) | 9 (7.9 - 9.9) |
| NPPs | 7 (4.7 - 7.6) | 4 (3 - 5) | 7 (4.7 - 9.2) | 3 (1.8 - 3.7) | 1 (0.7 - 1.9) |

### LPAZ ZUM-2 (33 - 23 cm) (1878 - 1921 CE)

In this second zone, tree pollen increases, reaching percentages between 19.1 and 39.1% (Fig. R.40). However, at taxon scale, very similar percentages for four of the five previously mentioned forms are found: *Pinus pinaster* (3.2 - 10.1%), *Betula* (3 - 8.8%), deciduous *Quercus* (4.3 - 5.6%) and *Alnus* (1.6 - 8.9%). *Castanea* has percentages between 0.2 - 1.9%. In addition, the presence of *Eucalyptus* sp. (0 - 0.2%) has been detected for the first time in this core. The rest of the taxa identified in this LPAZ ZUM-1 exhibit percentages lower than 2% individually.

Shrub pollen, in contrast, shows lower values than those observed in the previous basal zone (5 - 8.5%) (Fig. R.40). The taxa identified are *Erica* type (2.4 - 7.1), *Arbutus* type (0.4 - 2%), *Cistus* type (0.2 - 1.6%) and *Prunus* type (0 - 0.8%).

Herbaceous pollen continues to predominate in this lower part of the core. As seen in Figure R.41, the overall percentages (55.2 - 73.9%) decreased slightly. The Apiaceae family still dominates (18 - 33.1%). Despite the general decrease in herbaceous taxa, Poaceae shows a rise in the range of its percentages between 15.5 and 23.2%. Regarding Cichorioideae, a small reduction can be observed (6.2 - 13.8%). *Cerealia* type (3 - 7.9%) maintains a relatively high value. The same taxa as in the previous LPAZ ZUM-1 have been identified, with the new appearance of *Polygonum aviculare* (0 - 0.2%). None of these taxa exceed 2% in any case.

The hydro-hygrophilous pollen shows a similar trend to the one observed in the previous pollen zone (28.9 - 41.9%) (Fig. R.42): Cyperaceae (6.1 - 11.3%), Filicales Monolete (6.2 - 9.7%) and Filicales Trilete (7.6 - 12.5%).

As for the non-pollen palynomorphs (NPPs), a small decrease in their overall percentages (3 - 5%) is observed (Fig. R.42). Each taxon (*Chaetomium* sp., *Glomus* cf. *fasciculatum*, *Pseudoschizaea circula* and *Spyrogira* sp.) is below 4% abundance, with *Sordaria* sp. (1.8 - 3.8%) having the highest presence.

### LPAZ ZUM-3 (23 - 13 cm) (1921 - 1963 CE)

The trend of increasing arboreal pollen observed during the previous zone continues here. This increase is even greater, reaching percentages between 40.1 and 67.1% (Fig. R.40). For the first time in this core, arboreal pollen is predominant over herbaceous pollen. As for the individual values, *Pinus pinaster* (11.5 - 20.1%), *Betula* (7.1 - 22.3%) and *Alnus* (6.2 - 20%) are the three taxa with the highest abundance. The presence of deciduous *Quercus* (4.7 - 8.3%) also shows an increase. The other forms identified, below 2% each, are *Castanea*, *Corylus*, evergreen *Quercus*, *Fagus sylvatica*, *Fraxinus*, *Pinus sylvestris* type, *Salix* and *Tilia*.

Shrub pollen, on the contrary, decreases slightly in this zone (2.5 - 5.4%) (Fig. R.40). All taxa identified (*Arbutus* type, *Cistus* type, *Erica* type and *Prunus* type) are below 3% individually.

Herbaceous pollen continues to decline during this LPAZ ZUM-3. The total percentages now range from 30.4 to 54.7% (Fig. R.41). Indeed, this decreasing trend also seems to affect the invidual taxa, since Poaceae (15.4 - 18%) is now the dominant herb above Apiaceae (3.7 - 10.1%) which is even surpassed by Cichorioideae (3.4 - 16.1%). *Cerealia* type (1.6 - 7.5%) also maintained its relative abundance. The rest of the identified taxa (*Artemisia*, *Asphodelus albus* type, *Aster* type, Cardueae, Caryophyllaceae, *Centaurea nigra* type, Chenopodiaceae, Fabaceae and *Plantago lanceolata* type) do not exceed 3% abundance individually.

Hydro-hygrophilous pollen decreases slightly (23.3 - 40.7%) (Fig. R.42). The same three taxa as in previous zones have been identified here: Cyperaceae (4.4 - 12%), Filicales Monolete (4.9 - 7.7%) and Filicales Trilete (4.8 - 11.7%).

Finally, the abundance of non-pollen palynomorphs (NPPs) increases slightly (4.7 - 9.2%) (Fig. R.42). *Sordaria* sp., the most representative taxon, ranges between 2.7 and 5.5%. The rest of the NPPs identified do not exceed 1.5% individually.

### LPAZ ZUM-4 (13 - 7 cm) (1963 - 1988 CE)

This pollen zone continuous the increase in arboreal pollen along this core. The percentages of this type of pollen are between 79.2 and 82.9% here (Fig. R.40). The major difference with regard to the previous pollen zone is that *Pinus pinaster* (20.8 - 34.6%) is now the dominant taxon, above *Alnus* (20.7 - 28.2%) and *Betula* (13.1 - 19.7%). The rest of the species maintain very similar values to those recorded in the previous zone, except that the presence of *Eucalyptus* sp. is again detected here (0 - 0.2%).

Shrub pollen continues its decreasing trend (1.6% - 3.6%). All identified taxa (*Arbutus* type, *Cistus* type, *Erica* type and *Prunus* type) are below 2.5% each (Fig. R.40).

In Figure R.41 we can see how the decreasing trend also of herbaceous plants becomes more evident (15.4 - 17.3%). Now, all the previously identified taxa are still present, but only Poaceae (9.4 - 12.1%) overcomes 1.5% abundance.

The presence of hydro-hygrophilous pollen continues to decrease, with percentages now between 8.1 and 15.7% (Fig. R.42). The three commonly identified hydro-hygrophilous taxa do not exceed 4.5% individually.

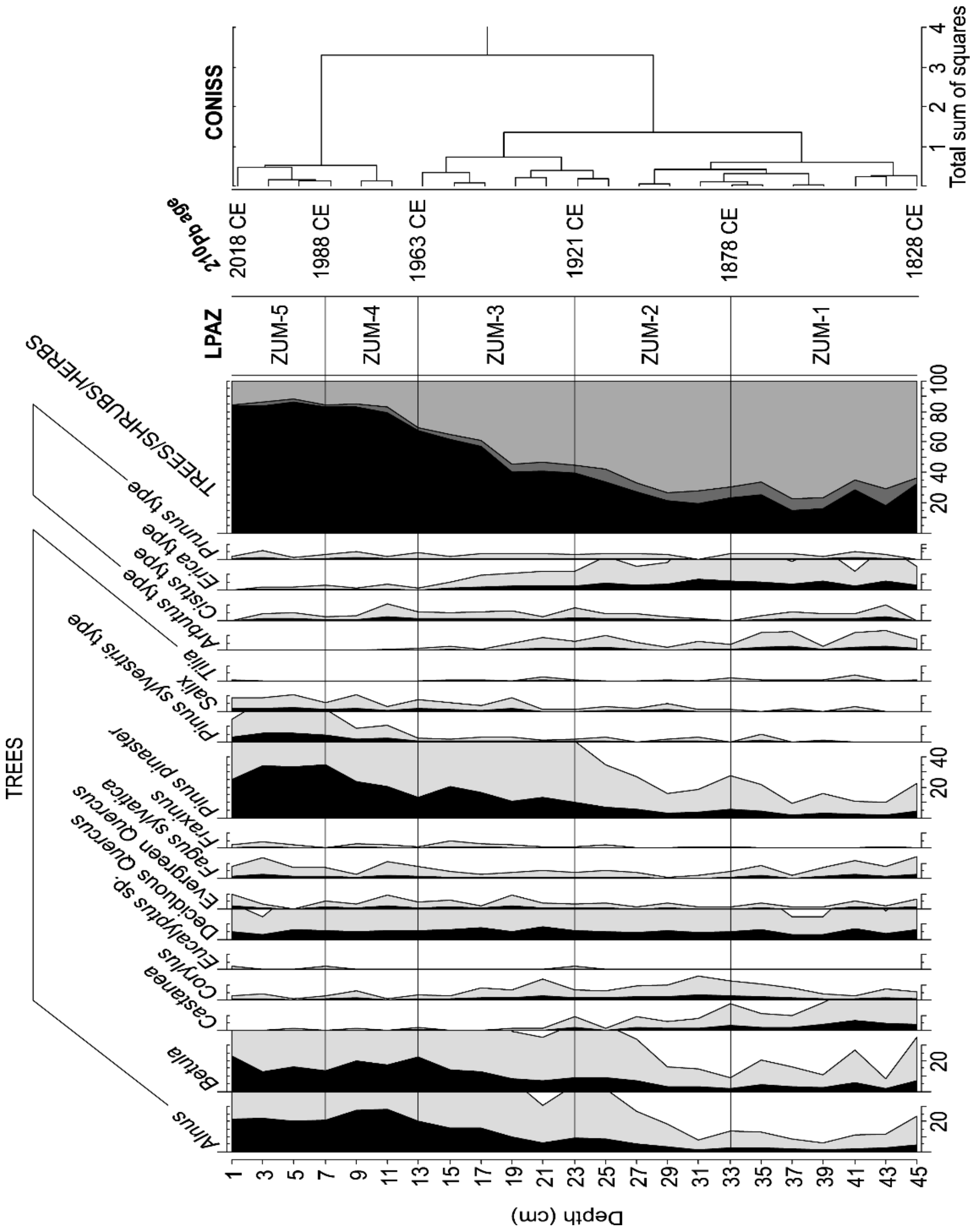


**Figure R.40** - Pollen diagram corresponding to the arboreal and shrub pollen along the Zumaia core. Depth at centimeter scale, the evolution of arboreal and shrub taxa, the defined local pollen assemblage zones (LPAZ), the $^{210}$Pb dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

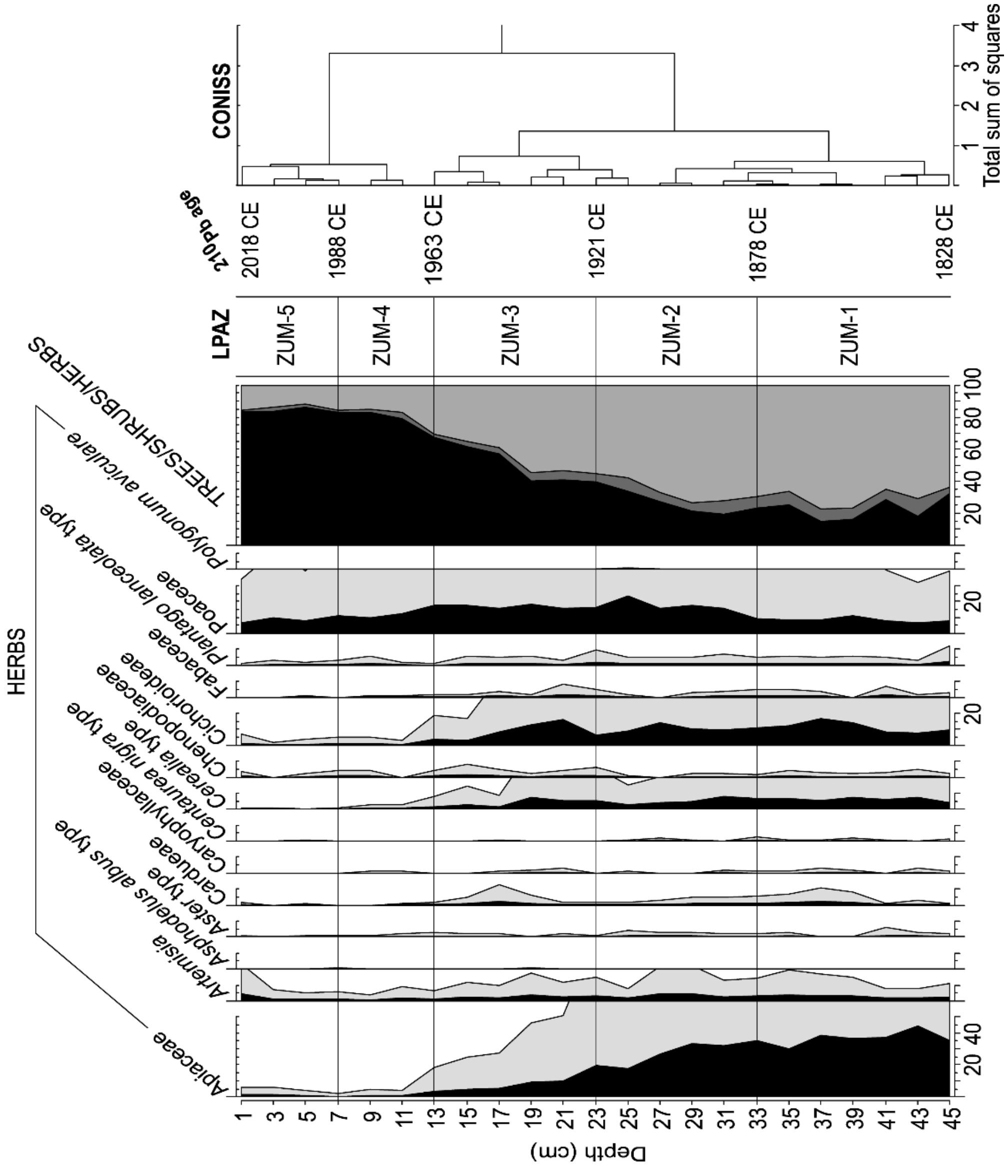


**Figure R.41** - Pollen diagram corresponding to the herbaceous pollen along the Zumaia core. Depth at centimeter scale, the evolution of herbaceous taxa, the defined local pollen assemblage zones (LPAZ), the $^{210}$Pb dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

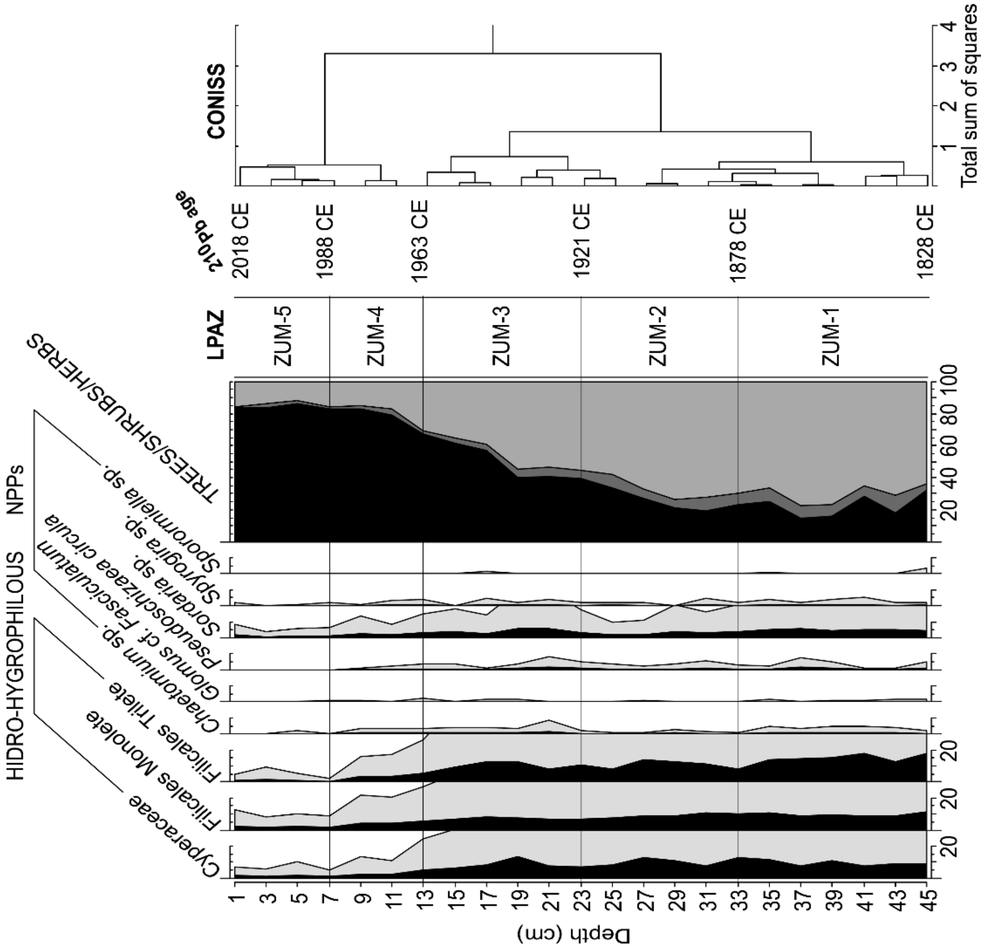


**Figure R.42** - Pollen diagram corresponding to the hydro-hygrophilous pollen and non-pollen palynomorphs (NPPs) along the Zumaia core. Depth at centimeter scale, the evolution of hydro-hygrophilous and the NPPs taxa, the defined local pollen assemblage zones (LPAZ), the $^{210}$Pb dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

The non-pollen palynomorphs (NPPs) identified in this LPAZ ZUM-4 (*Chaetomium* sp., *Glomus* cf. *fasciculatum*, *Pseudoschizaea circula*, *Sordaria* sp. and *Spyrogira* sp.) maintain a decreasing trend (1.8 - 3.7%) as well (Fig. R.42).

### LPAZ ZUM-5 (7 - 0 cm) (1963 - 2018 CE)

This final zone culminates the increasing trend of arboreal pollen observed in the previous pollen zones (83.8 - 86.4%), although not in such a pronounced way as in the previous zone (Fig. R.40). The dominant taxon continues to be *Pinus pinaster* (25.3 - 34.2%). *Alnus* (20.4% - 21.9%) and *Betula* (12.5% - 22.8%) remain prominent forms. The presence of *Eucalyptus* sp. (0 - 0.2%) is still detectable. Deciduous *Quercus* (3 - 6.4%) and *Pinus sylvestris* type (2.9% - 5.6%) increased slightly. The other taxa identified (*Castanea*, *Corylus*, evergreen *Quercus*, *Fagus sylvatica*, *Fraxinus*, *Salix* and *Tilia*) represent no more than 3% each.

Shrub pollen keeps decreasing (0.4 - 2.4%) (Fig. R.40). The taxon *Arbutus* type disappears. *Cistus* type, *Erica* type and *Prunus* type are individually below 2.5%.

Herbaceous pollen (12 - 15.8%) (Fig. R.41) stays at low rates comparable to its abundances in the previous pollen zones. Poaceae is the taxon with the highest presence (6.8 - 9.9%) followed by *Artemisia* (1 - 4.7%). Apiaceae, *Aster* type, Cardueae, *Centaurea nigra* type, *Cerealia* type, Chenopodiaceae, Cichorioideae, Fabaceae and *Plantago lanceolata* type have been identified below 1.5% abundance.

As observed also in the previous pollen zones, in LPAZ ZUM-5 the hydro-hygrophilous pollen continues to decrease (7.9 - 9.9%) (Fig. R.42). The individual percentages of Cyperaceae, Filicales Monolete and Filicales Trilete do not exceed 2.5%.

The same can be said for the non-pollen palynomorphs (NPPs) in this zone. The decrease results in a total percentage range between 0.7 and 1.9% (Fig. R.42). Only three taxa, *Chaetomium* sp., *Sordaria* sp. and *Spyrogira* sp. have been identified here, all of them below 2% abundance.

### 3.3.2. Geochronology

The results on the geochronology of the Zumaia core have already been published in Cearreta et al. (2021). The core studied in this thesis dissertation is a direct replica of the Z-1 core described there.

Radioisotope analyses showed $^{210}Pb_{ex}$ activity in ranges between -1 and 61.9 Bq $kg^{-1}$. Its increase occurs to a greater degree from 20 cm upwards (Fig. R.43).

The $^{137}$Cs concentrations detected show ranges between 1.2 - 9.9 Bq kg$^{-1}$(Fig. R.44). In fact, a peak can be observed starting around 20 cm and ending at 10 cm depth, corresponding to the $^{137}$Cs increase dated to about 1963 CE.

Using the CIC (Constant Initial Concentration) model (Appleby & Oldfield, 1978; Robbins, 1978), it was possible to calculate the sedimentation accumulation rate (SAR) (0.22 ± 0.02 cm/yr) and therefore to determine the dating of the Zumaia core, resulting in a geochronological timeframe between 1828 and 2018 CE.

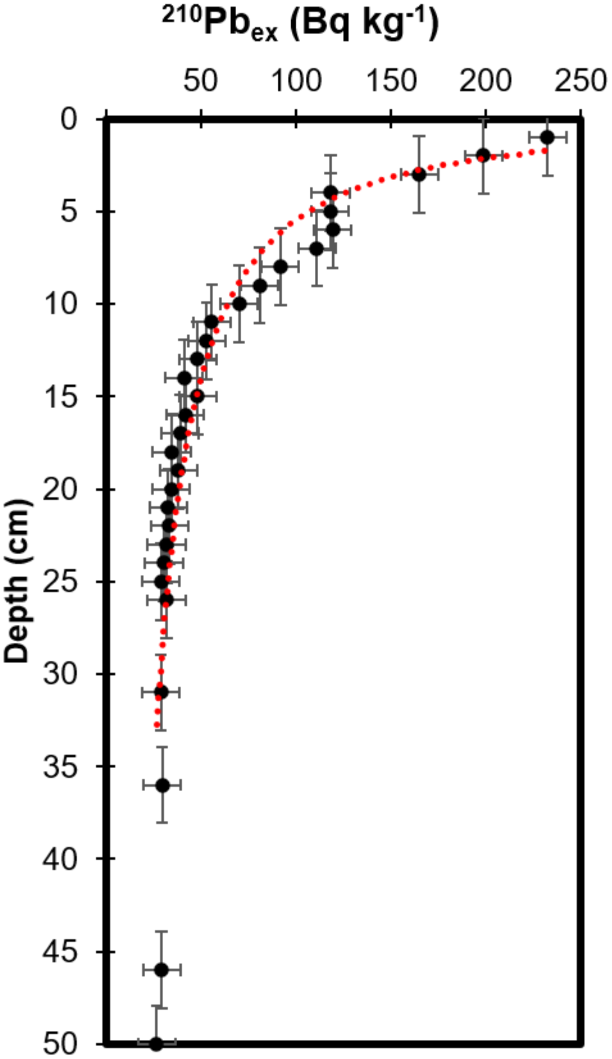


**Figure R.43** - Distribution of $^{210}$Pb$_{ex}$ (Bq kg$^{-1}$) with depth along the Zumaia core. Readapted from Cearreta et al. (2021).

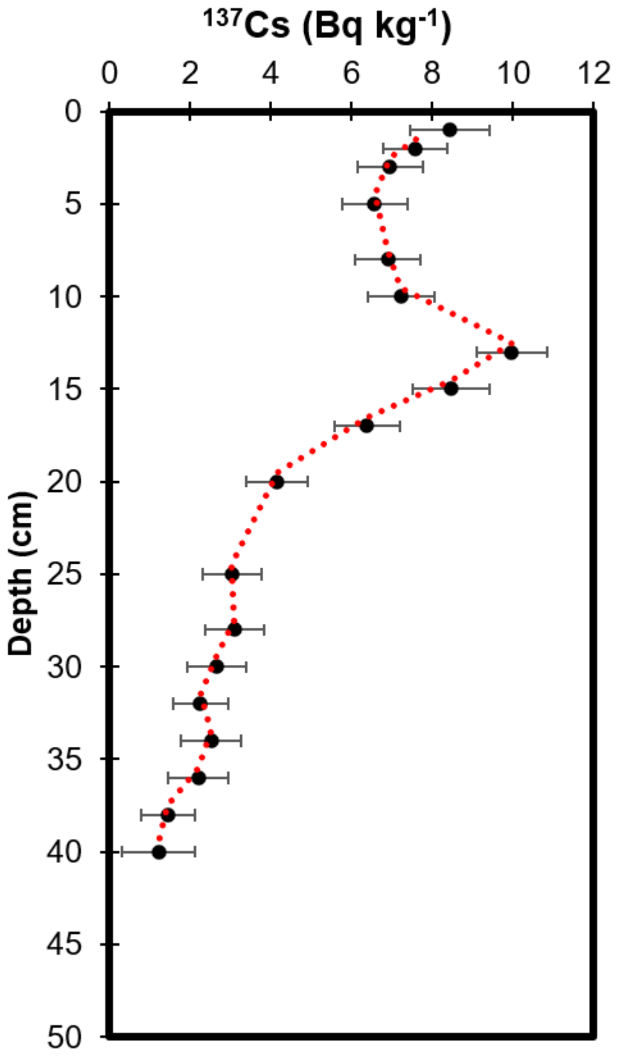


**Figure R.44** - Distribution of $^{137}$Cs (Bq kg$^{-1}$) with depth along the Zumaia core. Readapted from Cearreta et al. (2021).

## 3.4. Basque Mud Patch: KI03 and KI06 cores

Along with the rest of the coastal boreholes and cores in this study, a stratigraphically constrained cluster analysis by the incremental sum of squares (CONISS) has been performed for both cores retrieved from the continental shelf and different local pollen assemblage zones (LPAZ KI) have been identified. For both marine cores, KI03 and KI06, three pollen zones have been established. The following pollen results were published in Irabien et al. (2020) together with their radioisotopic dates presented here that were obtained from a different core (KS04) in the same geographical area.

**Table R.15 -** Summary of the most representative taxa (relative abundance %) identified in the KI03 core. The single value represents the average and those in parentheses give the range. The percentages of hydro-hygrophilous taxa and NPPs are calculated separately together with the rest of the taxa.

| | **KI03 - 1** | **KI03 - 2** | **KI03 - 3** |
|---|---|---|---|
| *Eucalyptus* sp. | 0.1 (0 - 0.2) | 0.1 (0 - 0.2) | 0.1 (0 - 0.2) |
| deciduous *Quercus* | 7 (1.9 - 9.3) | 4 (3.3 - 4.5) | 4 (3.2 - 4.2) |
| *Pinus pinaster* | 57 (40.7 - 82.9) | 72 (70 - 74.7) | 75 (70 - 80) |
| Apiaceae | 6 (0.8 - 9.2) | 2 (1.6 - 2.4) | 1 (0.4 - 0.8) |
| *Cerealia* type | 0.1 (0.2 - 0.4) | 0.1 (0 - 0.2) | 0 (0 - 0) |
| Cyperaceae | 9 (2.6 - 14.5) | 4 (3.6 - 4.5) | 3 (3 - 3.5) |
| Filicales Monolete | 9 (2.1 - 13.5) | 6 (4.6 - 6.5) | 3 (2.3 - 4.2) |
| Filicales Trilete | 10 (2.3 - 15.3) | 6 (4.3 - 7.3) | 3 (3.3 - 3.4) |
| TREES | 78 (68.5 - 93) | 89 (89.3 - 90) | 95 (92.6 - 96.6) |
| SHRUBS | 7 (2.1 - 10.8) | 4 (3.7 - 3.9) | 1 (0.6 - 2.2) |
| HERBS | 15 (5 - 20.7) | 7 (6.3 - 6.7) | 4 (2.8 - 5.2) |
| HYDRO-HYGROPHILOUS | 37 (12.9 - 49.8) | 20 (19.5 - 19.7) | 15 (15.2 - 15.3) |
| NPPs | 2 (0.3 - 2.9) | 2 (1.5 - 1.9) | 1 (0.5 - 0.8) |

**Table R.16 -** Summary of the most representative taxa (relative abundance %) identified in the KI06 core. The single value represents the average and those in parentheses give the range. The percentages of hydro-hygrophilous taxa and NPPs are calculated separately together with the rest of the taxa.

| | **KI06 - 1** | **KI06- 2** | **KI06- 3** |
|---|---|---|---|
| *Eucalyptus* sp. | 0 (0 - 0) | 0.1 (0 - 0.2) | 0.1 (0 - 0.2) |
| deciduous *Quercus* | 12 (6.3 - 14.1) | 5 (3.3 - 8.4) | 4 (2.3 - 5.9) |
| *Pinus pinaster* | 41 (34.7 - 47.5) | 65 (54.9 - 71.4) | 77 (69.3 - 84.8) |
| *Pinus sylvestris* type | 5 (1.5 - 8.9) | 7 (3.6 - 11.9) | 8 (4.1 - 11.2) |
| Apiaceae | 10 (7.2 - 13.9) | 4 (2.3 - 5.7) | 2 (1 - 3.2) |
| *Cerealia* type | 0.5 (0 - 0.9) | 0.2 (0 - 0.6) | 0.2 (0 - 0.6) |
| Cyperaceae | 7 (2.4 - 11.1) | 4 (1 - 7.1) | 2 (0.3 - 3.5) |
| Filicales Monolete | 8 (3.9 - 14.3) | 6 (1.7 - 12.3) | 3 (0.8 - 4.3) |
| Filicales Trilete | 11 (4.9 - 15.4) | 5 (1.3 - 12.9) | 2 (0.3 - 4.5) |
| TREES | 68 (62.1 - 75.4) | 86 (78.7 - 92.2) | 94 (90.5 - 95.1) |
| SHRUBS | 10 (5 - 14.9) | 5 (1.6 - 9.1) | 1 (1 - 1.8) |
| HERBS | 22 (13.2 - 26) | 9 (5.4 - 14) | 5 (3.8 - 8.1) |
| HYDRO-HYGROPHILOUS | 40 (28.6 - 47.1) | 25 (13 - 34.2) | 11 (9.1 - 14.5) |
| NPPs | 3 (1.5 - 4) | 2 (0.8 - 2.4) | 1 (0.2 - 1.6) |

## 3.4.1. KI03 & KI06

### 3.4.1.1. KI03 Pollen analysis

### LPAZ KI03-1 (17 - 9 cm) (1845 - 1920 CE)

Starting with the arboreal pollen, as shown in Figure R.45, trees predominate over the rest of the pollen. Their percentage ranges are high, between 68.5 and 93%. Among all the taxa identified, *Pinus pinaster* is clearly the dominant species (40.7 - 82.9%). The remaining forms have a lower abundance, with deciduous *Quercus* (1.9 - 9.3%), *Pinus sylvestris* type (1.8 - 4.8%), *Alnus* (0.9 - 5.6%) and *Betula* (0.8 - 4%) as secondary. Other taxa are also present: *Castanea*, *Corylus*, *Eucalyptus* sp., evergreen *Quercus*, *Fagus sylvatica*, *Fraxinus*, *Juglans* and *Salix*. Their percentages do not exceed 3% individually.

In the same Figure R.45, on the right, the content of the shrub pollen in this basal zone can be observed, ranging from 2.1 to 10.8%. *Arbutus* type, *Cistus* type, *Erica* type and *Prunus* type were the taxa identified and, with the exception of *Erica* type (0.8 - 5.2%), all the others are found in values below 5% each.

Herbaceous pollen has a higher presence (5 - 20.7%) in this zone (Fig. R.46). The two families with the highest abundance are Apiaceae (0.8 - 9.2%) and Poaceae (1.3 - 5.7%). The remaining taxa identified (*Artemisia*, *Aster* type, *Asphodelus albus* type, Cardueae, Caryophyllaceae, *Centaurea nigra* type, *Cerealia* type, Chenopodiaceae, Cichorioideae, Fabaceae and *Plantago lanceolata* type) do not exceed individually 3% abundance.

The hydro-hygrophilous pollen ranges between 12.9 and 49.8%, which are quite high abundance values (Fig. R.47). The three taxa identified, Cyperaceae (2.6 - 14.5%), Filicales Trilete (2.3 - 15.3%) and Filicales Monolete (2.1 - 13.5%) show here similar values.

Non-pollen palynomorphs (NPPs) (*Chaetomium* sp., *Glomus* cf. *fasciculatum*, *Pseudoschizaea circula* and *Sordaria* sp.) have also been identified in percentages less than 3% each (Fig. R.47).

### LPAZ KI03-2 (9 - 4 cm) (1920 - 1976 CE)

During this zone of the core, arboreal pollen continues to be predominant, maintaining very high values (89.3 - 90%) (Fig. R.45). *Pinus pinaster* continues to be the main taxon (70 - 74.4%). The percentages of *Pinus sylvestris* type increase slightly (6.9 - 8.3%). However, the percentages of deciduous *Quercus* (3.3 - 4.5%) and *Alnus* (1 - 2.2%) decreased compared with the previous zone. The rest of the taxa remain at similar values, below 3% each, including *Tilia*, which is detected for the first time in the core.

On the other hand, shrub pollen is decreasing and is now between 3.7 and 3.9% (Fig. R.45). *Arbutus* type, *Cistus* type, *Erica* type and *Prunus* type, whose percentage ranges do not exceed 2% individually in LPAZ KI03-2, have been identified.

Herbaceous pollen also decreased (6.3 - 6.7%) in this pollen zone (Fig. R.46). Furthermore, three taxa identified in the previous pollen zone disappear here: *Asphodelus albus*, *Centaurea nigra* type and Fabaceae. The remaining forms do not exceed 2.5% individually at any time.

The decreasing trend of hydro-hygrophilous pollen is also evident (19.5 - 19.7%) (Fig. R.47). Each of the three identified taxa, Cyperaceae, Filicales Monolete and Filicales Trilete, barely exceed 7% (only in the case of Filicales Trilete).

Non-pollen palynomorphs (NPPs) exhibit lower abundance values (1.5 - 1.9%) (Fig. R.47). In this intermediate zone, only the taxa *Glomus* cf. *fasciculatum*, *Pseudoschizaea circula* and *Sordaria* sp. have been identified, and none of these present abundances higher than 1.5%.

### LPAZ KI03-3 (4 - 0 cm) (1976 - 2004 CE)

The abundance of arboreal pollen increases in the most recent zone (92.6 - 96.6%) (Fig. R.45). *Pinus pinaster*, dominant taxon in the previous pollen zones, increases again (70 - 80%). In addition, *Pinus sylvestris* type also increased (10.3 - 13.2%). *Castanea* and *Tilia* have not been identified in this final zone of the core. The rest of the taxa display abundance rates very similar to those observed in the previous jntermediate pollen zone.

Shrub taxa continue to show a decreasing trend (0.6 - 2.2%) (Fig. R.45). In this zone, *Arbutus* type, *Cistus* type, *Erica* type and *Prunus* type have been detected. None of these taxa individually reaches 1% of abundance.

Figure R.46 reflects a continuation of decreasing herbaceous pollen percentages in this LPAZ KI03-3 (2.8 - 5.2%). However, only five herbaceous taxa have been identified in this pollen zone: Apiaceae, Cardueae, Cichorioideae, Chenopodiaceae and Poaceae, with less than 2% abundance in any case.

The hydro-hygrophilous pollen is also slightly reduced (15.2 - 15.3%) (Fig. R.47), continuing the trend already observed in the previous zone. The same three taxa have been identified: Filicales Trilete (3.3 - 4.4%), Cyperaceae (3 - 3.5%) and Filicales Monolete (2.3 - 4.2%).

The same occurs with the evolution of non-pollen palynomorphs (NPPs) over the length of the core (0.5 - 0.8%) (Fig. R.47). In this case, *Pseudoschizaea circula*, *Sordaria* sp. and *Spyrogira* sp. have been identified as the only NPPs in this final zone, with maximum percentages of 0.5% reached individually by these taxa.

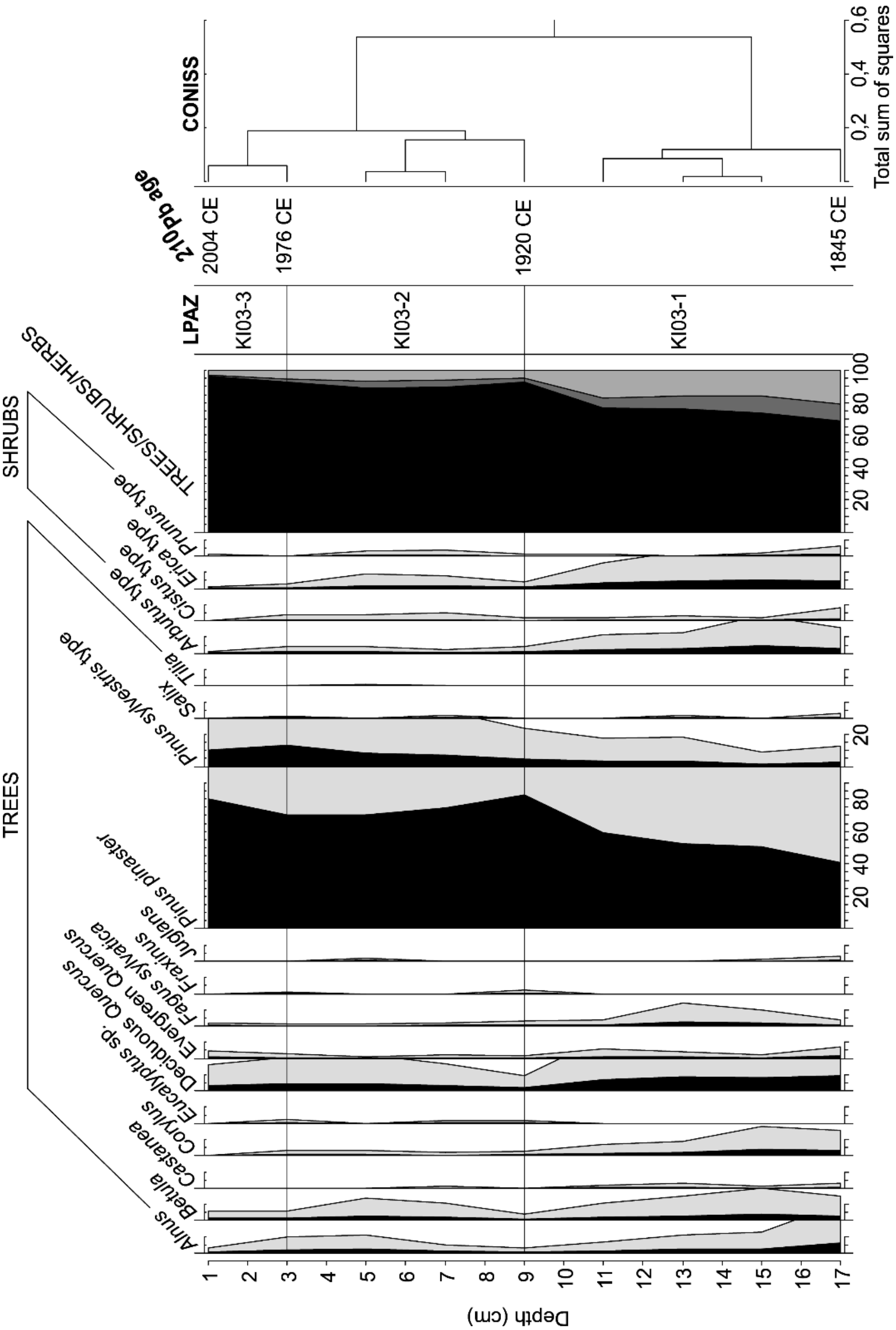


**Figure R.45** - Pollen diagram corresponding to the arboreal and shrub pollen along the KI03 core. Depth at centimeter scale, the evolution of arboreal and shrub taxa, the defined local pollen assemblage zones (LPAZ), the $^{210}$Pb dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

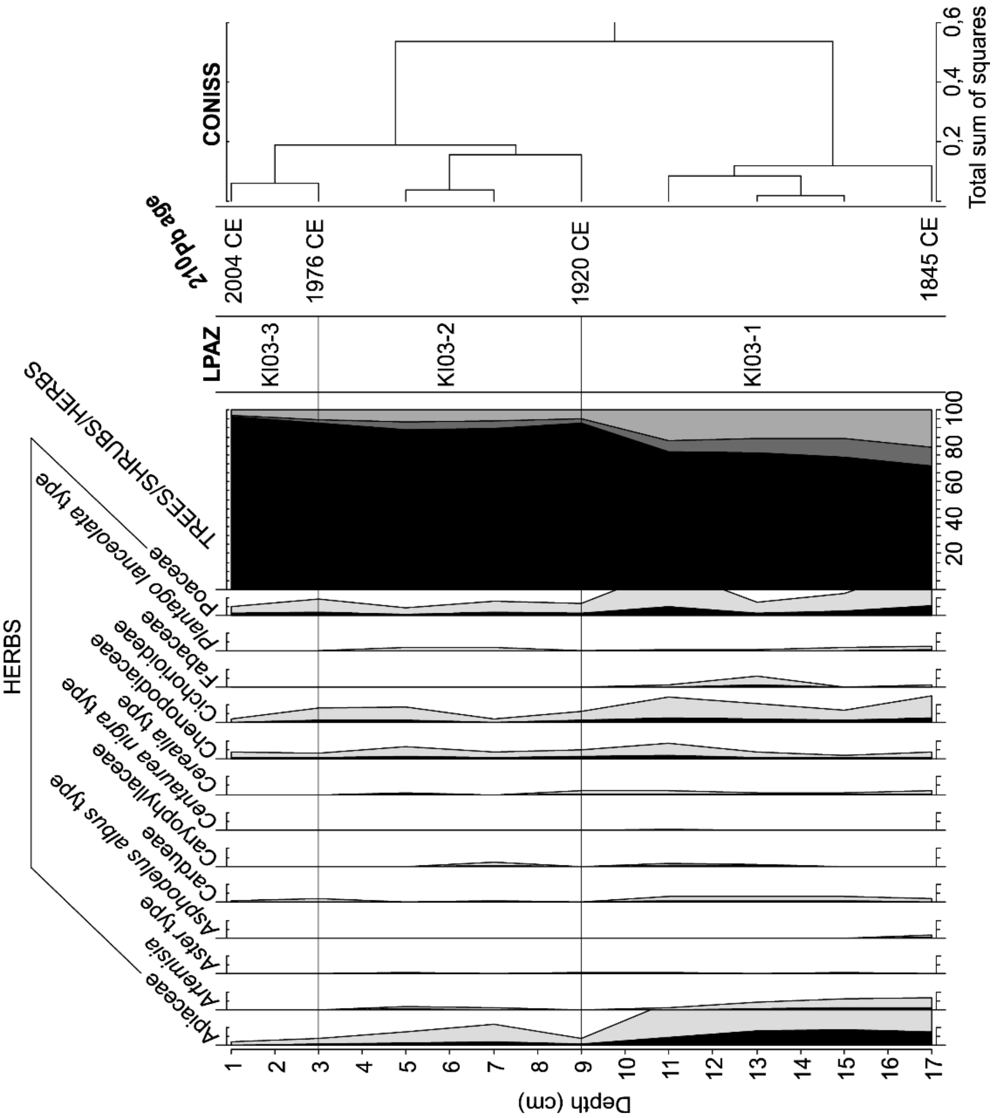


**Figure R.46** - Pollen diagram corresponding to the herbaceous pollen along the KI03 core. Depth at centimeter scale, the evolution of herbaceous taxa, the defined local pollen assemblage zones (LPAZ), the $^{210}$Pb dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

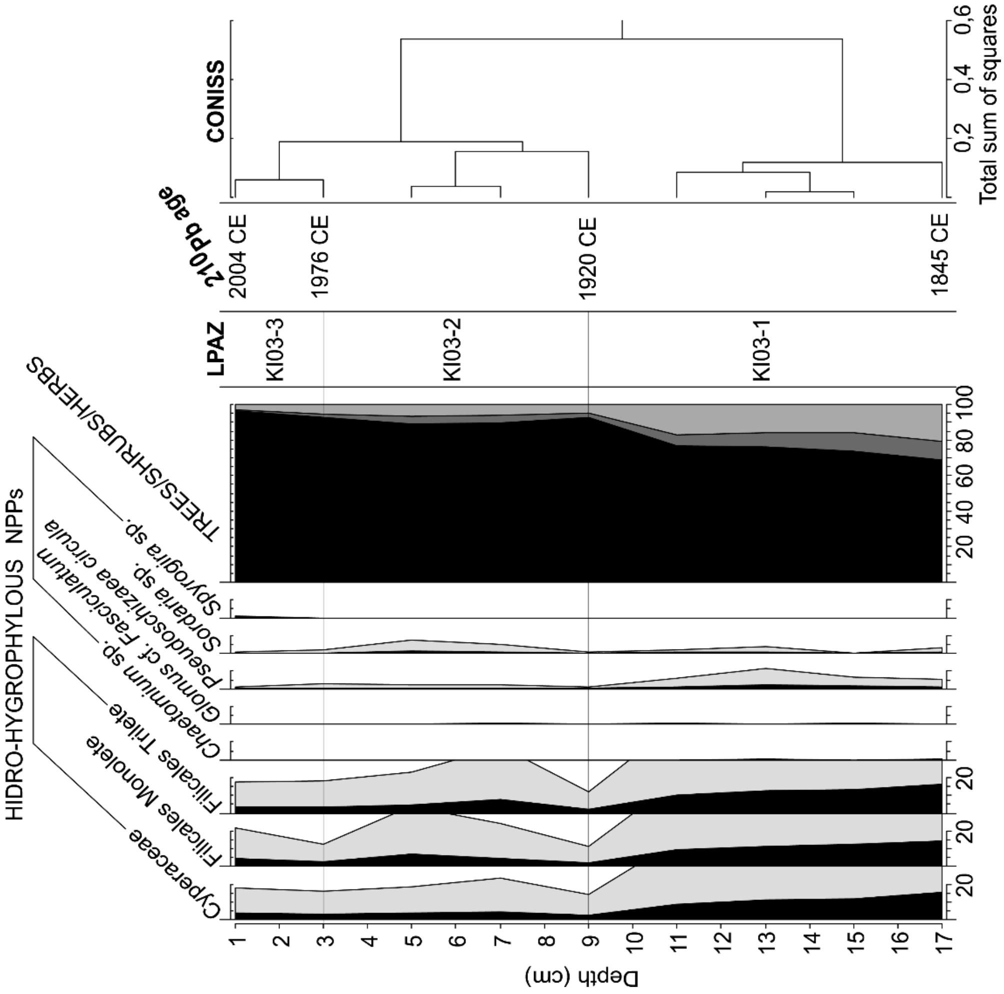


**Figure R.47** - Pollen diagram corresponding to the hydro-hygrophilous pollen and non-pollen palynomorphs (NPPs) along the KI03 core. Depth at centimeter scale, the evolution of hydro-hygrophilous and the NPPs taxa, the defined local pollen assemblage zones (LPAZ), the $^{210}$Pb dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

### 3.4.1.2. KI06 Pollen analysis

### LPAZ KI06-1 (20 - 15 cm) (1817 - 1864 CE)

The pollen analysis indicates a predominance of arboreal pollen in this basal zone of the core (62.1 - 74.4%), as observed also in the previous KI03 core (Fig. R.48). The dominant taxon is *Pinus pinaster* (36.1 - 47.5%). Deciduous *Quercus* (6.3 - 14.1%) and *Pinus sylvestris* type (1.5 - 8.9%) are secondary forms. The following taxa have also been identified here: *Alnus*, *Betula*, *Castanea*, *Corylus*, evergreen *Quercus*, *Fagus sylvatica*, *Juglans* and *Salix*. All these minor taxa appear in percentages of less than 5% each.

Shrub pollen presents percentage values between 5.6 and 14.9% (Fig. R.48). Five taxa were identified: *Erica* type (2.9 - 8.5%), *Arbutus* type (0.7 - 4.3%), *Cistus* type (0 - 3.4%), *Calluna* (0 - 1.6%) and *Prunus* type (0 - 0.4%).

In Figure R.49, we can observe that herbaceous pollen ranges from 13.2 to 26%. Apiaceae (7.2 - 13.9%) is the family with the highest presence within the herbaceous component. Cichorioideae (1.8 - 6.2%) and Poaceae (1.2 - 8.8%) also have remarkable values. The rest of the taxa identified (*Artemisia*, *Aster* type, Cardueae, Caryophyllaceae, *Centaurea nigra* type, *Cerealia* type, Chenopodiaceae, Fabaceae and *Plantago lanceolata* type) do not exceed 2% individually.

Regarding the hydro-hygrophilous pollen identified in this LPAZ KI06-1, the overall percentages are high (28.6 - 47.1%) (Fig. R.50). Filicales Trilete (4.9 - 15.4) is the taxon with the greatest dominance within this group. Filicales Monolete (4.6 - 14.4%), Cyperaceae (2.4 - 11.1%) and *Polypodium vulgare* type (0 - 1.1%) have also been identified.

Finally, the non-pollen palynomorphs (NPPs) have been scarce (1.5 - 4%) (Fig. R.50). The taxa *Chaetomium* sp., *Glomus* cf. *fasciculatum*, *Pseudoschizaea circula*, *Sordaria* sp. and *Spyrogira* sp. have been identified, each of them below 2.5% abundance.

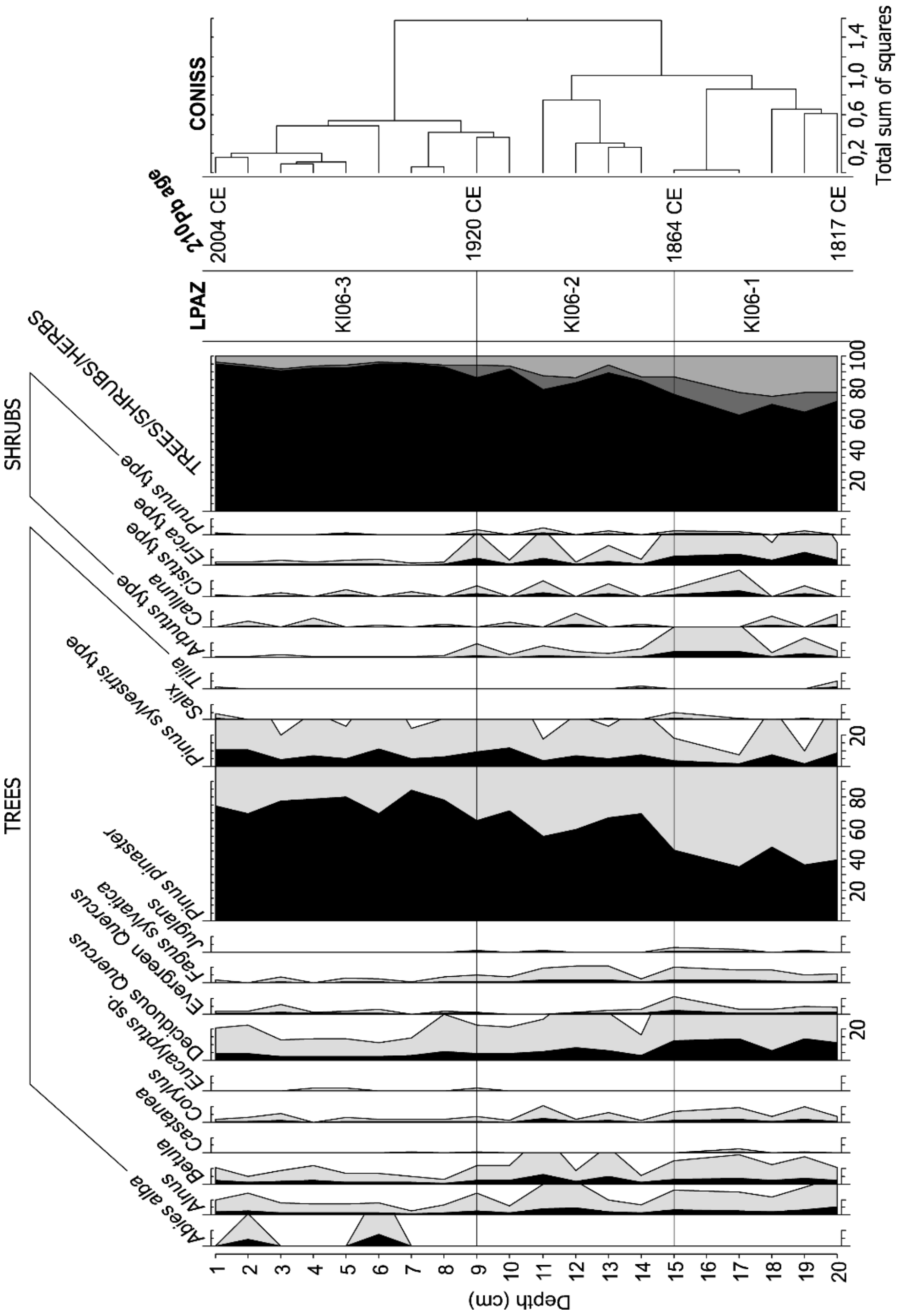


**Figure R.48** - Pollen diagram corresponding to the arboreal and shrub pollen along the KI06 core. Depth at centimeter scale, the evolution of arboreal and shrub taxa, the defined local pollen assemblage zones (LPAZ), the $^{210}$Pb dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

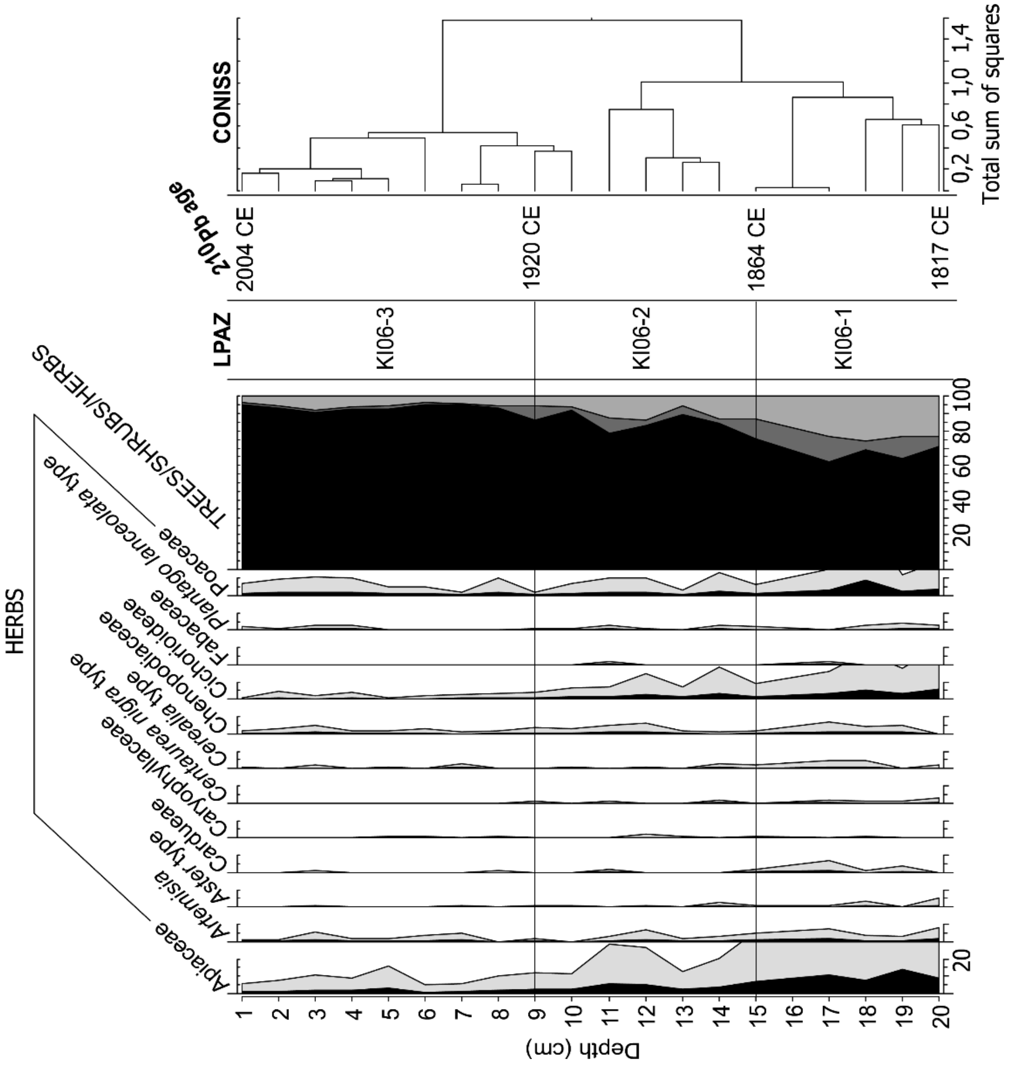


**Figure R.49** - Pollen diagram corresponding to the herbaceous pollen along the KI06 core. Depth at centimeter scale, the evolution of herbaceous taxa, the defined local pollen assemblage zones (LPAZ), the $^{210}$Pb dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

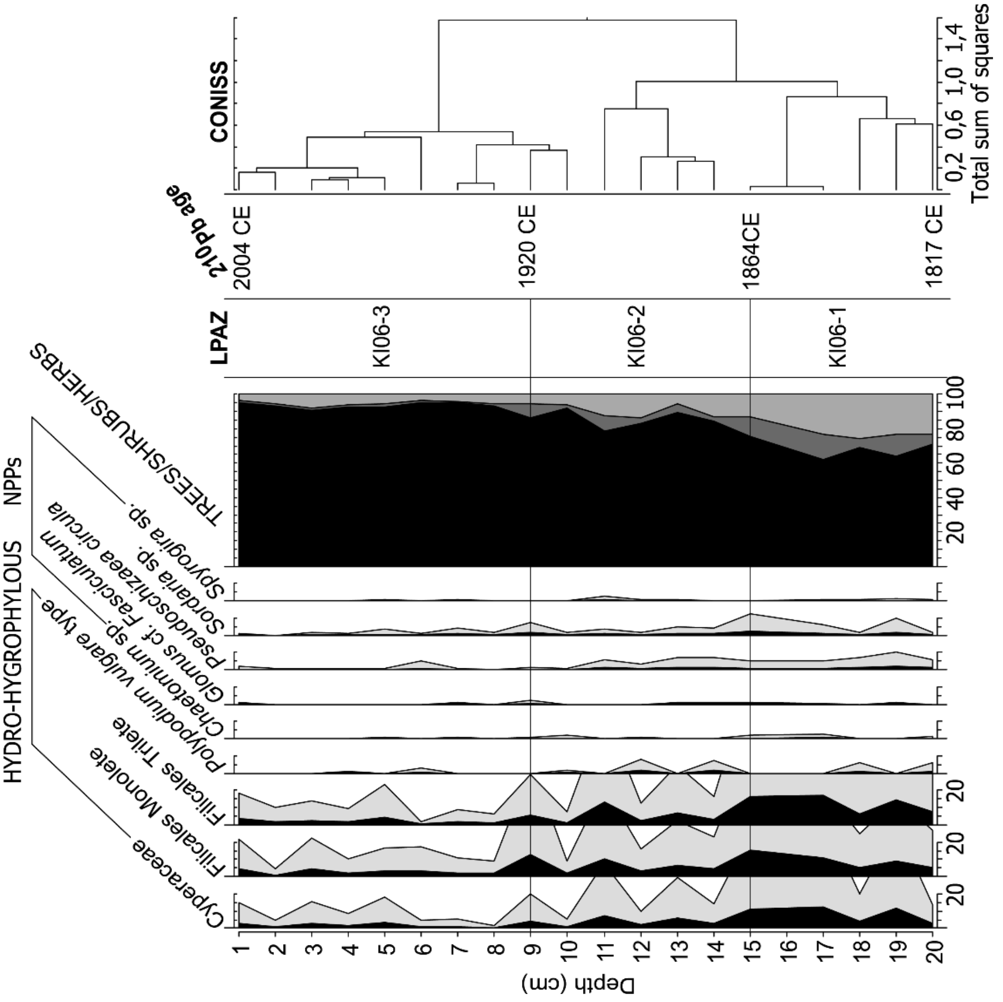


**Figure R.50** - Pollen diagram corresponding to the hydro-hygrophilous pollen and non-pollen palynomorphs (NPPs) along the KI06 core. Depth at centimeter scale, the evolution of hydro-hygrophilous and the NPPs taxa, the defined local pollen assemblage zones (LPAZ), the $^{210}$Pb dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are represented.

### LPAZ KI06-2 (15 - 9 cm) (1864 - 1920 CE)

The arboreal pollen experiences a large increase in this intermediate pollen zone (78.7 - 92.2%) (Fig. R.48). This mainly affects the individual percentages of the dominant species: *Pinus pinaster* (54.9 - 71.4%). The abundance of *Pinus sylvestris* type also increases (3.6 - 11.1%). However, the percentages of deciduous *Quercus* decrease (3.3 - 8.4%). *Alnus* (1.2 - 4.4%) and *Betula* (1.2% - 6.5%) maintain percentages similar to those observed in the previous zone. For the first time in this marine core, the presence of *Tilia* and *Eucalyptus* sp. was detected although, like the rest of the taxa identified (*Castanea*, *Corylus*, evergreen *Quercus*, *Fagus sylvatica*, *Juglans* and *Salix*), they do not exceed 3% individually.

In contrast, shrub taxa experienced a decrease (1.6 - 9.1%) (Fig. R.48). The same five taxa previously detected (*Erica* type, *Arbutus* type, *Cistus* type, *Calluna* and *Prunus* type) no longer exceed 5% each now.

The same decreasing trend is observed in the herbaceous pollen (5.4 - 14%) (Figure R.49). The previously identified taxa in the basal zone are still present here (Apiaceae, Cichorioideae, Poaceae, *Artemisia*, *Aster* type, Cardueae, Caryophyllaceae, *Centaurea nigra* type, *Cerealia* type, Chenopodiaceae, Fabaceae and *Plantago lanceolata* type) but now in lower percentages. For example, the abundance of Apiaceae, a family that dominated the previous pollen zone, is reduced to 2.3 - 5.7%.

The decrease also seems to affect the hydro-hygrophilous pollen. In Figure R.50, it can be observed that the percentages now range between 13 and 34.2%. Filicales Trilete continues to be the dominant form in this group (1.3 - 12.9%).

Non-pollen palynomorphs (NPPs) continue to be scarce (0.8 - 2.4%) The taxa with the greatest presence are *Sordaria* sp. and *Pseudoschizaea circula*, although none exceeds 1.5 % (Fig. R.50).

### LPAZ KI06-3 (9 - 0 cm) (1920 - 2004 CE)

A new increase is observed in the total percentages of arboreal pollen (90.5 - 95.1%) (Fig. R.48). *Pinus pinaster* now reaches values between 69.3 and 84.8%. The rest of the taxa maintain percentages very similar to those observed in the previous zone, except for two differences: *Juglans* disappears and *Abies alba* is identified for the first time in this core (0 - 7.5%).

The decreasing trend of the shrub pollen continues (1 - 1.8%) (Fig. R.48). *Calluna, Erica* type, *Arbutus* type, *Cistus* type and *Prunus* type are present, but they do not exceed 1.5% individually. In fact, *Calluna* (0 - 1.2%) is now the most common shrub genus.

Herbaceous pollen continues to decrease, but only slightly (3.8 - 8.8%) (Fig. R.49). Fabaceae and *Centaurea nigra* type are no longer present in this uppermost zone. Apiaceae (1 - 3.2%) continues to be the dominant herbaceous taxon. The remaining taxa identified do not exceed 2.5% individually.

As in the previous intermediate zone, hydro-hygrophilous taxa continue to decrease in abundance (9.1 - 14.1%) (Fig. R.50). The taxa identified here are the same as in the previous zones: Filicales Trilete (0.3 - 4.5%), Filicales Monolete (0.8 - 3.4%), Cyperaceae (0.3-3.5%) and *Polypodium vulgare* type (0.2 - 0.5%).

Finally, the percentage of non-pollen palynomorphs (NPPs) decreased slightly (0.2 - 1.6%) (Fig. R.50). *Chaetomium* sp., *Glomus* cf. *fasciculatum*, *Pseudoschizaea circula*, *Sordaria* sp. and *Spyrogira* sp. have been identified with less than 1% abundance individually.

### 3.4.1.3. Geochronology

The geochronology of the Basque Mud Patch (BMP) cores has been carried out through radioisotope analysis of $^{210}Pb_{ex}$ and $^{137}Cs$. For this purpose, another core was used, KS04, which was sent to the University of Cantabria in order to obtain a sedimentation rate and an age for the materials. This core is equivalent to KI03 and KI06 due to their geographic proximity.

Concerning the $^{210}Pb_{ex}$ activity, in Figure R.51 we can observe that the ranges oscillate from 13.1 - 230 Bq kg$^{-1}$ with its activity disappearing at 11 cm depth.

The $^{137}Cs$ concentrations (1.1 - 3.7 Bq kg$^{-1}$) (Fig. R.52), on the other hand, disappear at 6-7 cm without observing any clear peak that would allow us to date 1963 CE accurately.

The exponential decrease with depth observed in the $^{210}Pb_{ex}$ values has allowed us to calculate, by means of a linear regression, a mean sedimentation accumulation rate (SAR) of 1 ± 0.1 mm yr-$^{1}$ and a mass accumulation rate (MAR) of 97 ± 6 mg cm$^{-2}$ yr$^{-1}$. The applied Constant Flux: Constant Sedimentation (CF:CS) model (Appleby and Oldfield, 1978; Koide et al., 1973; Robbins, 1978) assumes constant $^{210}Pb$ flux and sedimentation rates for this sedimentary record.

Therefore, the considered time frame for the marine cores of the BMP (KI03 and KI06) is 1817 to 2004 CE.

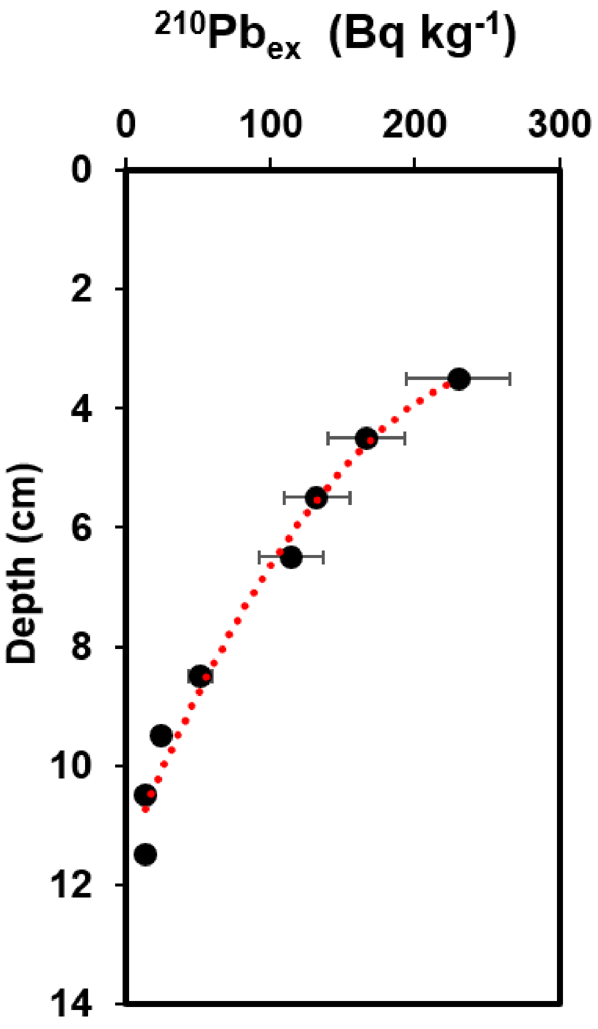


**Figure R.51** - Distribution of $^{210}Pb_{ex}$ (Bq kg$^{-1}$) with depth along the KS04 core. Re-adapted from Irabien et al. (2020).

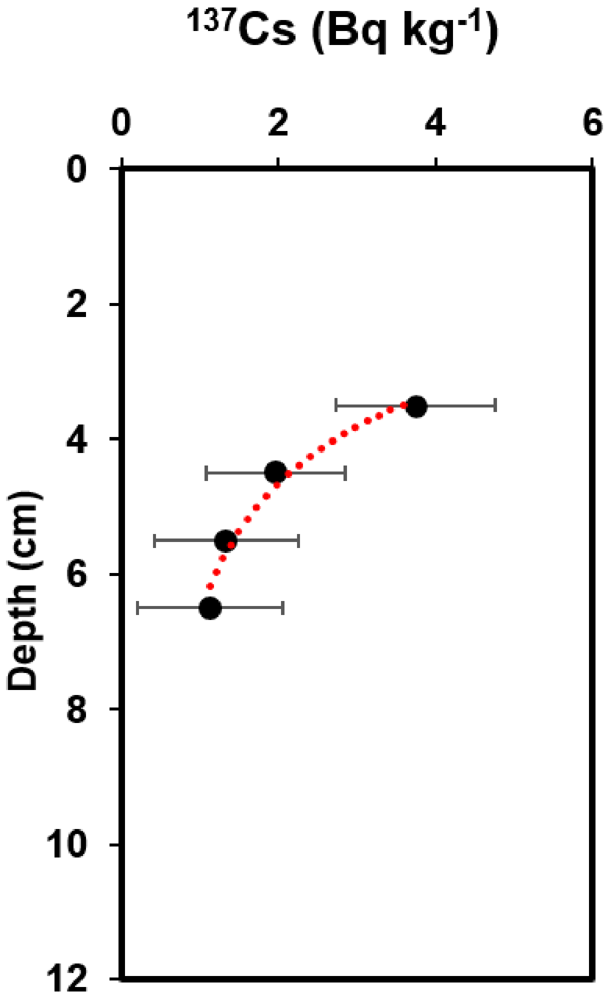


**Figure R.52** - Distribution of $^{137}$Cs (Bq kg$^{-1}$) with depth along the KS04 core**.** Re-adapted from Irabien et al. (2020).

# 4. Pleistocene

The raw data corresponding to the pollen analysis of this doctoral thesis are available in the following online cloud for further details:

https://drive.google.com/drive/folders/13GI02_4OWhwtkEJQaiKeSNv0MJHMWEuQ?usp=sharing

# Discussion

This chapter aims to provide an environmental interpretation of the sedimentary records through the information obtained from the different analyses (palynological, statistical and modelling) performed for 10 boreholes and cores from the eastern Cantabrian coast.

It is divided into three main temporal sections: Pleistocene, Holocene and Anthropocene. By organizing it in this way a linear and orderly discourse can be created, where the evolution of vegetation from the Pleistocene to the present day may be observed. This also allows us to better discern between natural and anthropogenic dynamics based on the increasing capacity of humans to transform the environment in more recent times versus the lower or null impact of humans in the older records.

# 1. Pleistocene

Pleistocene studies have been traditionally characterized by a strong paleoclimate focus. This is partly due to the added difficulty of studying this geological epoch, mainly owing to the partial pollen information that we can retrieve from such ancient sediments. This implies the need to follow an analytical discourse based on climate changes and, therefore, refer to the so-called Marine Isotopic Stages (MIS).

The Marine Isotopic Stages (MIS) are a series of alternating warm and cold intervals that serve, in turn, as a time scale in studies of the Earth's paleoclimate. These intervals have been inferred from oxygen isotope data as recorded in carbonate microfossil tests that reflect changes in temperature. This scale is not only temporal, but also typological, since those stages numbered with even numbers represent cold glacial intervals, while the odd-numbered stages represent warm interglacial intervals. In palynological studies of older geological epochs, as is the case of Liendo, MIS are of vital importance when contextualizing changes observed in the plant assemblages (Sánchez-Goñi et al., 1999; Heusser & Heusser, 2006; Mudie & McCarthy, 2006).

The case of Liendo is of special interest and its study opens up new opportunities for palaeoclimate and palaeoenvironmental knowledge of Pleistocene times. The peculiarities of this borehole lie not only in its impressive length (89 m), but also in the sedimentology, geochronology and pollen results obtained.

## 1.1. Sedimentology

The sedimentological profile of the Liendo borehole stands out for the frequent changes observed, forming well-defined sedimentary packages. These sedimentary packages follow one after the other along the borehole and although they are not uniform, alternating stretches of two or three sedimentary packages have been interpreted as sedimentary phases. In summary, the sedimentary types found in the borehole are: 1. yellow Keuper clays, 2. organic mud, 3. sand, 4. sandy mud, 5. peat, 6. brown mud, 7. soil and brick fill (Fig. D.1).

The geological knowledge of the area, one of the most important karstic systems in the north of the Iberian Peninsula, as well as the stratigraphy of the borehole, leads us to the conclusion that this deposit possibly formed in an ancient karstic lake (Morellón et al., 2009; Ábalos & Elorza, 2013; Valero-Garcés et al., 2014; Damnati et al., 2016; Elorza et al., 2019).

### 1.2. Geochronology

As with the rest of the boreholes, samples were collected for radiocarbon dating in all peat sedimentary strata, in order to have the most accurate geochronology possible.

Only two out of 13 samples provided reliable radiocarbon dates. These samples, located at 38 and 58 m depth, show approximate dates between 42,000 – 48,000 years BP. The rest of the radiocarbon dates obtained were older than 45,000 years and therefore, not datable by $^{14}$C. This is due to the fact that the half-life of $^{14}$C isotope is 5730 years, Therefore, we do not have very precise dating to make, for example, an age model that would allow us to better delimit the borehole's time frame. This also complicates the interpretation of the pollen results obtained (Barker, 1958; Stuiver, 1983; Linick et al., 1989; Haghipour et al., 2019).

**Table D.1 -** Vegetation groups and taxa included in in the synthetic diagrams

| VEGETATION GROUPS | TAXA |
|---|---|
| Riparian taxa | *Alnus*, *Fraxinus*, *Salix*, *Ulmus, Populus* |
| Deciduous taxa | *Corylus*, *Betula*, Deciduous *Quercus*, *Tilia, Ilex aquifolium Prunus* |
| Xerophytic taxa | Chenopodiaceae, Cichorioideae, *Aster* type, *Artemisia*, *Apiaceae*, *Centaurea nigra*, *Asphodelus albus* type |

**Figure D.1 -** Stratigraphic column of the Liendo borehole. According to colors: magenta: soil and brick fill; light brown: brown mud; black: peat; brownish gray: sandy mud; gray: sand; dark brown: organic mud; yellow: yellow Keuper clays.

## 1.3. Evolution of the vegetation

Considering the characteristics of the Liendo long sedimentary borehole and the objectives of the research presented in this doctoral thesis, we decided to carry out a study along the entire sequence. After obtaining the first results that demonstrated its particular interest, a more detailed study was carried out to improve the resolution from 687 to 282 cm depth. In this way, we obtained a higher pollen precision for the upper part of the borehole that, in addition, allowed us to carry out a first paleoclimate reconstruction of temperatures and precipitation.

Even so, we must be aware of the limitations of this analysis and the difficulty of establishing hypotheses that could relate changes in vegetation with possible climate changes without an appropriate geochronological framework. This is why the analysis that follows in this and the next sections will make reference to some Marine Isotopic Stages (MIS) together with the particular analysis of some specific taxa that we consider relevant for climate interpretations.

In spite of this, through certain taxa that are commonly diagnostic of possible specific climate events, a possible geochronological context will be proposed here. We consider that with the available information it is possible to draft an initial hypothesis on the chronological question by comparing the data obtained in Liendo with those published in other regional paleoclimate studies. In addition, a reconstruction of paleotemperatures and paleoprecipitation in the higher resolution LPAZ LIE (LIE-7 - LIE-11) was carried out (Fig. D.5). This paleoclimate reconstruction may also provide additional geochronological information.

In the basal LPAZ LIE-1, the significant values observed for deciduous taxa (*Fagus sylvatica*) would indicate a humid phase. Additionally, the progressive increase in the values of pines and silver fir (*Abies alba*) seem to indicate a cooling of temperatures (Fig. D.2). Both pine and spruce withstand relatively humid conditions, which would explain the predominance of *A. alba*. In fact, due to the process of aridification experienced by the Iberian Peninsula during the Holocene, this taxon has been relegated at present to the northeastern part in the areas bordering the Pyrenees mountain range (Wick & Möhl, 2006; Lebourgeois et al., 2010; Falk & Mellert, 2011; Serra-Diaz et al., 2012; Gazol et al., 2015, 2019).This taxa could be indicating very cold conditions in the region, although only punctually, since up to three large *A. alba* abundance peaks can be observed in zones LIE-1, LIE-3 and LIE-6 (Figure D.2). During the glaciations, fir was able to resist and even expand its territory, whereas when temperatures were higher, it would disappear or persist in small shelters where the climate was more favorable. This could explain why in the Liendo borehole we observed sections in which the presence of *A. alba* is dominant, but also moments in which the presence of this taxon has been detected but in lower percentages (Figs. D.2, D.3) (Scotti-Saintagne et al., 2021). Therefore, it has been shown that climate change does indeed affect the expansion/withdrawal of *A. alba* populations, although work carried out in the Holocene context suggests that silver fir populations were more impacted after the appearance of humans as a driver of environmental alteration (Carcaillet & Müller, 2005; Wick & Möhl, 2006; Kozáková et al., 2011).

In addition, in other studies in the northern Iberian Peninsula and in marine boreholes on the Atlantic coast, it has been observed that the presence of *Pinus* remained considerable during the Pleistocene, as also occurs in Liendo (Fig. D.2). In some Mediterranean boreholes, this translates into an increase of deciduous forest. This type of association (pine and silver fir) reminds us of the vegetation observed in various studies for the end of the MIS 3c (~60 - 55 ka BP), when the pollen assemblages seem to indicate a generalized cold climate gradually changing to wetter and somewhat warmer conditions, especially at ~55 ka BP (Roucoux et al., 2008; González-Sampériz et al., 2010; Sadori et al., 2016; Camuera et al., 2019).

In the LPAZ LIE-2 we observe how arboreal pollen values decrease notoriously. Pine reduces its percentages considerably while *A. alba* seems to disappear (Fig. D.2). The increased presence of Cichorioideae, as well as the fact that the values of deciduous taxa do not increase, may indicate a drop in temperatures. These conditions point to a rather cold and dry interval, with consequent reductions in moisture-demanding forests such as pine and silver fir, which seem to disappear (Camuera et al., 2019). The deciduous forest, however, is maintained. The specific conditions of the Cantabrian region probably soften the effect of environmental dryness, as seen in other works such as in Area Longa, Lugo province (Burjachs & Julià, 1994; Gómez-Orellana et al., 2007; González-Sampériz et al., 2010). These characteristics would fit with the end of MIS 3c and the beginning of MIS 3b (~52 - 40 ka BP).

The following LPAZ LIE-3 stands out for the new increase in tree pollen, where a new peak of *A. alba* appears, an increase in riparian vegetation is quite noticeable, as well as a general increase in pine and deciduous vegetation (Fig. D.2). Studies from González-Sampériz et al., 2010 have reported a reduction in precipitation and, therefore, in humidity during the MIS 3b, but that did not necessarily have to occur. We must keep in mind that the Cantabrian Coast of the Iberian Peninsula is characterized by its high precipitation conditions. This would imply a certain recovery phase with higher temperatures and, in the case of Liendo, higher humidity. In fact, several studies show a tree component dominated by *Pinus* and *Juniperus* with the presence of deciduous *Quercus* and other trees such as *Betula*, *Corylus*, *Alnus*, and *Tilia* during MIS 3 (González-Sampériz et al., 2010; Railsback et al., 2017; Columbu et al., 2019).

After this interval, a generalized decline in arboreal pollen in favor of herbaceous species is observed from LPAZ LIE-4 onwards (Fig. D.2). In fact, an increase in Apiaceae, *Centaurea nigra* and Cichorioideae species is present. Together with the aforementioned reduction of arboreal vegetation, this could be indicating a cold and, above all, dry phase. However, the reduction in deciduous taxa is not accentuated and the appearance of up to 40% of hydro-hygrophilous vegetation would indicate that the decrease in temperature and precipitation would not be excessive. Also noteworthy is the presence of evergreen *Quercus* with values of around 10%, which raises the question of the adaptation of holm oak to the Cantabrian coastal climate. This taxon is mainly identified in the LPAZs LIE-1 to LIE-6 (Fig. D.2, D.3). Holm oak is one of the most representative taxa of the Mediterranean forest, and in the Cantabrian Coast it adapts very well to the humid and temperate climate, and to the calcareous soils of the cliff areas.

Liendo, although it is now very close to the coast, is a little more inland than the rest of the locations studied in this doctoral thesis. Therefore, we must take into account that there are different types of evergreen *Quercus* and, on many occasions, they share the same habitat. On the one hand, the xerophytic holm oak groves that generally are biogeographically immersed in the Mediterranean Region. Secondly, the montane holm oak groves. These two most often appear together. Finally, the coastal holm oak grove that is scattered along the entire Cantabrian coast. It is possible that in Liendo we could have a combination of the three types of evergreen *Quercus*, although its modern presence in the area and the proximity to the coast of this enclave, make very possible that the taxa identified belong to the montane and/or coastal group (Varas-Cobo et al., 2006; Pérez-Obiol et al., 2016).

The scientific literature seems to explain that the presence of this Mediterranean taxon in the northern regions of the Iberian Peninsula may be due to its expansion from inland plateau areas during the driest intervals of the Quaternary period (Varas-Cobo et al., 2006; Loidi et al., 2011; Uzquiano et al., 2016). Although the coastal holm oak is not observed in inland areas, it is precisely in coastal areas where the climate is more favorable for this taxon, which would compete with the rest of the predominant deciduous taxa. Also, from the point of view of genetics, it has been hypothesized that the coastal holm oak appeared on the Cantabrian coast during the Paleogene period, when the prevailing subtropical conditions would favor its expansion, hybridizing with the more continental phenotypes during the driest periods, giving rise to the current coastal holm oak (Peñalba, 1989, 1994; Ramil-Rego et al., 1998, Carrión et al., 2012). In any case, the relict character of the Cantabrian coastal holm oak seems to be clear, since the persistence of this taxon in the region must respond to previous climatic conditions that are not currently present (Varas-Cobo et al., 2006; Loidi et al., 2011). Therefore, it is very possible that the presence of this taxon in Liendo during Pleistocene times could be indicating a greater aridification of the Cantabrian region (Varas-Cobo et al., 2006; Loidi et al., 2011; Uzquiano et al., 2016).

All this has already been also observed in the Dead Sea in the Levant or even in Lake Van, Turkey (Pickarski & Litt, 2017; Chen & Litt, 2018). Both the radiocarbon dates obtained for this interval and the vegetation association suggest the Heinrich Event 5. This event, which occurred during the last glaciation, has been chronologically framed around ~45 ka BP (Vidal et al., 1999; Hemming, 2004). This type of event is generally considered as indicative of very cold periods prior to the rapid warming times known as Dansgaard-Oeschger events (D-O). As we do not have a very high pollen resolution for this borehole section nor a precise chronology, we can only tentatively interpret the intervals in which the forest vegetation seems to recover and the taxa indicate an increase in humidity, as the alternation between the Heinrich and the Dansgaard-Oeschger events. However, previous works in which pollen has been used as a proxy have characterized the first and last phases of the Heinrich events 5 and 4 (H5, H4) as temperate and humid climates in southwestern Europe and associated them with the European origin of ice detritus (Vidal et al., 1999; Sánchez-Goni et al., 2000: Hemming, 2004; Sepulchre et al., 2007; Naughton et al., 2009; Pickarski & Litt, 2017; Chen & Litt, 2018). Nevertheless, during the intermediate chronological phases of these Heinrich events, those pollen records suggest colder and drier climates possibly due to the maximum contribution of glacial detritus from the ice surges of the Laurentide ice sheet. Vegetation changes in southwestern Europe seem to be related to cold winter air masses arriving from more intermediate latitudes (Sánchez-Goni et al., 2000; Sepulchre et al., 2007; Naughton et al., 2009).

All this fits well with observations at the end of the LPAZ LIE-4 and beginning of LPAZ LIE-5 where an upturn in arboreal pollen (AP) is found (Fig. D.2). As commented previously, the improvement in climate conditions would cause an increase in arboreal taxa in general, but especially of pines and deciduous taxa. In addition, very low values of *Artemisia* and Cichorioideae, cold indicators, are observed, as well as an increase in Cyperaceae. This would suggest that, in addition, environmental conditions would be somewhat more humid and warmer during this interval in Liendo. These conditions are similar to those observed in other studies such as Villarquemado (Teruel), Padul (Granada) or Area Longa (Lugo) (Gómez-Orellana et al., 2007; González-Sampériz et al., 2010, 2020; Camuera et al., 2018, 2019; Garcia-Ibaibarriaga et al., 2019).

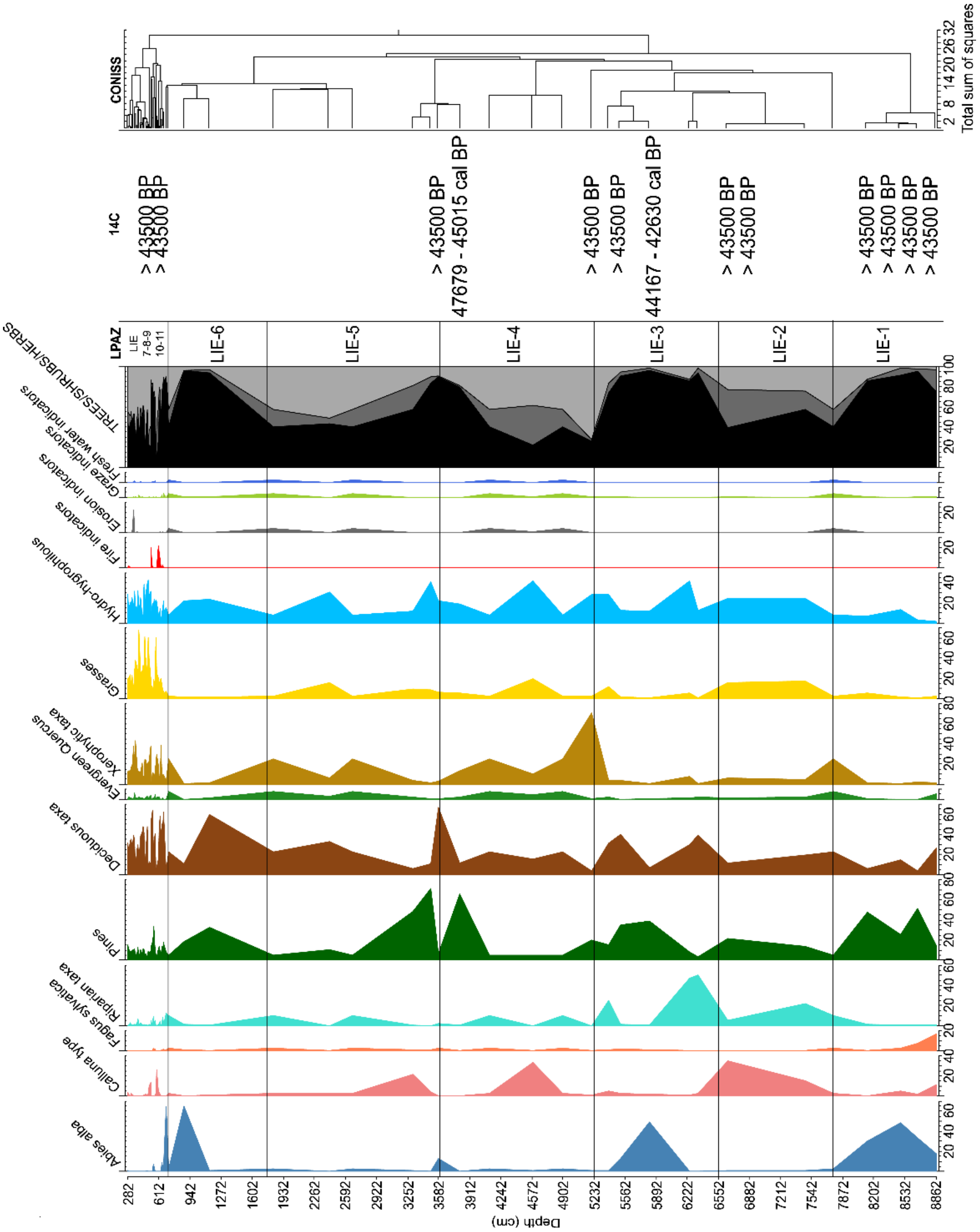


**Figure D.2 -** Synthetic pollen diagram of the complete Liendo borehole. The different vegetation groups and/or most relevant taxa are represented. In addition, the depth (cm), the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates, and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are also represented.

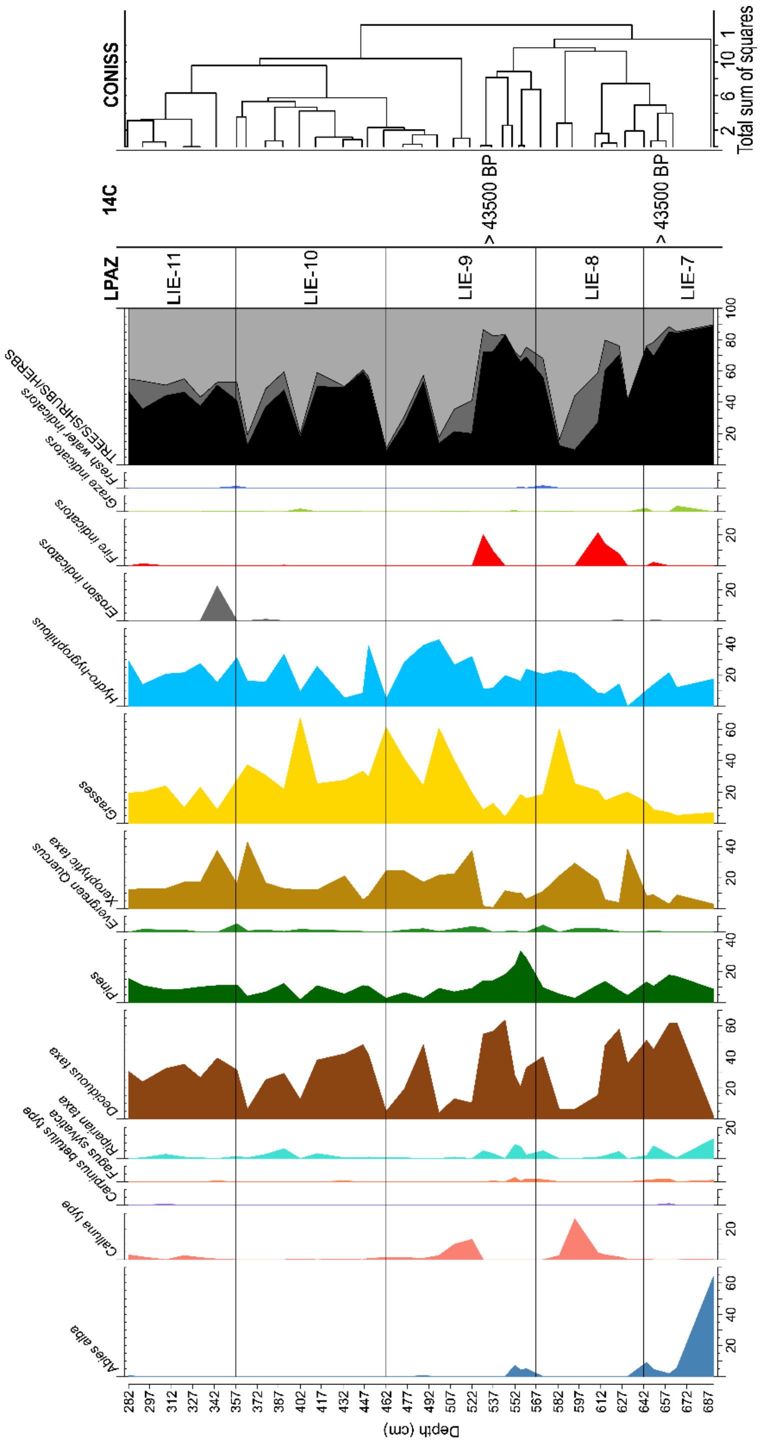


**Figure D.3 -** Synthetic pollen diagram of the upper section of the Liendo borehole analysed at higher resolution. The different vegetation groups and/or most relevant taxa are represented. In addition, the depth (cm), the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are also represented.

Even so, most of the LPAZ LIE-5 exhibits a generalized decrease in AP, especially pine (Fig. D.2). An increase in Cichorioideae and *Artemisia* is also observed in this zone, which could indicate a cold climatic event together with the reduction of arboreal taxa. This event would be relatively rapid allowing some arboreal species to persist. Despite the similarities observed in the pollen results, we cannot affirm that the vegetation association observed in LPAZ LIE-5 corresponds to a stage after the Dansgaard-Oeschger events and, therefore, to the Heinrich 4 event (~37 ka BP). The low resolution of both pollen and radiocarbon dating available only allows to hypothesize this possibility (Sánchez-Goñi et al., 1999; Gómez-Orellana et al., 2007; González-Sampériz et al., 2010, 2020; Biltekin et al., 2019).

**Figure D.4** - Map showing the location of the points studied in other Pleistocene research and mentioned throughout the discussion.

In the last lower-resolution LPAZ (LIE-6), a clear increase in arboreal vegetation and hydro-hygrophilous taxa can be observed (Fig. D.2). This increase in the AP is mainly due to higher percentages of pine and deciduous vegetation. In addition, a new peak of *A. alba* also appears at the end of this pollen zone, which coincides with the decrease in deciduous vegetation and pines (Fig. D.2). This has also been observed in other boreholes, as at Villarquemado (Teruel) in the NE or Area Longa (Lugo) in the NW of the Iberian Peninsula where, after a decline in woody taxa, forest associations seem to recover (Gómez-Orellana et al., 2007; González-Sampériz et al., 2010, 2020).

LPAZ LIE-7 initiates the higher resolution analysis of the Liendo borehole (Fig. D.3). It is likely that this pollen zone continues the trend observed in the previous LPAZ LIE-6 (Fig. D.2). In this LPAZ the percentages of AP, specifically the deciduous taxa, experience a considerable increase and, in addition, other taxa such as Cichorioideae and those indicative of a dry environment decrease. This suggests warmer conditions than those observed during previous LPAZ LIE-4 and LIE-5, where the Heinrich events may be located (González-Sampériz et al., 2010, 2020).

In the following LPAZ LIE-8, a punctual decrease in tree taxa and a subsequent recovery of the same is observed. It is possible that, from the plant conditions observed, which are similar to those observed in the previous LPAZ, this pollen zone could correspond to one of the different colder stages detected at the end of MIS 3 (~30 ka BP) in numerous boreholes in the Iberian Peninsula and the rest of Europe (Ruiz-Alonso & Zapata-Peña, 2003; Gómez-Orellana et al., 2007; González-Sampériz et al., 2010, 2020; Biltekin et al., 2019; Camuera et al., 2019). It is a stage in which gradual cooling begins and it is also characterized by a drier climate, as xerophyte values increase considerably (Fig. D.3). It is clear that the vegetation indicates a trend towards a colder climate which would culminate in Liendo with the decrease in AP observed at the end of this LPAZ LIE-8. The reduction of deciduous and pine taxa together with the increase of *Calluna* type and xerophytic taxa (*Centaurea nigra*, Chenopodiaceae, *Artemisia*) are clear indicators of climatic cooling (Fig. D.3; Table D.1). In addition, there is also an interesting rebound in fire indicators, as detected in other studies, especially in the northern hemisphere (Bond et al., 1993; Combourieu et al., 2002; Masson-Delmotte et al., 2005; Daniau et al., 2010; Sanchez-Goñi & Harrison, 2010). It is true that during MIS 3 natural fires are not as common as during MIS 2, but it seems that they occurred and these could have occasionally affected the vegetation. Throughout MIS 4 and the early MIS 3, numerous studies agree that the increased presence of Poaceae, *Calluna* and *Erica* would create phases with a grassland-heathland type landscape that would gradually transform, at the end of MIS 3, to a more deciduous-type landscape (Gómez-Orellana et al., 2007; Fletcher et al., 2010; González-Sampériz et al., 2010).

This evolution towards a more deciduous-type vegetation is well observed in LPAZ LIE-9, where the percentage of AP increases considerably up to 520 cm depth after which it decreases again (Fig. D.3). This has been previously seen in different boreholes during the end of MIS 3, where different stages of deciduous vegetation expansion are observed and correlated with the cold/warm cycles and fluctuations derived from the Heinrich events and Dansgaard-Oeschger cycles mentioned above (Ruiz-Alonso & Zapata-Peña, 2003; Gómez-Orellana et al., 2007; González-Sampériz et al., 2010). As these authors pointed out, the intermittent appearance of mesothermophyte-type vegetation (such as *Fagus sylvatica* and *Carpinus*) suggests the possibility of nearby refuge areas from which these taxa could expand after the coldest events (González-Sampériz et al., 2010; Loidi et al., 2011) The appearance of *Fagus sylvatica* already in the Pleistocene (Fig. D.2, D.3), is particularly interesting. Beech is a species that generally requires cool soils and high humidity. It is usually a tree that tends to form monospecific forests and competes with oaks. The presence of *Fagus sylvatica* along the borehole coincides with a lower presence of *Abies alba*, which may indicate a somewhat higher humidity. The expansion of beech during the Holocene is a very interesting topic that is extensively treated in the literature. The most widely accepted hypothesis at present argues that the expansion of beech would occur in some regions such as the Iberian Peninsula through a series of natural refugia where the beech could survive the different processes of climate change and from where it would expand regionally during the Holocene (Huntley & Birks, 1983; Peñalba, 1989, 1994; Ramil-Rego et al., 1996). The presence of *Fagus sylvatica* in Liendo during the Pleistocene is indicative of a clear presence of beech in the Iberian Peninsula before the Holocene, supporting its survival in refugia and its subsequent expansion (Ruiz-Zapata et al., 1995; López-Merino et al., 2008; Magri, 2008; Brus, 2010; Loidi et al., 2011, Ruiz-Alonso et al., 2019).

Moreover, the identification of *Carpinus betulus* in some of the samples from the Liendo borehole was also surprising (Fig. D.2, D.3). It has been detected mainly in the LPAZs from LIE-1 to LIE-6. In the higher resolution pollen zones, hornbeam has been identified in much lower values. *Carpinus betulus* is a much studied species because of its practical disappearance during the Holocene in the Iberian Peninsula despite the fact that, as in the case of Liendo, it was relatively common at least during the Middle and Late Pleistocene (Sánchez-Goñi et al., 2008; González-Sampériz et al., 2010; Magri et al., 2017; Muñoz-Sobrino et al., 2018; López-Sáez et al., 2020). Hornbeam usually forms mixed deciduous forests and prefers nutrient-rich soils, as it grows with difficulty in excessively dry or siliceous soils. A humid, temperate climate is ideal for this taxon. Some research on hornbeam (deep-sea cores in the Bay of Biscay, Area Longa studied by Gómez-Orellana et al., 2007) indicates the presence of this species in coastal areas during MIS 3, but after the expansion of *Quercus* its frequency was reduced, although it could persist until the beginning of the Holocene.

With a more oceanic climate and a rising sea level during this late epoch, the coastal areas previously occupied by hornbeam may have been flooded, creating unfavorable environmental conditions for *Carpinus betulus* (Sánchez-Goñi et al., 2008; Muñoz-Sobrino et al., 2018) but which favored the appearance of *Alnus* and other hygrophilous taxa so characteristic of saltmarsh areas (Loidi et al., 2011). Numerous studies have detected that during the Holocene *Carpinus betulus* practically disappeared from the Iberian Peninsula (with the exception of the western Pyrenees region in Nafarroa, and some valleys in the Bidasoa basin). Climate changes from 2500 cal yr BP onwards, together with increasing human impact, are responsible for the disappearance of this species from the rest of the Cantabrian Coast (Pearman et al., 2008; Magri et al., 2017; Muñoz-Sobrino et al., 2018).

These cycles and fluctuation dynamics are quite clear if we look at Figure D.3, where a higher pollen resolution shows how an alternating predominance succession between AP vegetation and non-arboreal pollen vegetation (NAP) is observed in LPAZ LIE-10 and LIE-11. Considering the information available, where the vegetation association indicates cooling, it is highly probable that the upper part of the Liendo borehole corresponds to the end of MIS 3 and the beginning of MIS 2 (González-Sampériz et al., 2010, 2020; Uzquiano et al., 2016). The higher presence of *Artemisia* and Cichorioideae in general mark a cooler and somewhat drier climate, but we should not forget the particular climate conditions of the Cantabrian Coast, a region in itself more humid than, for example, Villarquemado (Teruel) or Padul (Granada) (González-Sampériz et al., 2010, 2020; Camuera et al., 2018, 2019). *Artemisia*, *Centaurea nigra* and Cichorioideae (especially the first) have been commonly used in Mediterranean contexts as indicators of glacial or cold phases (González-Sampériz et al., 2010; Pérez-Díaz & López-Sáez, 2021). In the case of Liendo, and taking into account the low-resolution analysis of the borehole performed below 700 cm depth, the greater presence of *Artemisia* and *Centaurea nigra* seems to coincide with other taxa that usually indicate cold climate conditions (such as Cichorioideae). In the case of *Artemisia* and *Centaurea nigra*, they are indicative of cold and dry climates, and they never coincide with the presence of *A. alba*, a species that, as mentioned before, needs cool and moist soils, and does not tolerate summer drought. This could indicate cold phases of a long duration where climate conditions vary in humidity (González-Sampériz et al., 2010; Pérez-Díaz & López-Sáez, 2021). In the case of Cichorioideae, its presence does seem to coincide with higher percentages of *Artemisia* and *Centaurea nigra*, as for example in LPAZ LIE-4 and LIE-5 (Fig. D.2). Also, in the higher resolution diagram (Fig. D.3), we can observe a generalized presence of this zoophilous taxon, a cold climate indicator. Considering this simultaneous occurrence, this assemblage could be indicating a cold and dry climate (González-Sampériz et al., 2010; Giraudi et al., 2011; Biltekin et al., 2018). All this would explain the continuous presence of deciduous vegetation throughout MIS 3 in

Liendo, as also recorded previously in other regions, such as Navarrés (Valencia), Laguna de San Benito (Valencia-Albacete) or Cueva de la Carihuela (Granada) in the Mediterranean Spain (Dupre et al., 1996; Carrión et al., 1998; Carrión & Van Geel, 1999;) and Lagoa de Lucenza (Lugo), Laguna de Sanguijuelas (Zamora) and Cueva del Conde (Asturias) in the Cantabrian region (Muñoz-Sobrino et al., 2001, 2004; Uzquiano et al., 2008).

Studies on boreholes taken from the Atlantic margins also show an expansion of arboreal taxa during interstadials, including *Abies alba* during MIS 4, and of deciduous forest during MIS 3 (Naughton et al., 2007, Sánchez-Goñi et al., 2008). The appearance of *Abies alba* during MIS 4 could also have been recorded in Liendo and corresponds to some of the peaks observed in this taxon at greater depths of the borehole (LPAZ-1). Those studies also observe moments where open field type vegetation becomes more relevant, coinciding with the stadial periods, when herbaceous vegetation such as Cyperaceae, Poaceae and Ericaceae increase as is the case with some sections of the Liendo borehole (Fig. D.2, Fig. D.3) (Naughton et al., 2007, Sánchez-Goñi et al., 2008).

## 1.4. Paleoclimate reconstruction

A paleoclimate reconstruction of the LPAZ LIE-7 to LIE-11 (Fig. D.5) has been carried out in order to better understand climate evolution in this upper section of the Liendo borehole. As mentioned above, this last interval of the borehole could correspond to the end of MIS 3. From a depth of 700 cm to almost 650 cm, we observe a drop in temperatures and precipitation that coincides quite well with the gradual cooling during the end of MIS 3 and beginning of MIS 2 detected in other studies (Lokrantz & Sohlenius, 2006; González-Sampériz et al., 2010; Camuera et al., 2018, 2019). After that, from 650 cm to 540 cm depth, temperatures and precipitation increase and decrease, possibly due to the alternation of the Heinrich events and the Dansgaard-Oeschger cycles that characterized the last glacial phase. From 540 cm depth onwards, temperatures and precipitation increase, establishing a much more regular trend, varying between 8º and 13ºC in the case of temperatures and 1100 and 620 mm/yr in the case of precipitation. These climate conditions could respond to progressive to the end of MIS 3 (Muñoz-Sobrino et al., 2001, 2004; Ruiz-Alonso & Zapata-Peña, 2003; Gómez-Orellana et al., 2007; Uzquiano et al., 2008; González-Sampériz et al., 2010).

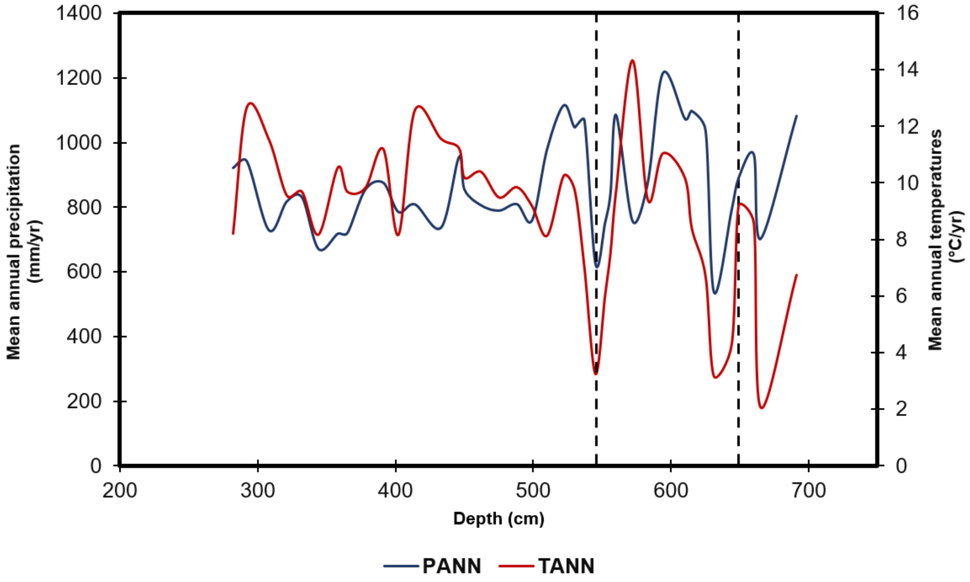


**Figure D.5 -** Quantitative paleoclimate reconstruction for the final 700 cm (higher resolution analysis) of the Liendo borehole. In red, the evolution of the mean annual temperature. In blue, the evolution of the mean annual precipitation. At 650 and 540 cm vertical lines separate the climatic intervals described in the text.

# 2. Holocene

## 2.1. Early Holocene (Greenlandian age: 11,750 – 8,200 cal yr BP)

### 2.1.1. Geochronology

Only the Requejada borehole contains a sedimentary record that dates back to before 8000 yr BP and informs about the evolution of estuarine vegetation along the Cantabrian Coast during the Early Holocene (Greenlandian age).

This evolution is linked to the sedimentary hiatus detected at 792 cm depth. As seen in Figure R.11, the evident lack of materials preserved between 7380 – 1850 cal yr BP causes a clear differentiation between the vegetation assemblages in the pre- and post-hiatus times, which is also observed in the case of other analyzed micropaleontological proxies, such as foraminifera (Serrano-García, 2020). The interpretation of this hiatus is complex, mostly because of its magnitude. It can respond to diverse geological processes, such as changes in sediment supply, lateral migration of the estuarine channel or subaerial erosion of sediments exposed to sea-level stabilization, among other possible causes (Hayward et al., 2004; García-Antón et al., 2006).

### 2.1.2. Vegetation evolution

Initially, and especially between 1572 – 792 cm depth (~9000 – 7500 cal yr BP), the diagram shows the predominance of a deciduous forest with a large presence of taxa such as *Betula*, deciduous *Quercus* and *Corylus* (Fig. D.7). This vegetation assemblage tends to colonize humid valley areas with relatively siliceous soils and, in addition, although it can often be located at different altitudes, it is usually close to rivers. In particular, birches usually grow at higher altitudes than hazels and oaks, which often share an ecological niche with other species such as linden, ash and chestnut. Oak is also a taxon that is found today in areas near the littoral, especially on the Cantabrian Coast. Although there are different types of oaks, the common oak (*Quercus robur*) is usually the most abundant (Biurrun, 1999; Loidi et al., 2011).

Accompanying this deciduous forest, pines are detected (Fig. D.7), showing a regional presence, even though pine is characterized by its great production and high dispersion capacity of its pollen grains. When the presence of pine pollen does not exceed 60%, we can consider the existence of pine forests on a more regional scale whereas, when these values are exceeded, the presence could be considered as the existence of a pine forest in the area (Caseldine et al., 2007; Richardson et al., 2007; Poska & Pidek, 2010; López-Sáez et al., 2013; Robles-López et al., 2018). In addition, pine forests tend to be quite territorially dominant, limiting the growth of other plant species in their domains (Loidi et al., 2011; Pretzsch et al., 2020). The non-dominance of pine pollen would indicate that its presence would be in secondary forests or that the pollen comes from regional catchment areas of the estuary, providing us with information of regional rather than local origin. In fact, the most abundant pine species is *Pinus pinaster*, commonly known as maritime pine precisely because its frequent presence near the coast and its abundance in the eastern Cantabrian Coast.

It is also interesting to note the increase in grasses (Poaceae) observed through this basal LPAZ RE-1 (Fig. D.7). This growth, despite the fact that some of the samples are sterile, could be due to the specific environmental conditions around the estuary. Vegetation of this type is usually well adapted to marshland areas, rapidly colonizing the muddier intertidal areas, which implies the appearance of halophyte grasses (Sanchez-Goñi, 1996; Biurrun, 1999; García-Antón et al., 2006; Loidi et al., 2011; Calleja-Apéstegui, 2019)..

The presence of hydro-hygrophilous taxa in high percentages is also relevant. As mentioned above, the most abundant vegetation type indicates humid environments and has a predilection for areas near rivers or coastal environments. It is not surprising, therefore, that ferns and mosses are abundant in these surroundings (García-Antón et al., 2006; Loidi et al., 2011).

Together with the dates obtained for this lower section of the Requejada borehole, the vegetation assemblage suggests a correlation with that observed in the literature during ~10,000 – 8000 cal yr BP in south-western Europe. Following the Younger Dryas, there is a very rapid rise in temperatures, which would correspond to the Holocene Climate Optimum that favored the widespread growth of forest vegetation. In general, the pollen biozones defined for this time interval tend to establish *Pinus* as the most dominant genus followed by *Betula* (Bos & Urz, 2003; Bos et al., 2007; Carcaillet et al., 2010). In the case of Requejada, the dominance is reversed, with *Betula* being the most dominant taxon, a phenomenon that is observed particularly in Mediterranean regions due to their more temperate climate. However, in the Cantabrian Coast, it seems also that more humid conditions favored the expansion of *Betula*.

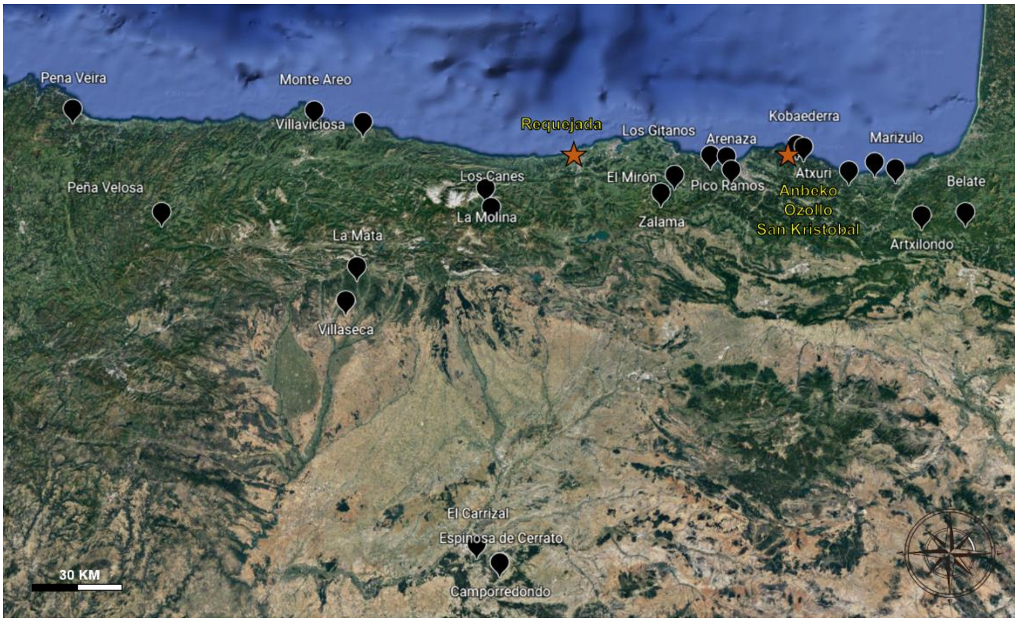


**Figure D.6 -** Map with the location of the sites studied in other Holocene research and mentioned throughout the discussion.

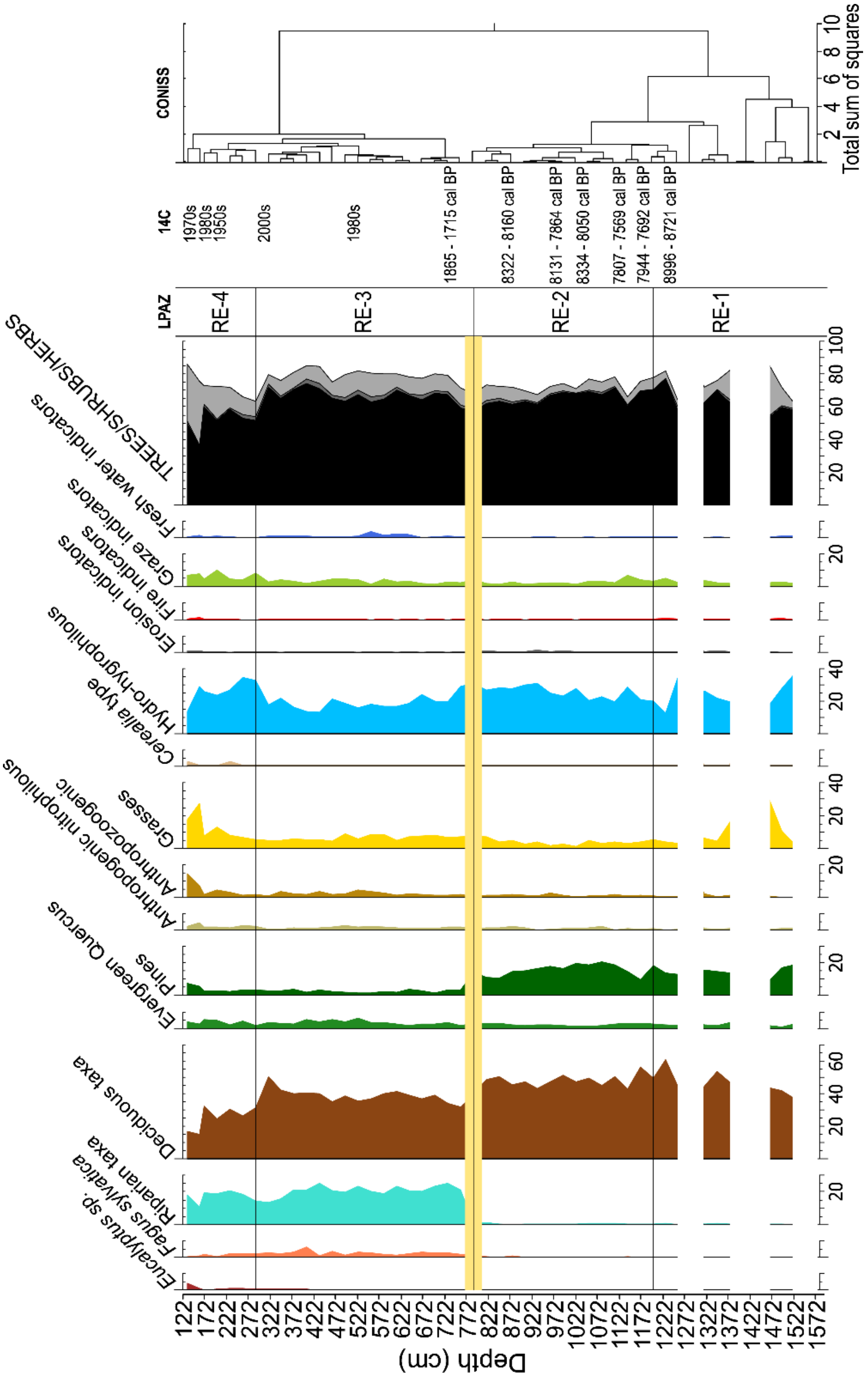


**Figure D.7 -** Synthetic pollen diagram of the Requejada borehole. The different vegetation groups and/or most relevant taxa are represented. In addition, the depth (cm), the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are also represented.

The increase in temperatures and precipitation also benefits the increase of other taxa, such as *Corylus* and *Quercus* (Uzquiano et al., 2016; Morellón et al., 2018;). Other studies, such as those carried out in Camporredondo (Valladolid), Espinosa de Cerrato (Palencia) and El Carrizal (Valladolid), show that pine forests are generally predominant during the early Holocene (Fig. D.6) (Franco-Múgica et al., 2001, 2005; García-Antón et al., 2011). However, this predominance is not regular, and pollen percentages vary greatly as the Holocene progresses, probably due to the climate improvement that characterizes this epoch. This climate improvement in the Iberian plateau region would imply an arboreal expansion where species better adapted to somewhat cooler conditions could persist. In the case of the Cantabrian Coast, it is likely that the higher humidity together with the climatic improvement of the Holocene gave way to a more deciduous vegetation, thus explaining its greater predominance over pine forests. In fact, the predominance and expansion of deciduous taxa such as *Betula* has also been recorded in other works such as the one carried out on the Cantabrian Coast in La Molina (Cantabria) or those carried out in Villaseca (León), La Mata (León) and Peña Velosa (Asturias) (Jalut et al., 2010; Muñoz-Sobrino et al., 2012; Sánchez-Morales et al., 2022). These works also argue for the expansion of deciduous taxa as a result of the Holocene climate improvement and higher regional humidity.

## 2.2. Middle Holocene (Northgrippian age: 8,200 – 4,200 cal yr BP)

### 2.2.1. Geochronology

As in the previous age, Middle Holocene (Northgrippian age) paleopalynological information is provided only by one sedimentary record: the Anbeko borehole.

The evolution of its vegetation is particularly interesting because fairly high pollen resolution and dating allow us to contextualize this borehole environmentally and temporally.

In the lower part of Anbeko, specifically in LPAZ ANB-1 and ANB-2, we observed several sandy intervals that did not allow a fruitful pollen analysis. However, we have obtained enough data to acquire a rough idea of what the vegetation was like at that time.

Precise dating has been obtained for these zones, which contextualizes quite well the changes in the vegetation occurring at that time and to make an age-depth model (Fig. R. 20). The changes would result from several processes: 1. Stabilization of the temperature increase after the Early Holocene would consolidate the expansion of deciduous forest; 2. The rise in sea level that formed the current estuaries and, therefore, created larger marsh areas; and 3. The increase in anthropogenic activities in the area (livestock and agriculture, deforestation).

### 2.2.2. Vegetation evolution

During the development of the basal pollen zone in Anbeko (LPAZ ANB-1), before 4239 cal. BP, we observed both a decreasing trend of the deciduous forest and an increasing presence of pine trees (Fig. D.8), with total values reaching 60%. In spite of the low resolution of this part of the borehole, it is probable that this could be due to the regional expansion and persistence experienced by *Pinus* previously during the Early Holocene (Franco-Múgica et al., 2001, 2005; García-Antón et al., 2011). During this interval a sudden rise in temperature sharply changed ecosystems, causing forest to replace open land in Europe (Bos & Urz, 2003; Bos et al., 2007; Carcaillet et al., 2010). On the other hand, the typical tree taxa of the riparian forest (*Alnus*, *Fraxinus*, *Populus* and *Salix*) maintain a relative regularity. As we have seen above, deciduous forests are often accompanied by species such as alder, ash and holm oak (Loidi et al., 2011). However, in the case of Anbeko, the presence of these taxa is much lower than observed in the rest of the boreholes studied in this doctoral dissertation.

The great presence of hydro-hygrophilous plants is remarkable (Fig. D.8). Even so, in this case, the low presence of anthropozoogenic, anthropogenic nitrophilous and grasses taxa is striking, while Chenopodiaceae, Poaceae and Cichorioideae, typical of marshy areas, are found abundantly (Sanchez-Goñi, 1996; Biurrun, 1999; García Antón et al., 2006; Loidi et al., 2011).

In LPAZ ANB-2, pine trees experience a gradual decline, while the deciduous forest remains at the values previously observed in the basal zone. In general, there are no major changes in this pollen zone except for the appearance of *Fagus sylvatica*. As shown in Figure D.8, the radiocarbon dates give ages around 4200 cal yr BP at about 320 cm depth. The appearance of *Fagus sylvatica* begins at 590 cm depth and since then its presence will be continuous, although not regular. *Fagus sylvatica* is a mainly montane species that usually inhabits the middle and upper-middle altitudes of the mountains in southern Europe and the lowlands of northern Germany, France, Denmark, southern England and Sweden (Huntley & Birks, 1983; Huntley, 1988; Loidi et al., 2011) This is a question that Huntley & Birks (1983) already discussed and, in synthesis, proposed that the present beech was confined to the Balkan-Dinaric shelters during the last glaciation (115,000 - 11,700 cal yr BP) and, from there, spread to the rest of Europe in different phases. According to their hypothesis, the beech expansion would reach the Iberian Peninsula in its last phase (~15,000 – 10,000 cal yr BP) (Sanchez-Goñi, 1996; Biurrun, 1999; García Antón et al., 2006; Loidi et al., 2011).

However, based on different pollen studies, other authors point out that the beech expansion occurred from different refuge areas in southern Europe during the last glaciation such as Greece, the Adriatic Sea, the Mediterranean, the southern Alps, the Apennines, the Pyrenees and the Cantabrian and North Portuguese Mountains (Ruiz-Zapata et al., 1995; Ramil-Rego et al., 1996; Ramil-Rego et al., 2000; Magri, 2008; Brus, 2010; Loidi et al., 2011).

The climate improvement during the middle Holocene (Northgrippian age, 8200 - 4200 cal yr BP) would favor beech expansion. Different studies on the presence of *Fagus sylvatica* in the Western Pyrenean Region (Northern Iberian Peninsula) have shown that this species was already present in the region in the Pleistocene, although its record appears discontinuous chronologically (López-Merino et al., 2008; Ruiz-Alonso et al., 2019). During the middle and late Holocene, numerous works show how the exploitation of beech forests by humans increases (López-Merino et al., 2008; Pérez-Díaz et al., 2016; Ruiz-Alonso et al., 2019; Sánchez de Dios et al., 2021). The initial expansion of *Fagus sylvatica* probably took place from small refugia in the north of the Iberian Peninsula although its Central European origin cannot be ruled out. It would mainly occupy the mid-mountain areas and more humid slopes, even displacing the *Quercus* forests (López-Merino et al., 2008; Loidi et al., 2011; Pérez-Díaz et al., 2016; Ruiz-Alonso et al., 2019; Sánchez de Dios et al., 2021). This would create positive conditions for beech proliferation, with mild winters and fresh summers. This expansion was probably supported by other transport agents, such as animals, river currents, etc. (Pott, 2000; Bradshaw, 2004; Loidi et al., 2011).

However, the major transport vector behind of the expansion of *Fagus sylvatica* during the Holocene is anthropogenic. Humans, especially from the Neolithic, and above all during the Roman period and later during the Middle Ages, generalized the exploitation of beech wood. During the Bronze Age (~2500 cal yr BP), humans became more active and began to transform the surrounding environment, causing deforestation which, in turn, led to the appearance of open spaces that were quickly colonized by beech trees due to favorable climate conditions (López-Merino et al., 2008; Magri, 2008; Brus, 2010; Loidi et al., 2011; Ruiz-Alonso et al., 2019).

The increase in anthropogenic dynamics during this middle phase of the Holocene can be attested by the growing presence of anthropozoogenic and anthropogenic nitrophilous taxa that, together with the detection of NPPs indicative of grazing and the first appearances of cereal pollen, signal human presence in the area before 4000 cal yr BP (Fig. D.8) (Zapata et al., 2004). In numerous works carried out in the boreholes of Artxilondo (Nafarroa), Atxuri (Gipuzkoa), Belate (Nafarroa) and Pareko Landa (Urdaibai-Bizkaia) (Fig. D.6) (Galop et al., 2001; 2004; Iriarte et al., 2007; Peñalba, 1989; Pérez-Díaz et al., 2015; Ruiz-Alonso et al., 2019), a close relationship can be observed between beech expansion and the increased presence of anthropozoogenic and anthropogenic nitrophilous taxa.

Holocene sea-level rise directly contributed to the formation of the present estuaries and the vegetation would therefore respond to this change. Previous works carried out along the Cantabrian Coast show that it was during the postglacial rapid sea-level rise (8500 - 3000 cal yr BP) when the modern estuaries began to develop (Leorri & Cearreta, 2004; Cearreta & Monge-Ganuzas, 2013; García-Artola et al., 2018; Cearreta et al., 2021). This would explain the increase in estuarine plant taxa such as Chenopodiaceae, Poaceae and Cichorioideae during this time interval, as can be observed in Figures D.8 and R.18. In addition, it is also accompanied by an increase in hydro-hygrophilous taxa, since the more humid conditions would lead to the formation of more favorable ecosystems for these types of plants (Cearreta & Murray, 1996; Leorri & Cearreta, 2004; Leorri et al., 2011, 2013; García-Artola et al., 2018).

From LPAZ ANB-3 (~4239 cal yr BP) to the borehole top it is possible to perform a pollen analysis at a much higher resolution as muddier sediments favoured pollen preservation. Pine abundance, although still decreasing, is not regular (Fig. D.8) whereas the deciduous type vegetation experienced an increase of up to 80%. This agrees with previous observations in a large number of studies that show how *Quercus* and deciduous forests in general underwent an expansion, even in Mediterranean areas, despite the cold climatic oscillations that occurred during the Middle Holocene (Aranbarri et al., 2016; Pérez-Díaz et al., 2016; Revelles et al., 2018). For example, in Villaviciosa (Asturias), García-Antón et al. (2006) characterized the climate optimum of the Middle Holocene with percentages of AP (tree pollen) between 80 and 90%, as also observed here in Anbeko. This climate optimum allowed the expansion of deciduous forest often together with holm oak. In addition, the appearance of riparian vegetation, which seems to increase slightly at the end of this borehole section, coincides with higher abundances of *Fagus sylvatica* (beech) together with the first evidence of cereal pollen. All this would indicate human presence and, therefore, its footprint on the landscape. Furthermore, alder and ash trees usually coexist and share space very often with the deciduous forest (Loidi et al., 2011). In fact, the reduction of pine prior to ~4200 cal yr BP (Fig. D.8) possibly favored proliferation of other types of arboreal vegetation, such as oak groves, which increase during LPAZ ANB-3 and ANB-4.

Most previous studies along the Cantabrian Coast detected a reduction in the *Pinus* taxon around ~7500 cal yr BP (Santos et al., 2000; Roucoux et al., 2001; Moreno et al., 2011; Stoll et al., 2013). This decrease seems to respond mainly to climate reasons, as in the case of *Quercus*. The increase in precipitation and temperature during the initial middle Holocene, as detected in lakes, marshes, marine sediments and speleothem records from the northern Iberian Peninsula, resulted in the recolonization of deciduous forest especially in the Atlantic areas of northern Iberia together with an early decline of pine forests (Muñoz-Sobrino et al., 2007; Rubiales et al., 2008, 2010, 2012). *Quercus*, *Corylus* and *Betula* were able to compete with the generally more dominant conifers, allowing the deciduous forest to colonize more humid and temperate regions (such as the Cantabrian coast) and to limit the presence of *Pinus* to the more continental, colder and drier areas of the Cantabrian region (Jalut et al., 2010; Muñoz-Sobrino et al., 2012; Pérez-Díaz et al., 2016).

Moreover, the presence of hydro-hygrophilous vegetation continues to be remarkable during LPAZ ANB-4, related to the aforementioned changes in sea level and the development of the modern estuaries. The appearance of new marsh areas favored the expansion of typical marsh species, which coincided with the notable growth observed in the anthropogenic nitrophilous and anthropozoogenic vegetation groups (Fig. D.8). Within these groups, the presence of Chenopodiaceae, Cichorioideae and *Plantago coronopus* stands out (Fig. R.18). Again, the greater presence of these taxa is clearly indicative of marked marsh environmental conditions. At the end of the borehole, in the LPAZ ANB-4, a reduction is observed in the general arboreal vegetation in favor of herbaceous vegetation. As the marsh areas expanded, it is probable that the soil nature altered and affected vegetation that is not adapted to higher salinity and humidity conditions. This would result in a reduction of deciduous tree taxa in favor of herbaceous marsh vegetation. In turn, Figure D.8 shows that riparian vegetation maintains certain stability. This is congruent as it represents a typical vegetation of riverine areas where, for example, alder (*Alnus*) has the capacity to withstand very humid soils with higher salinity (Mariscal, 1993; Peñalba, 1994; Loidi et al., 2011;).

Finally, although still not on a regular pattern, cereal pollen and NPPs indicative of agricultural and livestock activities have been detected at this time (4257 cal yr BP) (Fig. D.8). The presence of agriculture in the coastal region of the Basque Country, as indicated by both carpological and palynological data, seems to be confirmed since at least the mid-8th millennium BP, especially in areas such as Urdaibai (Biscay) (Zapata-Peña et al., 2004; Zapata-Peña, 2005). In cases such as the Zalama peat bog (Biscay, Basque-Cantabrian mountains) (Fig. D.6), grasslands seem to have occupied greater areas during the Middle Holocene (6460 cal yr BP) along the mountain range (Pérez-Díaz et al., 2016), as also observed in LPAZ ANB-3. Grazing indicators, consisting mainly of anthropogenic taxa (such as *Sordaria* sp.) and coprophilous fungi, indicate that productive economic activities related to early agriculture and livestock farming were already taking place on the Cantabrian coast at that time (Zapata et al., 2004; Zapata-Peña, 2005; Pérez-Díaz et al., 2016).

Consequently, reduction of arboreal vegetation groups could be due to human deforestation creating open spaces for crop fields and pastures for livestock. Other studies along the Cantabrian Coast have observed similar trends to those preserved in LPAZ ANB-3 and ANB-4, such as a reduction in tree taxa (especially *Quercus*) (García-Antón et al., 2006; Rubiales et al., 2008).

This evidence has been refined in the region through the study of Lower Neolithic (late 8th and first half of the 7th millennium BP) archaeological sites such as Los Canes, Los Gitanos, El Mirón (Cantabria), Kobaederra, Pico Ramos, Lumentxa, Arenaza (Biscay), Herriko Barra and Marizulo (Gipuzkoa) (Zapata-Peña et al., 1997; Alday & Mujika, 1999; Iriarte et al., 2004; Arias, 2005; Zapata-Peña, 2005; Zapata et al., 2007; Ontañón et al., 2013). This greater human impact during the Middle Holocene has also been detected in other pollen records from natural deposits such as the Monte Areo (Asturias) and Pena Veira (Lugo) peatlands (Rego et al., 1993; López-Merino et al., 2010; Pérez-Díaz et al., 2016). In the case of Monte Areo, patterns of relationship have been found between the results obtained from soil analysis and erosion, and the evolution of the forests. López-Merino et al. (2010) observed how prehistoric agriculture (~6760 and ~3860 cal yr BP) can be a factor of soil disturbance and how the impact it exerts is not only closely related to the intensity of the activity, but also to its proximity. Moreover, the evolution of herbaceous vegetation cover is also related to human pressure on the landscape. With increasing human pressure, the studies mentioned above also show a general increase in herbaceous species. This is interpreted as the consequence of agricultural practices that increasingly promoted the expansion of pastures (Rego et al., 1993; López-Merino et al., 2010; Pérez-Díaz et al., 2016).

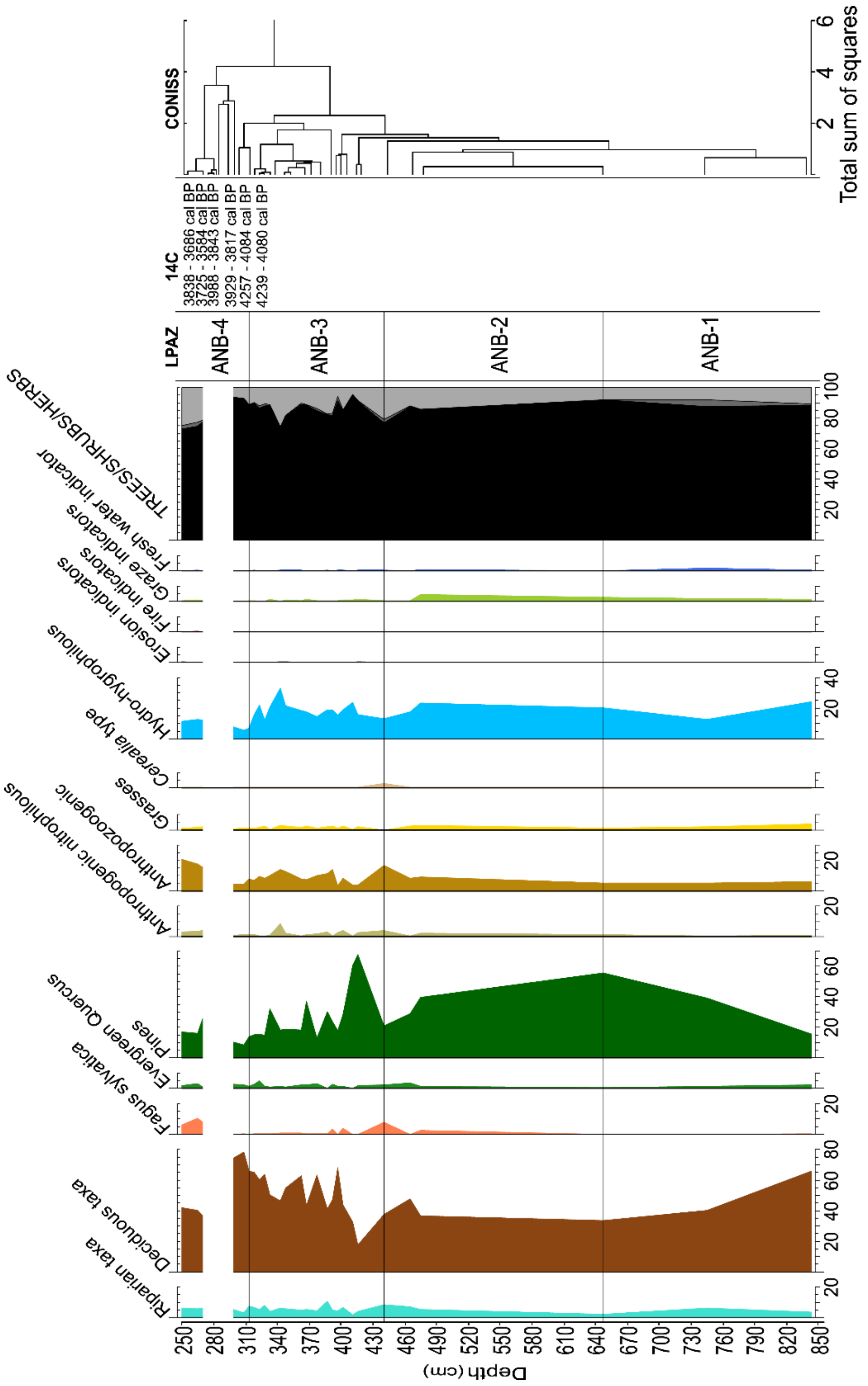


**Figure D.8 -** Synthetic pollen diagram of the Anbeko borehole. The different vegetation groups and/or most relevant taxa are represented. In addition, the depth (cm), the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are also represented.

## 2.3. Late Holocene (Meghalayan age: 4200 cal yr BP – 1950 CE)

### 2.3.1. Geochronology

The San Kristobal borehole, drilled originally to locate the initial development of the marsh environment in the Oka estuary, could not be precisely dated for its entire sedimentary sequence (Table R.7, Figure D.10). Its pollen contents, with the presence of *Eucalyptus* sp., herbaceous taxa related to human presence, and the increase in pine trees in the uppermost section, seem to indicate that the borehole is quite recent. Due to the impossibility of accurate dating, it has been included in the general "Holocene" group of boreholes.

Conversely, the radiocarbon dates obtained for the Ozollo borehole provide a precise time frame, although some difficulties are encountered. The main one is that the ages obtained from the shell samples are older than those obtained from plant remains. This is probably related to the deficit of the radiocarbon reservoir in the ocean compared to that of the atmosphere (Fig. R. 24). Furthermore, the ages obtained from the shells are sometimes inverted, with older dates in the upper sections and younger ages from the lower samples. A possible explanation for this is reworking of the older sediments, a phenomenon that has also been invoked in previous works on the high-energy Basque coast (Cearreta & Murray, 2000; Soares, 2015; Rodríguez-Beraza, 2021).

### 2.3.2. Vegetation evolution

During the Late Holocene (Meghalayan age), changes in plant associations were also observed, especially affecting the riparian taxa. Due to the maximum altitude of sea level during this time, the estuaries presented their greatest development and this, evidently, favoured expansion of typical riparian vegetation such as *Alnus* (alder), as observed along the Requejada, San Kristobal and Ozollo boreholes (Figs. D.7, D.9, D.10). Development of alder forests around the estuaries in response to the availability of large areas of freshwater near the coast (Huntley & Birks, 1983) can be particularly observed in the case of the Ozollo and Requejada boreholes. Increase in riparian vegetation in Ozollo during LPAZ OZO-1, OZO-2 and OZO-3 zones is the highest observed in all the Urdaibai boreholes (Fig. D.9). As already mentioned, deciduous forest is often a mixed type of forest, which allows the appearance of other plant species with different biological characteristics. This is the case of riparian vegetation such as alder, elm and ash, trees that grow among the oak groves (Mariscal, 1993; Peñalba, 1994; Loidi et al., 2011).

In the case of Requejada, deciduous forest continues to be the most predominant vegetation type in LPAZ RE-3 and RE-4 (Fig. D.7). The most abundant taxa continue to be *Betula*, deciduous *Quercus* and *Corylus* (Fig. R.8). In general, these wooded areas present high plant diversity and usually constitute mixed forests (Loidi et al., 2011). The arboreal element is mostly made up of oaks that filter the light through their foliage, which allows a remarkable undergrowth biomass. In the rainiest regions, generally located at its highest altitudinal range (about 650 m), it is mixed with *Fagus sylvatica*, which is common in deciduous forests in the eastern Cantabrian region. In addition, birches can also show some prominence, as secondary forests. Furthermore, after the sedimentary hiatus, the vegetation assemblages changed and, although the dominance of deciduous forest continues, the riparian forest takes prominence, replacing pine trees as the second most predominant arboreal vegetation (Fig. D.7). This is evident from 1865 - 1715 cal yr BP, just after the sedimentary hiatus at 792 cm depth, to the present (LPAZ RE-3 and RE-4), as the youngest dated samples supplied ages around the 1990s. The typical genera of the riparian forest detected in this Requejada borehole were *Alnus*, as the most predominant, *Fraxinus* and *Salix*. As mentioned above, alder is a species whose natural habitat is generally found in wet soils near rivers, ponds and lakes. In fact, this tree needs to have its roots deeply embedded, which does not mean that it cannot sometimes thrive in drier places, forming mixed forests. One of the characteristics of this species is also its tolerance to a wide variety of soil types, from acidic to alkaline and even brackish, as is the case of soils near saltmarsh areas. It usually forms gallery forests (Mariscal, 1993; Peñalba, 1994; Loidi et al., 2011).

Alder expansion seems to be linked to the alteration of river courses, which leaves high water table floodplains very suitable for the development of this type of forest (García-Antón et al., 2006). There are different studies that point to an early general development of alder forests in the Cantabrian coast between 6000 - 4500 years BP in low and medium altitude areas related to deceleration of sea-level rise (Mary, 1990; Garzón et al., 1996; Sánchez Goñi, 1996). In this doctoral thesis, representative values of riparian forest are observed at times chronologically prior to ~3000 cal yr BP, although its greatest presence coincides with a chronology close to ~3000 cal yr BP and extending even to the present.

Furthermore, the species *Fagus sylvatica* (beech) has been identified in percentages of up to 10% in Requejada and 25% throughout the Ozollo borehole (Figs. D.7 and D.9). Indeed, it is in Ozollo where the highest presence of beech from all the Urdaibai boreholes has been detected, where it appears from the lowest samples and maintains a relatively regular trend, with some occasional increases, such as the one observed at 250 cm depth (2259 cal yr BP). During the Holocene, an expansion of beech has been reported throughout Europe (López-Merino et al., 2008;

Loidi et al., 2011; Pérez-Díaz et al., 2016; Ruiz-Alonso et al., 2019; Sánchez de Dios et al., 2021). The greater presence of *Fagus sylvatica* in the Ozollo borehole is probably related to its greater proximity to the Airo beech forest in the area bordering the Urdaibai Biosphere Reserve.

A change in the deciduous plant associations is also observed in the LPAZ ANB-4 at Anbeko, where a decrease in the percentage of tree pollen (AP) and more specifically of deciduous taxa is observed (Fig. D.8). On the other hand, the arboreal vegetation in the first three pollen zones in Ozollo shows the predominance of deciduous *Quercus* and *Betula* (Figs. R.21 and D.9). However, despite being dominant, AP percentage values are lower in Ozollo (50%) than in Anbeko (80%) before 4000 cal yr BP. From that time on, a decrease of *Quercus* and deciduous forest in general is observed (Figs. D.8 and D.9).

Similarly, during the first two LPAZ SK-1 and SK-2 in the San Kristobal borehole (pre-1950 CE), the dominance of deciduous forest is also evident. Although a decreasing trend with time is observed, *Betula* and deciduous *Quercus* taxa are predominant, accompanied by a relevant presence of *Alnus*. However, the presence of riparian forest genera, such as *Alnus*, *Fraxinus* and *Salix*, remains constant throughout the borehole (Fig. D.10). As previously mentioned, it is common for riparian species, such as alder, to settle close to the river courses. It is quite usual to find the combination of these two types of forests on the Cantabrian Coast mainly in valley areas where the riparian forest generally grows at lower altitudes and the deciduous forest expands uphill (Mariscal, 1993; Peñalba, 1994; Loidi et al., 2011). Nevertheless, in the following LPAZ SK-3 and SK-4 the growth of pine vegetation, which implies a decrease in the deciduous forest, is observed (Fig. D.10). Beech, which enjoyed a certain prominence during the previous pollen zones, disappears almost completely. This drastic disappearance may be related to the fact that this taxon came from remote areas, and it was through fluvial transport that it was more prominent than would be expected. As mentioned above, there are no beech forests in the area to explain those pollen abundances observed. Even so, its sporadic presence could indicate a reduced fluvial contribution through time (Moss et al., 2005; Brown et al., 2007).

Increasing human impact occurring from the Early-Middle Neolithic and, especially, during the Middle Ages (Sobrino et al., 1997; Santos, 2004; Mighall et al., 2006; Revelles et al., 2015; Pérez-Obiol et al., 2016; García-Ruiz et al., 2020; Quirós, 2020) explains this reduction in deciduous forests, and especially of *Quercus*, due to the increasing deforestation by human populations to create open grassland spaces that, sometimes, would be occupied by taxa such as *Fagus sylvatica*. In fact, it is at this time when the taxon *Cerealia* type begins to appear more regularly together with ruderal taxa, such as *Plantago*, which also indicates the use of land for agriculture and livestock activities (García-Antón et al., 2006; Pérez-Díaz et al., 2016).

Among the arboreal vegetation recorded in San Kristobal during the first two LPAZs, the presence of eucalyptus (*Eucalyptus* sp.) and beech (*Fagus sylvatica*) is noteworthy (Fig. D.10). Simply the presence of eucalyptus already indicates that sediments were deposited in very recent historical times. Although this taxon was introduced in the region for the first time in the 19th century, it was not until the mid-20th century that it began to be replanted intensively (Martin de Agar et al., 1992; Espinel et al., 1995; Duñabeitia et al., 2004; Veiras & Soto, 2011; Soto-Caba, 2013). On the other hand, there is a quite relevant expansion of beech during the Holocene although, in the case of San Kristobal, it is striking that it is not a continuous expansion, but it increases until 290 cm depth, where it reaches its maximum, and then declines again until it practically disappears. This may be due to the fact that pollen of *Fagus sylvatica* comes from areas higher than the estuary itself, as beeches usually have better rooting in temperate-cold or cold climates, and prefer the fertile soils of the high mountains (altitude 600-1200 m) (López-Merino et al., 2008; Loidi et al., 2011).

In fact, the beech forest of Airo (Fig. D.11), on the Iluntzar hill, is located on the periphery of the Biosphere Reserve of Urdaibai, which would explain the presence of this species in the sedimentary record at San Kristobal. It is interesting to note how the decrease in *Fagus sylvatica* coincides with the exponential increase in pine trees (Fig. D.8). It is quite possible that we are observing an increase in pine as a result of the first pine plantations (*Pinus radiata, Pinus pinaster* and *Pinus sylvestris*) carried out in the 1940s after the implementation of the “Plan Nacional de Repoblaciones”. The logging shift of these trees is around 30-35 years, which already implies the maturity of the tree and, therefore, also standardizes the pollen production of the specimens (López-Merino et al., 2008; Loidi et al., 2011; Pérez-Díaz et al., 2016; Ruiz-Alonso et al., 2019; Sánchez de Dios et al., 2021).

The appearance of *Eucalyptus* sp. around 420 cm depth in the Requejada borehole during the 20th century according to radiocarbon analysis is of great relevance (Fig. D.7, D.11). The presence of this taxon already indicates a temporal proximity with the present and informs about more sophisticated processes of anthropization of the environment, as will be explained in the following section (Duñabeitia et al., 2004; Espinel et al., 1995; Martin de Agar et al., 1992; Soto-Caba, 2013; Veiras & Soto, 2011).

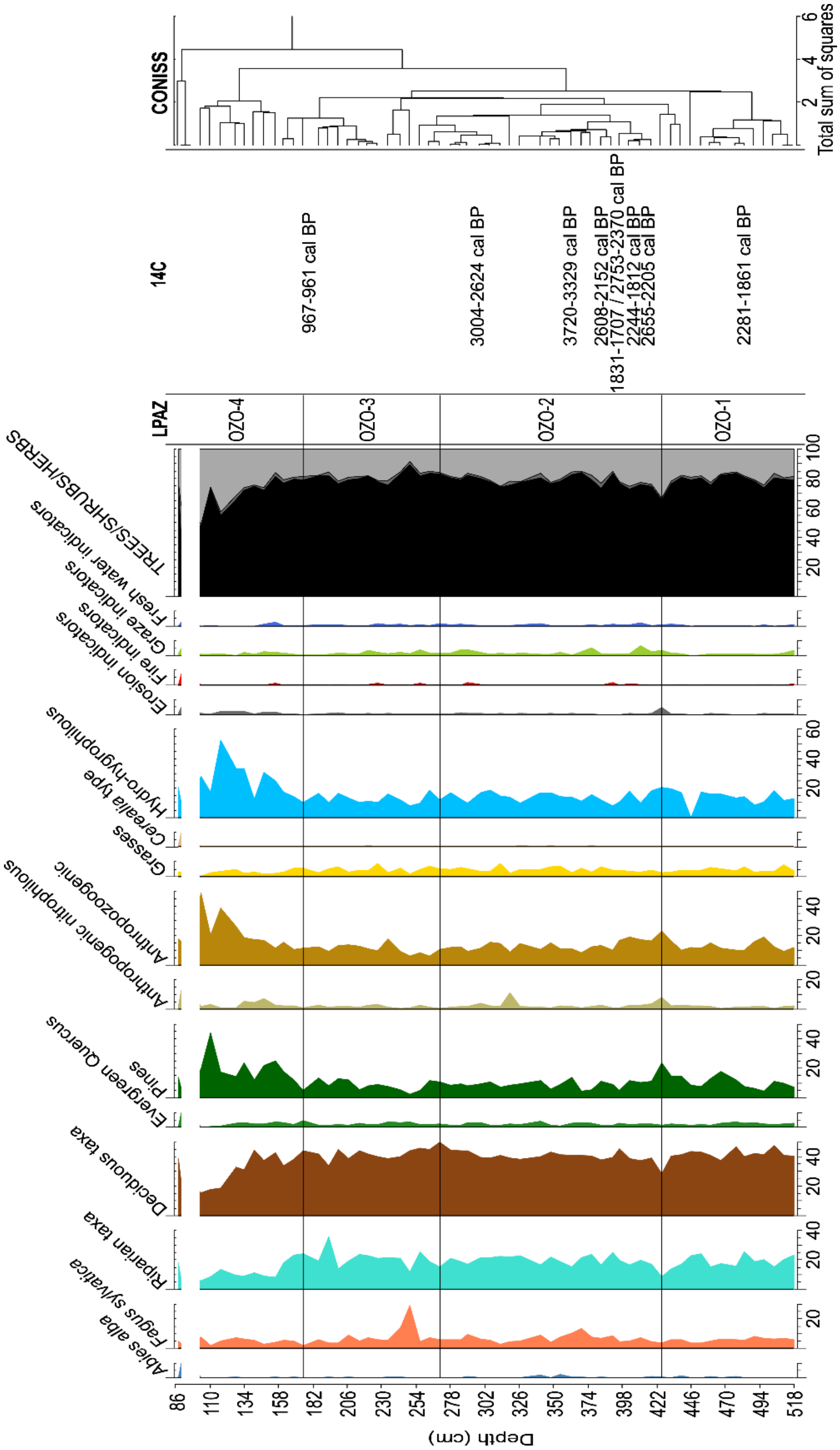


**Figure D.9 -** Synthetic pollen diagram of the Ozollo borehole. The different vegetation groups and/or most relevant taxa are represented. In addition, the depth (cm), the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are also represented.

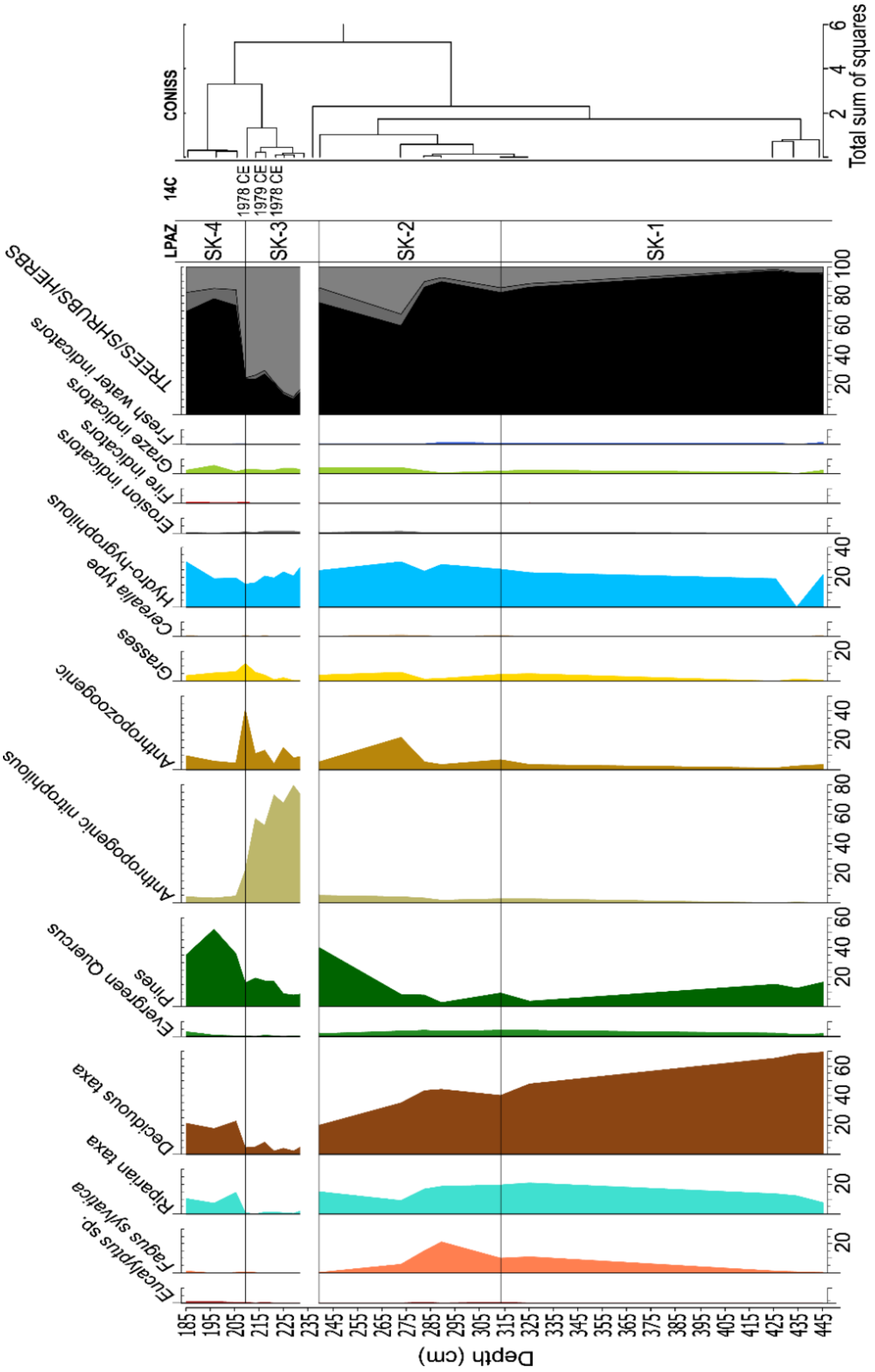


**Figure D.10 -** Synthetic pollen diagram of the San Kristobal borehole. The different vegetation groups and/or most relevant taxa are represented. In addition, the depth (cm), the defined local pollen assemblage zones (LPAZ), the radiocarbon raw dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are also represented.

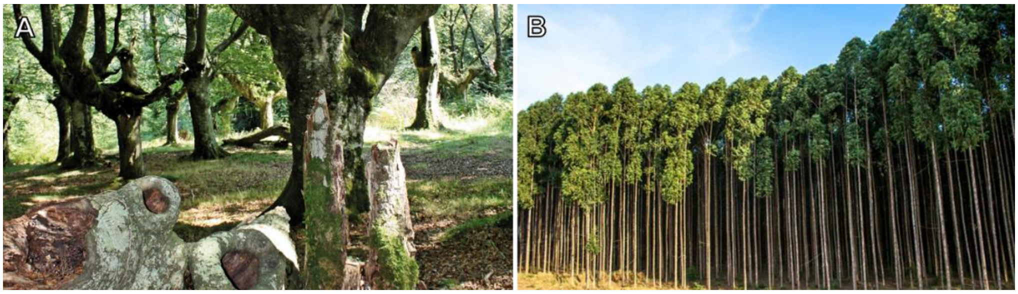


**Figure D.11 -** A) Photograph of the Airo forest (Bizkaia); B) Photograph of a Eucalyptus sp. plantation Sources: Provincial Council of Bizkaia, GazteizBerri (2020).

Important values of herbaceous vegetation have also been detected, specifically anthropozoogenic taxa. This type of vegetation is also accompanied by anthropogenic nitrophilous vegetation and grasses (Figs. D.7, D.8, D.9 and D.10). In our boreholes, the appearance of cereal pollen always began after 5000 years BP although the oldest agricultural activity recorded in the Cantabrian coastal region dates back to about 6000 years ago (Zapata et al., 2004; Zapata, 2005). In addition, through the study of non-pollen palynomorphs (NPPs), it has been possible to identify grazing indicators, erosion indicators and fire indicators. All these indicators usually appear in soils where different types of agricultural activities have been carried out, such as cattle-raising in the case of grazing indicators, or arable farming in the case of erosion and fire indicators. The latter indicators are the result of those actions carried out by humans to condition the land in order to use it for livestock and/or agriculture. For example, humans have frequently used fire to open wooded areas in order to create new pastures, croplands or even for the construction of new infrastructures (Zapata, 2005; Kaal et al., 2011; García-Ruiz et al., 2016; Robles-López et al., 2018, 2020; Narbarte-Hernández et al., 2019, 2021; Camarero et al., 2021; Shen et al., 2021). Moreover, many of these taxa (Cichorioideae, Chenopodiaceae, Apiaceae, Poaceae, *Plantago* sp.) are opportunistic, and colonize the spaces recently opened by humans if they find an appropriate ecological niche (Li et al., 2008; Jadczyk, 2009; Galop et al., 2013; García-Rivero et al., 2019).

In the case of the Requejada borehole, changes are also observed in this type of vegetation after the hiatus at 792 cm depth (Fig. D.7). The first change is the progressive increase of grasses (Poaceae), highlighting their growth in the uppermost borehole, around 220 cm depth and the 20th century (Fig. D.7). Some genera of Poaceae (*Spartina, Puccinellia, Elymus, Phragmites*, etc.) are quite abundant in marsh areas. Grasses not only respond to human presence in the sense of agricultural activities and cereal cultivation, but also as a consequence of the development of other anthropogenic activities such as construction and deforestation that favor grasses to be the first plants to colonize areas previously inhabited by other vegetation species (Zapata et al., 2004; Zapata, 2005; Tweddle et al., 2005; Zhao et al., 2013; Hostetler et al., 2021).

An increase in anthropogenic nitrophilous and anthropozoogenic taxa has been observed since about 575 cm depth (20th century, according to radiocarbon dating) (Fig. D.7). These groups include typical marsh taxa, such as Cichorioideae, Apiaceae and Chenopodiaceae. These taxa also tend to be highly related to human presence. However, we should bear in mind that during the Late Holocene, changes to foraminiferal assemblages in the estuaries on the Bay of Biscay (Cearreta & Murray, 1996; Leorri & Cearreta, 2004; Cearreta & Monge-Ganuzas, 2013; Serrano-García, 2020) suggested extensive development of high marsh environments related to a high sea level position. This conditioned the development of marsh vegetation, leading to an increase in these taxa with respect to previous times. The most predominant taxon is usually Chenopodiaceae, which, together with Poaceae, is characterized by its occurrence both in marsh areas and in those areas with human presence (Fig. R.22). In Ozollo, indicators of human presence, such as grazing and fire indicators, have been identified (Fig. D.9). Accordingly, we can assume that the vegetational dynamics observed in LPAZ OZO-1, OZO-2 and OZO-3 are of both natural and anthropogenic character.

Natural dynamics could be associated with the sea-level changes mentioned above. Previous studies have recorded a sea-level rise from the early Holocene of 5.5-7.3 mm $yr^{-1}$ that then declined to values of <1 mm $yr^{-1}$ from 7000 cal yr BP (Leorri et al., 2012; García-Artola et al., 2018). These sea-level variations formed the estuaries that we know today and, therefore, created those marshy environmental conditions. This would explain the appearance and, above all, the increase of typical marsh taxa throughout the Holocene record.

On the other hand, anthropogenic dynamics correspond mainly to grazing and agricultural activities during the last 5000 years (Zapata et al., 2004; Zapata, 2005). These dynamics changed during the last zone of the Ozollo borehole, the LPAZ OZO-4 (Fig. D.9) around 967 cal yr BP. During the Middle Ages important demographic growth took place, represented by the appearance of new human settlements and villages, especially in the northern regions of the Iberian Peninsula. This human expansion led to the creation of new crop fields, pastures and, in turn, large-scale deforestation to open spaces for new infrastructures (Zapata, 2005; Narbarte-Hernández et al., 2019, 2021; Quirós, 2020).

During the final LPAZ OZO-4, the arboreal vegetation in the Ozollo borehole shows a decrease of deciduous vegetation to the point that it ceases to be dominant in favor of pines, which experience a significant increase. Another type of arboreal vegetation that suffers a reduction is the riparian vegetation, which accompanies the decreasing trend of the deciduous forest (Fig. D.9). Besides, we can observe that the values of *Fagus sylvatica* are not reduced. This is probably due to the external origin of the beech pollen contribution that comes from an area farther away from the estuary (Zapata, 2005; Jouffroy-Bapicot et al., 2007; Pérez-Díaz et al., 2015; Ruiz-Alonso et al., 2017). Deforestation processes would also justify the increase in herbaceous plants detected, especially anthropozoogenic herbaceous plants. We have already discussed on previous pages that within these plant groups there are taxa such as Chenopodiaceae, Apiaceae and *Plantago coronopus* that usually colonize marsh areas. However, these taxa also have a marked anthropogenic character, as they are species that often appear precisely when humans interfere in the environment through deforestation processes. They are opportunistic taxa, which quickly colonize the emptied areas and are highly adaptable. The same occurs with the hydro-hygrophilous vegetation, which in LPAZ OZO-4 shows an increase (Fig. D.9). Deforestation processes in the areas closest to the estuary would cause an increase in the humidity of these soils. In part, because the riparian vegetation acts as a natural barrier in the river courses. At the same time, human interventions near the course of the river to facilitate the passage of water and obtain better agricultural yields cannot be discarded (Jouffroy-Bapicot et al., 2007; Pérez-Díaz et al., 2015; Ruiz-Alonso et al., 2017). Deforestation is a well-studied topic, and in areas of the Sierra de Cantabria (Burgos, La Rioja, Araba and Nafarroa), numerous studies have recorded this activity. Species such as *Quercus*, which was very abundant in the Sierra de Cantabria, *Pinus* sp. and *Corylus avellana* were used as firewood from the Neolithic onwards. With the intensification of anthropization, especially from the Chalcolithic (~5400 cal yr BP), deforestation increased and with it the increase in herbaceous communities of anthropogenic origin (González-Sampériz et al., 2008; Pérez-Díaz et al., 2015; Ruiz-Alonso et al., 2017; Alba-Sánchez et al., 2021).

In the San Kristobal borehole, non-arboreal pollen (NAP) contains anthropogenic nitrophilous and anthropozoogenic taxa along the LPAZ SK-1 and SK-2. In addition, these are accompanied by the presence of grasses which, together with taxa such as Cichorioideae and Chenopodiaceae, are indicative of marsh-type vegetation (Sánchez-Goñi, 1996; Biurrun, 1999; García-Antón et al., 2006; Loidi et al., 2011; Calleja-Apéstegui, 2019). The presence of this vegetation is in accordance with the indicative values of hydro-hygrophilous species, which are quite high not only in these first two pollen zones, but also throughout the entire borehole (Fig. D.10).

Another interesting anthropogenic indicator is the presence of cereal pollen (*Cerealia* type) from the beginning of the borehole (Fig. D.10). This would suggest a clear human presence in the area, with interventions in the estuarine zone mainly of agricultural nature. In fact, non-pollen palynomorph taxa (NPPs) have been identified indicating the presence of agricultural activities. The presence of Apiaceae, a taxon linked precisely to humans that appears whenever they impact the environment, reinforces the signal of human fingerprint in this sedimentary record.

Much more striking is the accentuated and even sudden decrease (at 210-230 cm depth) observed in arboreal taxa during LPAZ SK-3 (Fig. D.10). This decrease led to a very intense growth of anthropogenic nitrophilous taxa, particularly Cichorioideae. Such rapid growth has no explanation considering the time frame of natural dynamics in the estuary. Radiocarbon dating indicates calibrated dates of 1978-1979 CE for this section. Previous studies using other proxies (foraminifera, geochemistry and historical sources) carried out in the area have already detected intense dredging and dumping operations in the Oka estuary during the period 1973-1978. The main estuary reflux channel was dredged and 220 x $10^3$ $m^3$ of sand were deposited on the salt marshes of San Kristobal, causing the meandering channels of Busturia and Kanala to become straight and inactive (Monge-Ganuzas et al., 2019). These human activities would provide a reasonable explanation for the repeated increase in Cichorioideae, since the relocation and dumping of sediment would come from the areas closest to the estuarine course, an area colonized mainly by estuarine taxa such as Cichorioideae. Therefore, the anomalous increase in this taxon can be the result of the rapid contribution of new sediments to the area. Furthermore, the fact that the decline in arboreal taxa ends with a sudden recovery of their previous values and even their increasing trend (in the case of pines), clearly suggests that human intervention is the main cause for all these changes observed in the pollen record. All this is further supported by the presence of anthropozoogenic taxa, as well as the detection of indicators of both agricultural activity and erosion.

Finally, we should not forget that the presence of *Cerealia* type (~3000 cal BP), although not very remarkable and recorded intermittently, is indicative of agricultural activities in the area (Fig. D.7, D.8, D.9 and D.10). Besides, we have also detected the presence of non-pollen palynomorphs (NPPs) that support this hypothesis: grazing indicators, erosion indicators and fire indicators that can appear when conditioning and deforestation processes are carried out. Fire was used for the rapid opening of forested areas and has been a topic discussed at length in recent years (Santos, 2004; Pérez-Obiol et al., 2016; Ruiz-Alonso et al., 2017; Alba-Sánchez et al., 2021; Camarero et al., 2021). Numerous studies have shown how pine abundance shows a high frequency relationship with fires. There is a feedback between forest fires, human use of forests and shrub and pasture vegetation. One of the quickest ways for humans to obtain transhumant pasture was precisely through anthropogenic fires. This is seen in the Sierra de Gredos (Salamanca, Cáceres, Ávila, Madrid and Toledo), especially since the 19th century, although it has been recorded since the mid-18th century. This is something that we will be able to observe in more detail when analysing the short cores record (Camarero et al., 2021). The development of non-pollen palynomorph taxa indicative of grazing activities could be considered a potential determining factor. In Requejada, although the evolution of these taxa barely reaches 5% in the pollen zones prior to the sedimentary hiatus and up to 1865 - 1715 cal yr BP, from 670 cm depth onwards a gradual increase in grazing indicators can be observed, reaching 10% in the most recent times represented (20th century) (Fig. D.7). As observed in Figure D.12, the presence of agricultural fields around the area where the Requejada borehole was drilled is evident, which would also explain the appearance of *Cerealia* type in certain samples from the uppermost part of this borehole.

**Figure D.12 -** Aerial photographic sequence of the Saja-Besaya middle estuary. From bottom to top: 1957 - 2001 - 2020. Yellow square indicates location of the Miengo core. Orange dot signals location of the Requejada borehole. Farmland around the estuary channel reduced during the most recent times. Sources: 1957 American Flight, GeoEuskadi and Google Earth.

### 2.3.3. SiZer analysis

In order to understand the statistical significance of the observed change in arboreal and anthropogenic nitrophilous taxa in LPAZ SK-3 (San Kristobal borehole), a Significant Zero crossings of derivatives (SiZer) statistical analysis was performed. This tool has proven to be very useful for detecting significant changes in ecological data. Compared to many other methods of change point detection and statistical significance, SiZer analysis is a highly flexible tool. From trends in the data, it is able to detect multiple change points and changes in the temporal distribution of the sampling by adapting to temporal or depth changes in the variance of the signal error. Thus, a SiZer map helps to discover all significant dips and rises in the ecological data quickly (Sonderegger et al., 2009; Latałowa et al., 2019; Camuera et al., 2021; Ilvonen et al., 2022).

Through the SiZer method we can examine the derivatives of a curve to identify the presence of a threshold and to find where the derivative of a function changes significantly with respect to an environmental variable (Chaudhuri & Marron, 1999). This analysis has also been used to identify the significance of environmental and climate changes from various past and present paleoenvironmental data (Hald et al., 2004; Sonderegger et al., 2009)

In this case, the observed decrease in arboreal taxa in favor of anthropogenic nitrophilous taxa was striking. The SiZer takes into account not only the relative abundance data but also the resolution of the spatial/temporal data and, thanks to the good resolution obtained from the pollen analysis, the SiZer could be applied successfully.

The SiZer analysis was applied to two different taxa in the San Kristobal borehole: *Pinus pinaster* and Cichorioideae, the main protagonists of the observed change (Figs. R.15 and D.16). The results obtained show how effectively the SiZer analysis detects the significance of both the observed increase (in the case of Cichorioideae) and decrease (in the case of *Pinus pinaster*) in their respective pollen percentages. Increases are shown in red, while decreases are indicated in blue. The purple color represents the section with no statistical significance, which depends directly on the sample resolution of each borehole interval.

As shown by the SiZer maps, the dredging and dumping of sediments that took place in the San Kristobal area at the end of the 20th century and that left a clear signal in the palynological record are not only observable at graphical and percentage levels, but their impact is statistically representative as is supported by the analysis of the first derivative performed with SiZer for the taxa Cichorioideae and *Pinus pinaster*.

In the case of the the Ozollo borehole, the major vegetation change occurs in the LPAZ OZO-4 (post 967 cal yr BP). This change implies a reduction of tree pollen in favor of herbaceous pollen. This seems to be related to human presence and the impact of human activities in the estuarine environment. In order to test whether these observed changes in vegetation dynamics have sufficient statistical relevance, we selected the 4 main taxa involved: *Alnus*, deciduous *Quercus*, *Betula* and Chenopodiaceae. When performing the SiZer analysis, all the changes observed individually by any taxon showed statistically significant results. We would expect that in some cases the resolution or even the percentage values would not be sufficient. However, as seen in Figures R.26, R.27, R.28 and R.29, the three declining trends (blue) (*Alnus*, *Betula* and deciduous *Quercus*) and the increasing trend (red) of Chenopodiaceae are clearly detected by the software.

### 2.3.4. Paleoclimate reconstruction

A quantitative paleoclimate reconstruction of mean annual temperatures and precipitation has been carried out using pollen data from the Ozollo borehole. The application of WA-PLS-based transfer function model under cross-validation in late Holocene sedimentary records implies taking into account the increasing human impact already characteristic of this time interval (Birks & Seppä, 2004; Li et al., 2014; Strandberg et al., 2014; Ramos-Román et al., 2018). Another factor to be aware of in this case is the already mentioned inversion of the radiocarbon dates in this sedimentary sequence.

It can be observed that, in general, the temperature shows a slowly increasing tendency through time, with minima of approximately 8º C/yr and maxima of 11º C/yr (Figs. R.25 and D.13). On the other hand, interpretation of the reconstructed precipitation is more problematic, since there are many taxa, such as *Pinus*, which may indicate more precipitation than actually occurred. The ranges obtained after quantitative analysis oscillate from a minimum of 680 mm/yr to a maximum of 950 mm/yr.

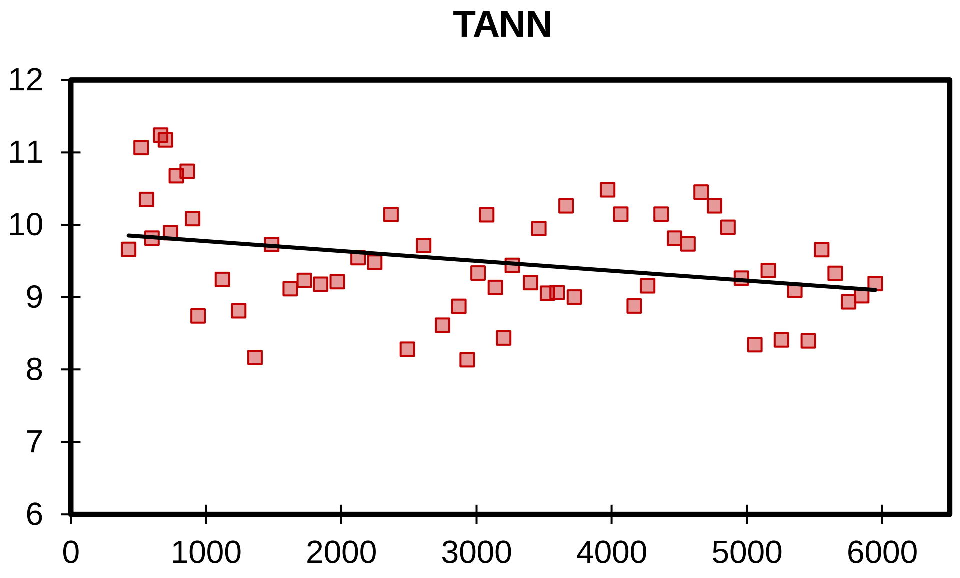


**Figure D.13 -** Linear regression of temperature data obtained by WA-PLS-based transfer function model under cross-validation. A trend of progressive increase in temperature through time is shown.

# 3. Anthropocene

## 3.1. Geochronology

A series of radioisotopic analyses have been performed on the recent core sediments to detect the exponential distribution of $^{210}Pb_{ex}$ and reconstruct their age. In the case of Miengo, through the $^{210}Pb_{ex}$ profile and by using the CIC (constant initial concentration) model (Robbins, 1978) and fitting the logarithm of the concentration with depth in the core, the sedimentation rate for each zone has been calculated (Fig. R.33).

No significant maxima have been identified for $^{137}Cs$ in the Miengo sedimentary record that would allow us to associate them with the year 1963 CE, the time when this artificial radionuclide reaches its maximum (Fig. R.34). Furthermore, the presence of $^{137}Cs$ has been detected in sediments older than 1952 CE when the atmospheric nuclear tests began. This is probably due to a post-depositional downward migration process of $^{137}Cs$ (Crusius & Anderson, 1995; Putyrskaya & Klemt, 2007; Zhang et al., 2019; Serrano-García, 2020).

A chronological framework for the Miengo core shows continuous sedimentation from the mid-19th century to the present.

The Axpe core is a replica of the one studied previously by García-Artola (2013) and, consequently, the same $^{210}Pb_{ex}$ radioisotopic results have been used here (Fig. R.38). These were interpreted using the CIC model (constant initial concentration of Robbins, 1978). In addition, García-Artola (2013) detected a peak of $^{137}Cs$ activity at 6 cm depth that she associated with the year 1963 CE (Fig. R.39). The chronological framework for the Axpe core extends from approximately the end of the 18th century to the present.

Radioisotopic analyses of the Zumaia core showed the $^{210}Pb_{ex}$ activity decreasing exponentially with depth and suggested a relatively steady accumulation. Concentration of this radionuclide cancelled out below 30 cm depth. Using the CIC (constant initial concentration) model (Robbins, 1978), Cearreta et al. (2021) determined the sedimentation rate which, in turn, allowed a date to be assigned to each sample analyzed (Fig. R.43). In addition, the analyses performed for the $^{137}Cs$ showed a concentration peak at 13-12 cm, corresponding to 1963 CE, the time of greatest activity of this radionuclide. The chronology obtained for this core extends from approximately 1828 CE to 2018 CE, covering the last 190 years (Fig. R. 44).

Due to the limited availability of sedimentary material to perform different types of analysis from the Basque Mud Patch (BMP) cores, the KS04 core was selected to perform the radioisotope analysis that would allow us to obtain an adequate geochronology for this marine deposit (Irabien et al., 2020).

Using the slope derived from the linear regression between $^{210}Pb_{ex}$ and depth (Appleby & Oldfield, 1992), the mean sedimentation rate ($1\pm0.1$ $mmyr^{-1}$) was calculated (Fig. R.51). This estimated that the sedimentation rate resembles the lowest rates defined by Jouanneau et al. (2008) for the BMP (between 1.3 and 5.0 $mmyr^{-1}$). On the other hand, radioisotopic analyses of $^{137}Cs$ have been applied to corroborate the sedimentation rates determined using $^{210}Pb_{ex}$. The peak of maximum global fallout for this radionuclide after atmospheric thermonuclear tests, dated between 1962-1964 CE, appears slightly deeper (1 cm) than the geochronology obtained by $^{210}Pb_{ex}$ (Fig. R.52). The anomalous penetration of radiotracers has been previously mentioned in the case of the Miengo core and represents a postdepositional effect extensively described in previous works (Livingston & Bowen, 1979; Jaakkola et al., 1983; Cochran, 1985; Crusius et al., 2004;). It is possible that the biological mixing effect was the process responsible for this alteration, as $^{137}Cs$ is more sensitive to it than $^{210}Pb$ (Johannessen & Macdonald, 2012).

### 3.2. Evolution of vegetation

The major difference between the more recent short cores and the older long boreholes discussed previously can be summarized in their respective responses to different natural and anthropogenic-derived changes. Variety and intensity of human impact increase through time in accordance with the cultural and technological development of human societies. The more technology, the greater the capacity to alter the environment, especially since industrial times (Meyer, 1996; Ponting, 2007; Goudie, 2013). If in the Holocene boreholes natural processes used to be predominant, in these recent cores anthropogenic impacts are the main cause of change. Therefore, the study of the core sediments deposited during recent times, named as Anthropocene in this doctoral thesis following Waters et al. (2016), allows a more detailed and higher resolution approach to trace the human impact on the vegetal biosphere during the last decades.

Starting with the arboreal vegetation of the Miengo core (1830 – 2018 CE), we can observe that deciduous forest predominates over the rest of the vegetation groups. Its dominance is practically regular throughout the entire core, without undergoing major changes. Similarly, riparian vegetation also maintains a relatively regular presence (Fig. D.14). As already commented, in the Cantabrian coastal vegetation it is common to find this type of mixed forest with a predominance of deciduous taxa where such taxa as alder and ash also develop (Loidi et al., 2011).

The presence of *Fagus sylvatica* along the core is also interesting (Fig. D.14). As mentioned for the Holocene boreholes, the expansion of *Fagus sylvatica* during this epoch has been detected early in the previous boreholes studied here (López-Merino et al., 2008; Loidi et al., 2011; Pérez-Díaz et al., 2016; Mónica Ruiz-Alonso et al., 2019; Sánchez de Dios et al., 2021). This pollen probably comes from the watershed of the Saja and Besaya rivers that flow from the Cantabrian Mountains.

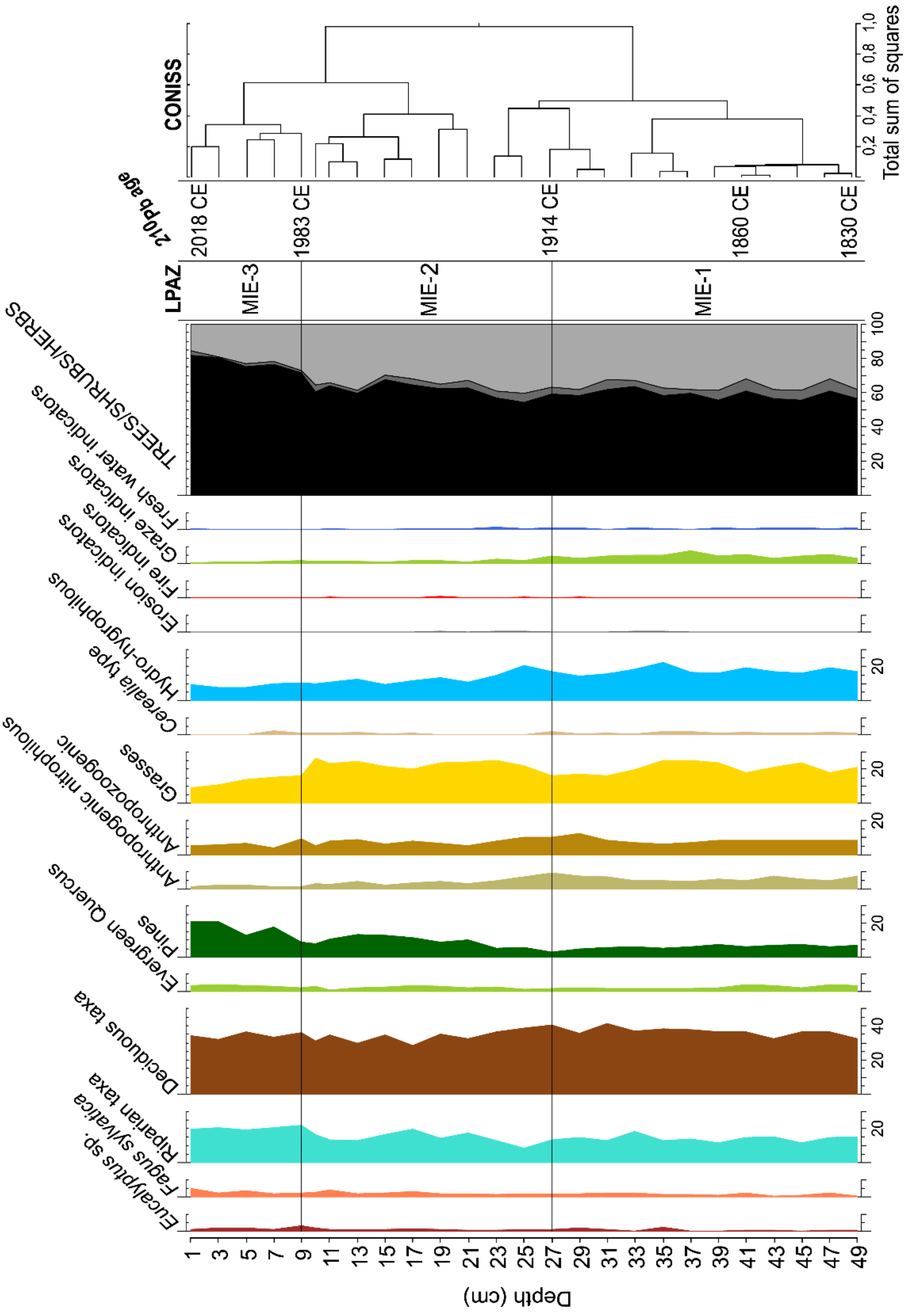


**Figure D.14 -** Synthetic pollen diagram of the Miengo core. The different vegetation groups and/or most relevant taxa are represented. In addition, the depth (cm), the defined local pollen assemblage zones (LPAZ), the $^{210}$Pb dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are also represented.

Pine begins to increase progressively in the LPAZ MIE-2, dated around 1914 CE, and its greatest increase occurs approximately since 1970 CE, reaching its maximum during those years (Fig. D.14). The reason for this increase is very likely related to the replanting carried out along the Cantabrian coast, particularly after 1940. From that date, the so-called "Plan Nacional de Repoblaciones" came into operation and consisted of replanting areas of previous natural forest with commercial, rapid-growing taxa with the main objective of exploiting them for timber. This implied that some of the species replanted were allochthonous, such as *Pinus radiata* that originally comes from California, North America. Unfortunately, its pollen type is difficult to discriminate from the autochthonous morphotype *Pinus pinaster* (Michel, 2006; Uriarte, 2010; Vadell et al., 2016, 2019). Although the percentage of pine does not allow us to talk of local pine forests, on a regional scale the repopulation of this taxon took place mainly in the Province of Cantabria, precisely in the Cuenca del Pas and in the surroundings of the Natural Park of Saja-Besaya and Alto Campoo (Ezquerra & Gil, 2004).

The introduction of *Eucalyptus* sp. is also noteworthy, as previously mentioned for the Requejada borehole (Fig. D.14). As a taxon with rapid growth and high profitability, it also responds partially to the aforementioned "Plan Nacional de Repoblacion" (Martin de Agar et al., 1992; Espinel et al., 1995; Duñabeitia et al., 2004; Veiras & Soto, 2011; Soto-Caba, 2013). The natural distribution of eucalyptus covers much of Oceania, Tasmania, Australia, New Guinea, Indonesia and the Philippines (Ladiges et al., 2003). The genus *Eucalyptus* has been introduced in many regions of the world because of the great adaptation of many of the eucalyptus species to different types of soils and climates, making this taxon suitable from the point of view of economic profitability (Elosegui et al., 2020). In terms of geographic distribution, eucalyptus trees have become one of the most representative plant formations in the lowlands of Cantabria, and their use is one of the bases of the forestry industry in that province (Ezquerra & Gil, 2004).

Another region where *Eucalyptus* is common in forestry is the Basque Country. Most of the plantations are on the coast of the Province of Biscay, whose benign climate is more conducive to these trees, although it is beginning to spread to other regional areas. Elosegui et al. (2020) shows that the municipalities with the greatest eucalyptus coverage are Maruri-Jatabe (50% of the municipal area), Lemoiz (44%) and Bakio (38%). In this region, eucalyptus has begun to replace Monterey pine or *Pinus radiata*. That is why the non-detection of this taxon in the Axpe core is striking, although this may be due to the low pollen resolution of this sedimentary record with multiple sterile samples (Fig. D.15).

Among the arboreal vegetation, pines seem to have a greater predominance throughout the Axpe core. In LPAZ AXP-1 the percentage values of different arboreal taxa are similar (pine 8%, deciduous taxa 10%), but during LPAZ AXP-2 pine increases considerably (Fig. D.15). Axpe does not show a clear dominance of deciduous forest, nor a frequent presence of riparian vegetation. This is probably due to the fact that this core is located in an area used traditionally for farmland, especially during the 19th and 20th centuries (Rodríguez-Loinaz et al., 2007; García-Artola, 2013; García-Artola et al., 2016). As in the previous Miengo core, the observed increase in pine taxa here responds to the replanting carried out since the early 20th century with a peak related to the "Plan Nacional de Repoblación". The presence of *Fagus sylvatica* in Axpe is also interesting. As in the already discussed boreholes of Ozollo, Anbeko and San Kristobal in the same Urdaibai estuary, it is very likely that this pollen arrives by fluvial transport from more inland areas.

In the case of Zumaia the presence of *Fagus sylvatica* is more continuous than in Axpe. Zumaia core has turned out to be a clear example of how vegetation change is affected by anthropogenic processes that leave an evident record in the sediments. There are two clearly marked phases in this core, mainly defined firstly by the increase of anthropogenic nitrophilous and anthropozoogenic taxa between 1828 - 1920 CE, and secondly by a dominance of arboreal vegetation, mainly pine and riparian taxa during 1920 - 2018 CE (Fig. D.16).

Evolution of arboreal vegetation shows the great regularity of deciduous forest along the whole core (from 1828 - 2018 CE). However, during the first two pollen zones (LPAZ ZUM-1 and ZUM-2), arboreal vegetation is not dominant (Fig. D.16) and high values are observed for shrub taxa such as *Erica* type. This taxon is typical of acid substrates and characteristic of humid forests or associated with the humidity provided by watercourses. Heather (*Erica arborea*) grows together with beech, pine and oak forests, and is grouped in extensive formations that can be found up to 2000 m above sea level (Loidi et al., 2011). The presence of *Fagus sylvatica* has also been detected in this core.

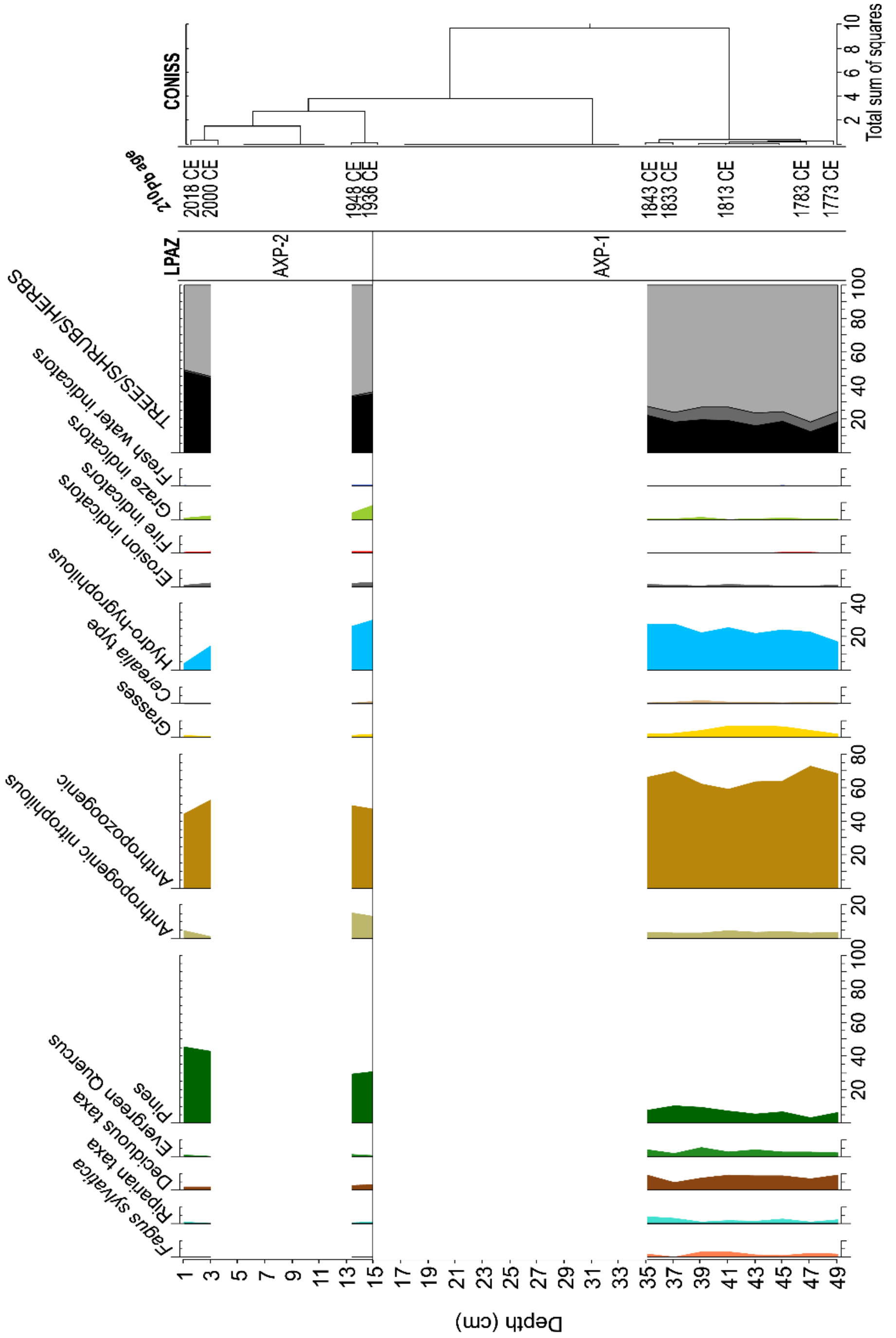


**Figure D.15 -** Synthetic pollen diagram of the Axpe core. The different vegetation groups and/or most relevant taxa are represented. In addition, the depth (cm), the defined local pollen assemblage zones (LPAZ), the $^{210}$Pb dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are also represented.

The following LPAZs, ZUM-3, ZUM-4 and ZUM-5 (~1990 CE), exhibit a progressive increase of arboreal vegetation (Fig. D.16) with two main protagonists: pine and riparian taxa. This increase in pine pollen would respond to its intensive and extensive replanting from the 20th century onwards that gave priority to pine taxa and even introduced new allochthonous species in Spain, such as *Pinus radiata* (Michel, 2006; Uriarte, 2010; Permán-García et al., 2017; Vadell et al., 2016, 2019). Some of the most important plantations are located in the mountains of Errialtadua Mayor, the mountains of Durango and Mount Irisasi (Biscay and Gipuzkoa provinces). Even so, today 85% of the Basque-Atlantic forests correspond really to plantation areas, of which practically half are pines that occupy almost all of the forest located below 600 m altitude. There are two arguments that would support this hypothesis: Firstly, the small increase observed in the pollen values of deciduous forest whose species were also replanted, although not prioritized. Therefore, after a first phase where deforestation was intensive and replanting scarcely occurred, a second phase began when replanting started to impact strongly on the vegetation around the Urola estuary. These plantations gave priority to pine trees over the autochthonous deciduous vegetation of the Cantabrian coast. Secondly, the appearance of *Eucalyptus* sp. in the pollen record since 1920 CE. This taxon was introduced from Australia during the 19th century, but it was not until the 20th century when it began to acquire a considerable extension. It is worth mentioning that *Eucalyptus* sp. is not a taxon characterized by high aerial pollination, instead, it normally depends on other agents (such as birds or insects). The study carried out by Sniderman et al., (2018) about the pollination of Eucalyptus has shown that pollination ranges are of 1130 - 327,000 pollen grains (although values >100,000 may be over represented) collected in honey traps from spring to January. This would explain how, despite having a large presence in the modern regional landscape, it does not appear in large percentages within the recent sedimentary record (Martin de Agar et al., 1992; Espinel et al., 1995; Duñabeitia et al., 2004; Loidi et al., 2011; Veiras & Soto, 2011; Soto-Caba, 2013; Permán-García et al., 2017).

On the other hand, the increase in riparian vegetation observed in these three pollen zones is likely to respond to the greater presence of this vegetation type both in the areas close to the core, as well as in other areas further inland in the Urola river catchment area. Their pollen contribution, especially alder (*Alnus*), would be supplied mainly by the river. In fact, along the Urola there are currently some areas where alders form small gallery forests. The abandonment of agricultural activities is probably one of the causes for this increase, since these riverine areas with brackish and very humid soils are very appropriate for the growth of riparian-type species such as alder and ash (Loidi et al., 2011).

Finally, KI03 and KI06 cores from the Basque Mud Patch (BMP) contain clearly dominant arboreal vegetation (1817 – 2004 CE) (Figs. D.17 and D.18). The most predominant taxon is pine since the beginning of both cores, experiencing an increase over time. Other tree groups also appear in these records, such as deciduous forest and riparian vegetation. Nevertheless, their abundance values never come close to those achieved by pines.

The dominance of pine in these marine cores probably responds to two main reasons. Firstly, to the pollination characteristics of pine species. Pines are taxa known for their high pollination capacity, which allows them to create monospecific forests. *Pinus pinaster*, for example, has a pollen production between $20.9 \times 10^6$ and $32.3 \times 10^6$ pollen grains per tree, which far exceeds the production of all *Quercus* species, which range between 119,190 and 550,450 pollen grains per tree (Jato et al., 2000; Gómez-Casero et al., 2004). Secondly, to the great dispersal capacity of pine pollen. Studies have been carried out to measure the pollination and germination capacity of pine over medium and long distances, obtaining a germination rate of between 2% and up to 57% over distances of 3 to 41 km respectively. This is due to the structure of the pine pollen grain. Thanks to its aerobic sacs, its dispersal and aerial transport is much more effective, allowing these grains to spread very long distances (Lill & Sweet, 1977; Jato et al., 2000; Frenguelli et al., 2002; Goubitz et al., 2002; Gómez-Casero et al., 2004; Robledo-Arnuncio & Gil, 2005). An example of the high pollination capacity of this taxon is provided by Sánchez-Morales (2021), where his pollen calibration study shows how pine can be dominant even in records collected in evergreen forests. Therefore, cores KI03 and KI06 would contain an overrepresentation of pine pollen, which would be derived from different coastal areas, where the dominant taxon is *Pinus pinaster* (Figs. R.45 and R.48). It is very likely that this pollen supply could also come from France, since we can observe in core KI06 a small presence of *Abies alba* (silver fir). This taxon is clearly a mountain tree, which can be found in core KI06 due of its proximity to the Pyrenean Mountains, where this species is known to be present. The presence of *Fagus sylvatica* has also been detected, especially in the first two LPAZs of both cores (Figs. D.17 and D.18).

It is interesting that despite its limited dispersion capacity, *Eucalyptus* sp. (Figs. D.17 and D.18) has been identified in these marine cores. Its presence suggests that the introduction of this taxon in around 1920 CE must have been relatively extensive, being a taxon with a low pollination rate which even in areas closer to its plantations leaves hardly any record in the sediments (Martin de Agar et al., 1992; Espinel et al., 1995; Duñabeitia et al., 2004; Loidi et al., 2011; Veiras & Soto, 2011; Soto-Caba, 2013; Permán-García et al., 2017).

Herbaceous vegetation also shows signs of human influence. In Miengo, the presence of anthropogenic nitrophilous and anthropozoogenic taxa, although not dominant, is quite regular (Fig. D.14). Moreover, the presence of cereal pollen (*Cerealia* type) throughout this core implies the presence of farmland nearby. This has been verified thanks to historical aerial photography (Fig. D.12). In addition, Figure D.14 shows a quite relevant presence of grasses. This vegetation tends to grow easily in marshy areas and, in addition, it is closely related to human presence, rapidly colonizing anthropogenic areas. The notable presence of grasses could be partially due to the species *Cortaderia seollana*. Although the time of its arrival in Spain from South America is uncertain, there is evidence that it reached different ports on the Cantabrian Sea through international trade, and from there it may have spread naturally or as a consequence of human action through its ornamental use in gardens (Sobrino et al., 2002; Domènech et al., 2005). Unfortunately, the pollen morphology of this taxon is very similar to that of its morphotype Poaceae. In fact, the Poaceae are practically indistinguishable from each other except for their size, which in the case of cereals allows easy distinction among them. We cannot be sure that the large amount of grass pollen observed in the Miengo core derives from this taxon, but we do know that regionally the presence of this invasive species is very high and persistent (Campos et al., 2004; Domènech & Vilà, 2008; Pardo-Primoy & Fagúndez, 2019; Cires et al., 2022).

Grazing, erosion and fire indicators have also been detected in the Miengo core and they are closely related to human activities, such as agriculture, livestock farming, deforestation or infrastructure construction (Figs. D.12 and D.14). This is relevant because during the 19th and 20th centuries, the Cantabrian coastal area became the industrial center of Spain. This led to the construction of numerous industrial and port facilities. In addition, the important Reocín zinc mine was located near Miengo. This mine was rediscovered in 1856 and since then, until its closure in 2003, the exploitation of mineral resources was intensive (Castro et al., 2001; Velasco, 2003; Symons et al., 2009; Serrano-García, 2020). This led to the location of new infrastructures related to the mine, which led to an increase in the exploitation of other resources such as, for example, timber. Indeed, there is a large paper company in the area, the "Sniace group", founded in 1939.

Regarding herbaceous vegetation in the Axpe core, the great predominance of anthropozoogenic taxa is striking as it represents the dominant vegetation in this core (Fig. D.15). Chenopodiaceae is the most dominant taxon (Fig. R.36) and is clearly related to marsh environments. The large presence of this taxon is congruent since the core was extracted from a recent medium/high marsh, where artificial dykes and agricultural structures were once found. These agricultural fields were abandoned during the last decades and the Urdaibai marsh areas experienced a rapid natural regeneration process (Cearreta et al., 2013; García-Artola, 2013; García-Artola et al., 2016, 2017) (Fig. D.19).

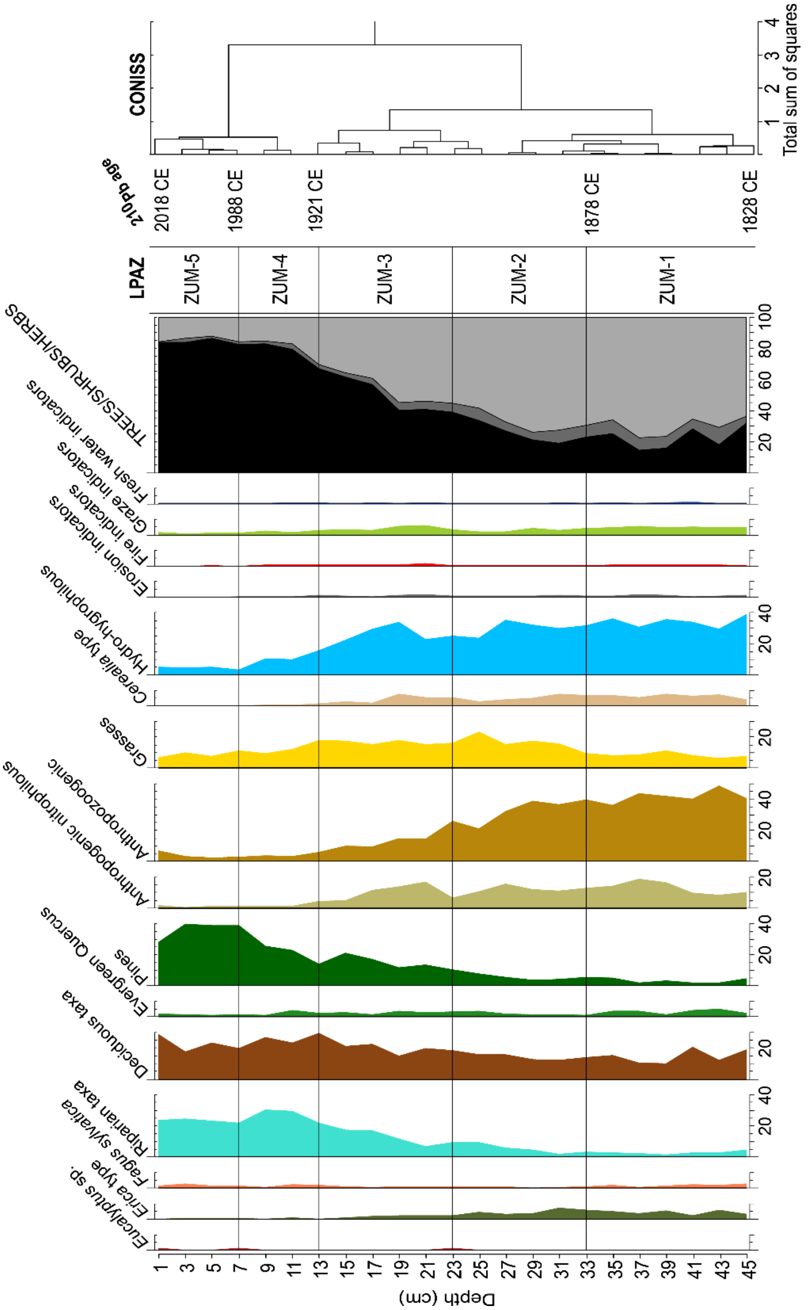


**Figure D.16 -** Synthetic pollen diagram of the Zumaia core. The different vegetation groups and/or most relevant taxa are represented. In addition, the depth (cm), the defined local pollen assemblage zones (LPAZ), the 210Pb dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are also represented.

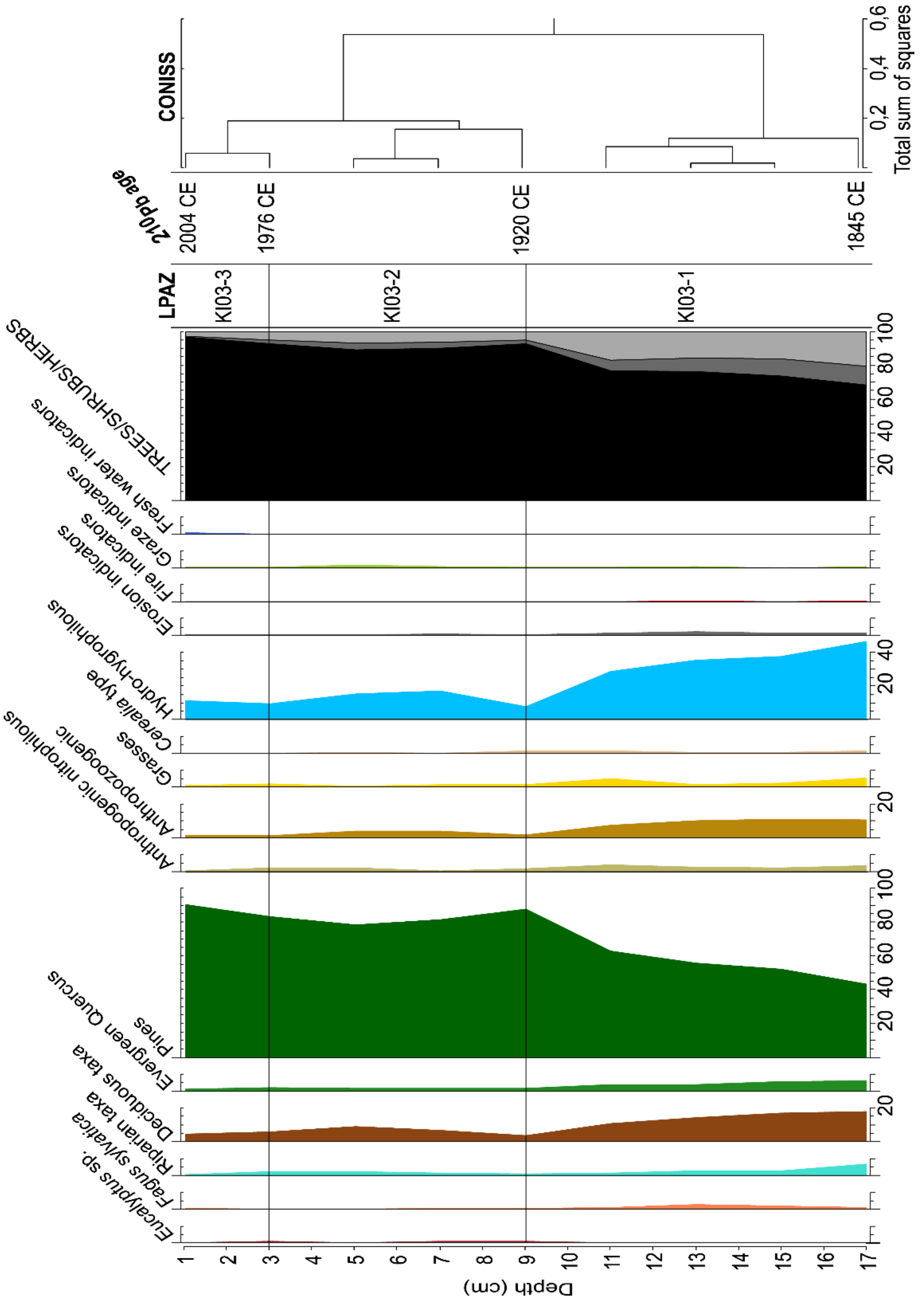


**Figure D.17 -** Synthetic pollen diagram of the KI03 core. The different vegetation groups and/or most relevant taxa are represented. In addition, the depth (cm), the defined local pollen assemblage zones (LPAZ), the 210$^{Pb}$ dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are also represented.

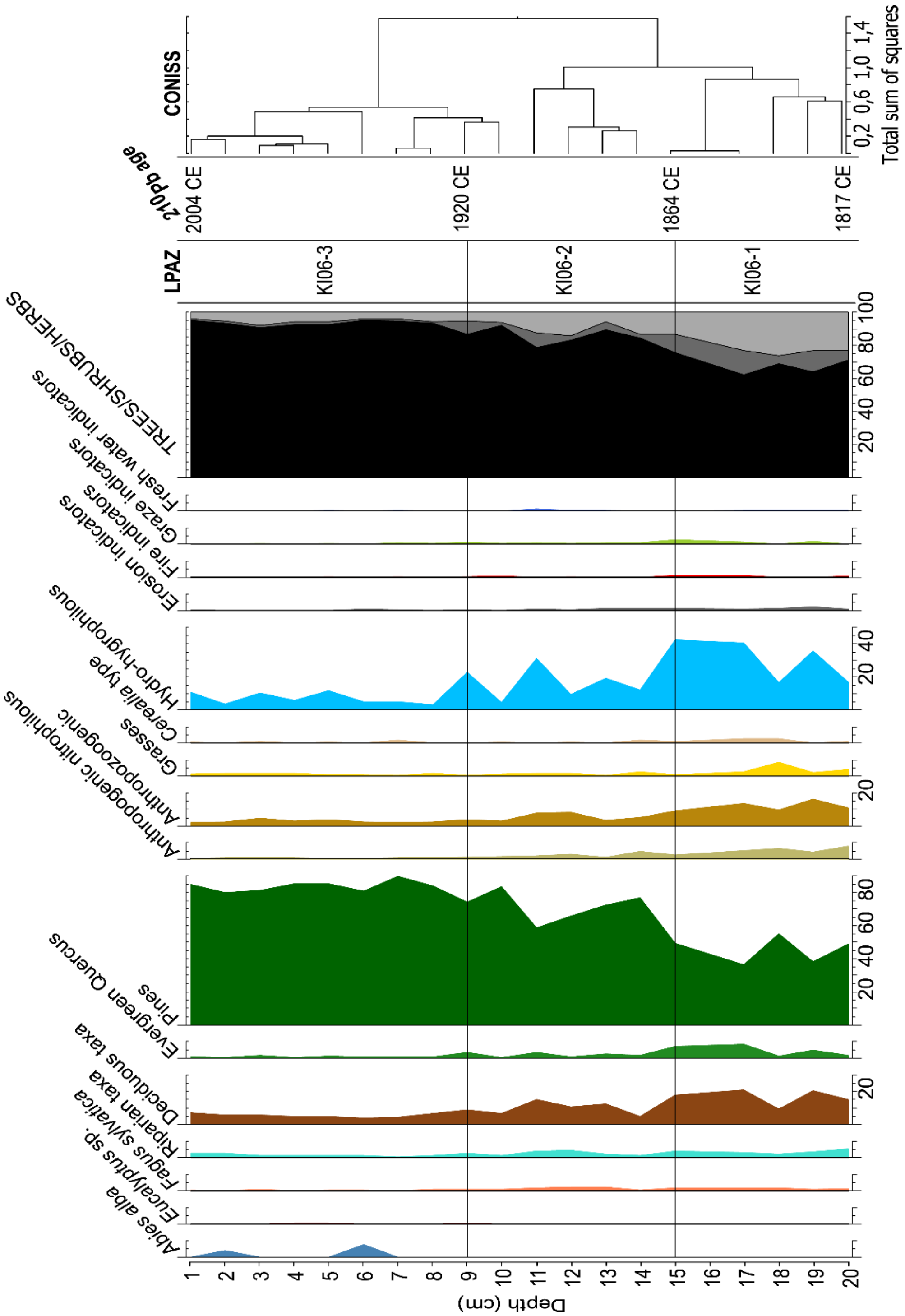


**Figure D.18 -** Synthetic pollen diagram of the KI06 core. The different vegetation groups and/or most relevant taxa are represented. In addition, the depth (cm), the defined local pollen assemblage zones (LPAZ), the 210$^{Pb}$ dates and the analysis of stratigraphically constrained clusters by the incremental sum of squares (CONISS) are also represented.

The prominent presence of hydro-hygrophilous vegetation is also in agreement with a clear marshy context. Human influence is also represented by *Cerealia* type pollen, whose appearance is basically regular until about 1940 CE. We also have information from non-pollen palynomorphs (NPPs). Both erosion and fire indicators have been detected and, with a greater presence, grazing indicators are also significant. However, since about 1940 CE these taxa saw their percentages significantly reduced. This is also probably due to the progressive reduction in farmland around the estuary in recent decades (García-Artola, 2013; García-Artola et al., 2016, 2017) as observed in Figure D.19.

Anthropogenic nitrophilous and anthropozoogenic vegetation (Chenopodiaceae and Cichorioideae) in the Zumaia core is also noteworthy although they are not dominant (Fig. D.16) (Fernández-Illescas et al., 2010; Loidi et al., 2011; Muñoz-Rodríguez et al., 2017). The dominant taxon during LPAZ ZUM-1 and ZUM-2 is Apiaceae (Fig. R.41). This is a taxon that, although also related to marsh environments, represents a clear indication of human impact (Galop & Jalut, 1994; Hjelle, 1997; Gómez et al., 2007; Loidi et al., 2011; Huang et al., 2018; Lullfitz et al., 2020). Many, but not all, Apiaceae species are colonizing taxa of human-modified spaces although they include even cultivated plants: dill, celery, coriander, carrot, fennel or parsley. If we add all this to the presence of *Cerealia* type pollen, it is very likely that this record is highly influenced by agricultural activities developed on the previous reclaimed marshlands. This is also supported by the presence of grazing indicators and the remarkable presence of hydro-hygrophilous vegetation. Altogether they are indicative of a clearly humid marsh environment that is being used for arable and livestock activities.

Regarding the herbaceous vegetation of its last three LPAZ ZUM-3, ZUM-4 and ZUM-5, the reduction in anthropogenic nitrophilous and anthropozoogenic taxa is noticeable. As can be observed in Figure D.20, agricultural fields around the Zumaia core were replaced by industrial activities (iron industry and various harbor facilities) and tree plantations through time. These activities required various channeling and dredging works of the Urola estuary, which provoked the disappearance of marshland areas (Cearreta et al., 2021). Almost certainly, this caused the reduction in hydro-hygrophilous vegetation together with anthropogenic nitrophilous and anthropozoogenic vegetation in the most recent sediments of this core.

Grasses (Poaceae), as well as anthropogenic nitrophilous and anthropozoogenic taxa, are opportunistic organisms that grow in marsh areas or even in human-impacted places. In the Miengo core, a large part of the pollen values attributed to this vegetation group may correspond to the invasive plant *Cortaderia seollana* (Campos et al., 2004; Domènech & Vilà, 2008; Pardo-Primoy & Fagúndez, 2019; Cires et al., 2022). It is possible that the same situation is occurring in Zumaia.

Finally, the herbaceous vegetation in both the KI03 and KI06 cores is characterized by the presence of cereal pollen transported to this marine environment by the numerous Cantabrian rivers (Figs. D.17 and D.18). The presence of anthropogenic nitrophilous and anthropozoogenic taxa would also derive from this fluvial and estuarine contribution. The same can be applied to the hydro-hygrophilous vegetation, which has a greater presence and experienced a rather sharp decrease around 1920 CE. This is a period when the north of the Iberian Peninsula underwent a more intense industrialization, which is observed in the geochemical records of these and other cores previously analyzed (Cearreta et al., 2013; 2021; García-Artola, 2013; García-Artola et al., 2016, 2017; Irabien et al., 2020).

The eastern Cantabrian Coast was one of the most industrialized areas in the Iberian Peninsula during the Industrial Revolution (regionally since the 1880s), and even today it still preserves numerous infrastructures derived from those historical activities. This made the region one of the most important economic centers in Spain but, at the same time, one of the regions with the most degraded environmental quality.

This industrial development was preceded by agricultural development that was also extensive and long-lasting (Narbarte-Hernández et al., 2019, 2021, 2022; Quirós, 2020). Agriculture and livestock have been present in the region since approximately the 7th or 8th millennium BP (Zapata et al., 2004; Zapata, 2005). The adoption of agriculture meant the development of new practices which brought about radical changes in the interaction of humans with the plant environment: differentiation of wild resources, knowledge of the reproduction of cereals and leguminous plants, care necessary for the good growth of these taxa... It also added the requirement for greater knowledge of the environment in order to be able to control production and deal with problems of soil fertility and competition from grasses and animals (Zapata et al., 2004; Zapata, 2005; Narbarte-Hernández et al., 2019, 2021).

The Cantabrian region is very fertile because of its high humidity, the presence of numerous rivers and high soil quality. As humankind developed both demographically and technologically, increasing quantities of natural resources were needed to sustain that population. Consequently, this increased the pressure on riparian zones, marshes and surrounding areas (Zapata et al., 2004; Zapata, 2005; Narbarte-Hernández et al., 2019, 2021). During the Middle Ages, these areas began to be systematically deforested in order to create open fields for grazing and agriculture; a situation that did not change much in the northern Iberian Peninsula until the arrival of the Industrial Revolution (Narbarte-Hernández et al., 2019, 2021, 2022; Quirós, 2020).

**Figure D.19 -** Aerial photographic sequence of the Oka estuary (Urdaibai). From bottom to top: 1957 - 2001 - 2020. Yellow square indicates location of the Axpe core. Orange dot signals location of the San Kristobal borehole. Farmland around the estuary reduced during the most recent times. Sources: 1957 American Flight, GeoEuskadi and Google Earth.

**Figure D.20 -** Aerial photographic sequence of the Urola estuary. From bottom to top: 1957 - 2001 - 2020. Yellow square indicates location of the Zumaia core. Farmland around the estuary reduced during the most recent times. Sources: 1957 American Flight, GeoEuskadi and Google Earth.

In different cores, such as Zumaia, Miengo and even Axpe, we can see that about 200 years ago herbaceous plants were either the dominant vegetation group or were quite even with the percentages of the arboreal group. This is very significant as the presence of humans and agricultural activities are usually represented in the pollen analysis through this replacement process. The anthropogenic nitrophilous and anthropozoogenic taxa, together with the grasses and the hydro-hygrophilous vegetation represent a marsh environment that together with the presence of cereal pollen and the NPPs indicators of fire, erosion and grazing confirm the development of these human activities in the estuarine area (Fig. D.14, D.15 and D.16).

However, as we move through time, all cores show the evolution of the vegetation changes, with a shift in the predominant plant associations. The arboreal pollen indicates a great recovery of forest areas especially since the beginning of the 20th century. Nevertheless, this is not a natural recovery. The need to repopulate extensive areas of deforested land in Spain began in the 18th century, as a result of the inadequate use of the territory through recurrent cycles of grazing-fire, stimulated by the policy of La Mesta (since the 13th century) which promoted deforestation for the creation of crop fields and pastures. This was aggravated by the liberal agrarian reform (1836) due to the demand of the growing population, the increase in the price of cereals and the incipient industrialization. All this led to a transfer process where public-owned mountains fell into the hands of private owners. Parallel to this process, the first ordinances began to be published with the aim of protecting forests and plantations, but they did not succeed due to the lack of political and social support. In 1833 the General Directorate of Forestry was created within the Spanish Ministry of Development thanks to the gradual awareness of the population. In the mid-19th century, the Spanish Forestry Administration was created and the first Forestry Districts appeared. Implementation of the first Forestry Law in 1863 and its Regulations in 1865 meant that, for the first time, a firm base to organize and restore the forestry sector in Spain was established (Permán-García et al., 2017).

Within this legislative framework, public and private reforestation began in 1877 thanks to the “Ley de Bosques” (1863), although its results were very limited (Valbuena-Carabaña et al., 2010). Even so, exotic species such as *Pinus radiata* and *Eucalytus* sp. were already being introduced. The main problem of these plantations and reforestation is the balance between environmental responsibility and economic profitability. This has been always a problem in Spain, where the economic interest was the only one to be prioritized. On the Cantabrian Coast, priority was given to reforestation with allochthonous tree species such as *Pinus pinaster*, *Pinus radiata* and *Eucalyptus* sp. as opposed to native taxa such as *Quercus*. This effect was exacerbated, above all, by the implementation of the "Plan Nacional de Repoblaciones” of 1940. Reforestation of *Pinus pinaster* in the north of the Iberian

Peninsula had a clear productive objective and was carried out at densities above 2000 ha$^{-1}$ (Vadell et al., 2017). Pine silviculture in regular forests and under plantation conditions has been characterized by the maintenance of high densities and the use of their highest productive capacity (Fig. D.21). It was during the second stage of the PNR (1960 - 1971) when priority was given to fast-growing species such as *Pinus radiata* and *Eucalyptus* sp. with a clear productive objective.

Taking into account the chronology of the short cores, this expansion of pine forests through human repopulations is clearly reflected in these pollen records from the estuaries on the eastern Cantabrian coast. The pine forests usually have a turn of 30-40 years, and in the sedimentary records studied in this doctoral thesis, maximum peaks of these taxa are observed at the end of the 20th century. Therefore, maximum pollen abundances detected correspond to those times when pollen production and arboreal development of these repopulated pines reached maturity during those years.

*Eucalyptus* sp. was introduced in reforestation to satisfy the demand for cellulose. Pines brought with them some specific problems, such as their high susceptibility to fire (Guijarro et al., 2017), which favor their replacement by *Eucalyptus* sp. This process occurred mainly in coastal areas because of the dominant mild temperatures that allowed rapid growth, and the regeneration capacity of this taxon after fires (Vega, 2003).

However, eucalyptus reforestation also generated environmental problems. Recent studies argue that the soils occupied by eucalyptus plantations experience an impermeability that slows the growth of other plant species and reduces the diversity of insects and fungi (Veiras & Soto, 2011; Permán-García, et al., 2017). Since 1990, eucalyptus plantations in the Basque Country have multiplied to occupy 2.6% of the total territory at present. This expansion is due to the use of its wood for the paper industry. Despite this abundance, low pollination makes its presence in the sediments very limited. Even so, *Eucalyptus* sp. has been identified in the sedimentary records analysed in this work and, therefore, it has become part of the paleontological record of human impact during the Anthropocene (Martin de Agar et al., 1992; Espinel et al., 1995; Duñabeitia et al., 2004; Loidi et al., 2011; Veiras & Soto, 2011 Soto-Caba, 2013; Permán-García et al., 2017; Williams et al., 2022).

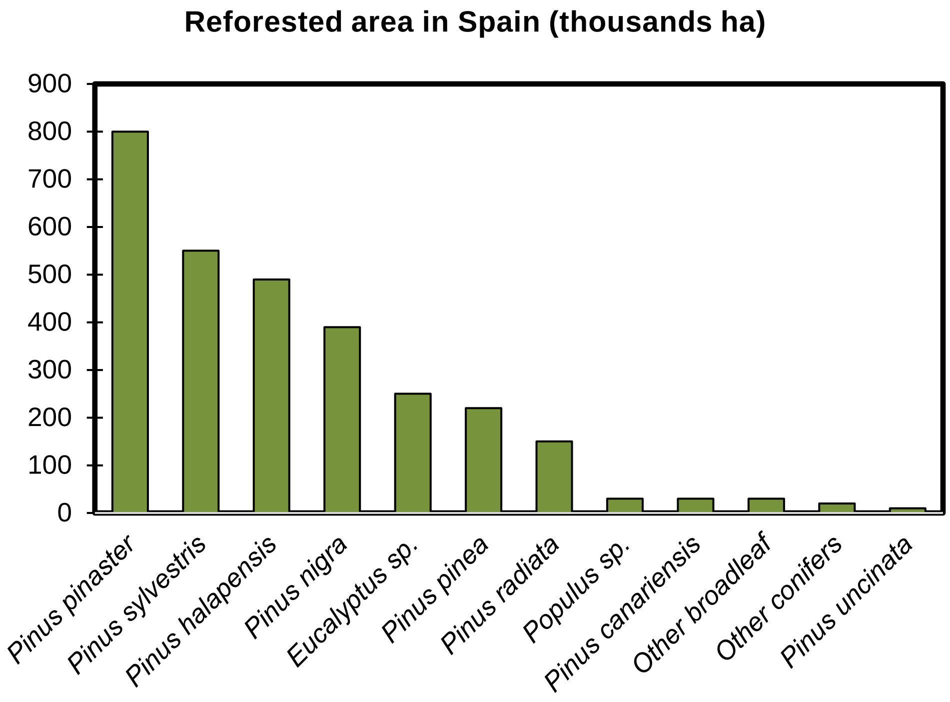


**Figure D.21 -** Different arboreal species used for historical reforestation in Spain between 1940 and 1984. Modified from Permán-García et al. (2017). Source: Memorias del Patrimonio Forestal del Estado, Dirección General de Bosques, Caza y Pesca Fluvial y el Instituto Nacional para la Conservación de la Naturaleza.

Finally, the possibility that the increase in the percentages of grasses found in recent sediments was due to the expansion of the invasive plant *Cortaderia selloana* has been already mentioned. *Cortaderia selloana* is a perennial cespitose grass, which forms clumps up to 3 or 4 m high and has long leaves up to 2 cm wide and 1.8 m long. Its flowers are arranged in spikelets of about 20 mm in length and are silver or slightly pink in color. Each flower can produce thousands of seeds per reproductive cycle and those seeds present long hairs that facilitate their wind dispersal over long distances. All this makes *Cortaderia selloana* a highly dispersive invader that, in addition, once it reaches maturity grows very fast and occupies a large area. This is crucial in its colonization and invasion process, since the clump arrangement hinders and prevents the settlement of native herbaceous and woody species (Campos et al., 2004; Herrera & Campos, 2006; Domènech et al., 2005; Domènech & Vilà, 2008; MITECO, 2018; Cires et al., 2022).

*Cortaderia selloana* tolerates both drought and waterlogged conditions in poor soils with little substrate, enduring even some salinity in the soil and surrounding waters. These low environmental requirements allow this taxon to be one of the first species to colonize and establish in degraded environments, such as disturbed land where the original vegetation cover has been removed, or areas where infrastructure has been built but organic soil remains available, such as roadsides, industrial land and railroad tracks (MITECO, 2018). It is a taxon originally from South America that was introduced to Europe as an ornamental plant at the beginning of the 19th century. Its highly invasive nature allows it not only to occupy degraded land but also other spaces of natural value (Fig. D.22). In addition, biodiversity and forage quality of pastures reduce greatly with its presence. Another important risk factor is that it produces large quantities of flammable material (Campos et al., 2004; Domènech et al., 2005; Herrera & Campos, 2006; Domènech & Vilà, 2008; GISD, 2018; MITECO, 2018; Pardo-Primoy & Fagúndez, 2019; Cires et al., 2022).

The recent increase in the percentages of grass pollen along the short cores analyzed here could be explained by the expansion of this invasive taxon. Estuarine and riparian areas are among the most effectively colonized by *Cortaderia selloana*, so it is congruent that part of this increase could be due to the germination of this species. However, it is hard to be sure as, being a Poaceae, pollen grains within this group are very difficult to distinguish taxonomically.

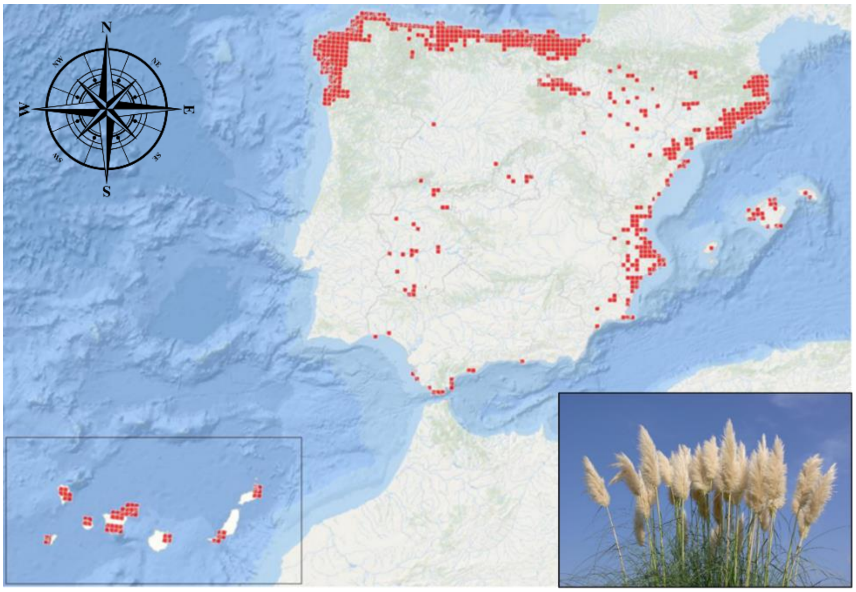


**Figure D.22 -** Distribution of the allochthonous *Cortaderia* sp. in Spain showing its great concentration on the Cantabrian coastal area, in UTM grids of 10x10 km. Source: Ministerio para la Transición Ecológica y el Reto Demográfico (MITECO) (2018).

# Conclusions

# Conclusions

The results presented in this doctoral thesis contribute to a better understanding of the evolution of vegetation cover along the eastern Cantabrian coast from the Pleistocene to the Anthropocene. This has been possible through the study of ten boreholes and cores in the Saja-Besaya, Oka and Urola estuaries as well as the marine Basque Mud Patch (BMP) and an ancient karst lake in Liendo. Through the paleopalynological study supported by radiocarbon and radioisotope dating of $^{210}$Pb and $^{137}$Cs, we can chronologically frame and characterize the change events that have occurred to the vegetation cover in coastal ecosystems.

The paleopalynological study presented here has shown that the Cantabrian Coast has been affected by both natural and anthropogenic alteration processes. This general conclusion is based on a series of particular observations that are presented as follows:

1. During the Pleistocene, in the areas near the coast, the changes observed in the plant associations indicate quite acute climate oscillations through the alternation in the dominance of arboreal and herbaceous vegetation. In the case of Liendo borehole, these changes in vegetation could be due to the climate oscillations during MIS 3. Firstly, we detect the appearance and predominance of taxa such as *Artemisia*, Cichorioideae, *Calluna* type, *Abies alba* and *Pinus sylvestris*, which would correspond to very cold and dry conditions (Heinrich/H-E events). Secondly, we observe the recovery of arboreal vegetation following the climate amelioration, leading to the expansion of taxa such as deciduous *Quercus*, *Fagus sylvatica*, *Betula* and *Pinus pinaster*. This may be associated with periods of rapid warming, known as Dansgaard-Oeschger (D-O) events.

2. In the Holocene epoch, our data obtained from Requejada, Anbeko, San Kristobal and Ozollo boreholes show an increase in arboreal vegetation, especially of deciduous-mixed forest type and typical riverside taxa (e.g. *Alnus*, *Ulmus*, *Populus*, marsh taxa such as Cichorioideae, Chenopodiaceae, Poaceae and hydro-hygrophilous taxa). These changes may correspond to the beginning of the Holocene Climatic Optimum, in which the higher temperatures produced a progressive rise in sea level, resulting in the formation of the modern estuaries.

3. Our sedimentary records with data from the Holocene register the so-called Holocene Expansion of *Fagus sylvatica* (beech), which has also been widely recorded in other regional records.

4. In the Holocene boreholes, we also observe the first traces of human activity and anthropogenic dynamics, particularly the presence of *Cerealia* type taxa and *Sordaria* sp., a non-pollen microfossil (NPP) indicative of pastoral activity.

5. In Anbeko, San Kristobal, Requejada and Ozollo boreholes, our data from the Middle Ages and onwards show that herbaceous plants appear as the dominant vegetation group, although in equal proportion to arboreal taxa in some cases. This is accompanied by the appearance of typical marsh vegetation together with cereal pollen and NPPs indicative of fire, erosion and grazing. All these data together may indicate systematic deforestation processes to create open fields for pastoral and arable farming, which would have been important human activities in the areas near the estuaries.

6. The dynamics of successive increases and decreases in the percentages of tree pollen observed in the Miengo, Axpe, Zumaia and KI03-KI06 cores since the 19th century would respond to the arrival of industrialization. An increase in forest vegetation has been observed in these cores, which seems to indicate an arboreal recovery of these spaces to the detriment of herbaceous vegetation. This growth of forests is linked to the plantations that began to take place at the end of the 19th century. Industrialization process would cause an increasing demand for timber resources, which led to a greater exploitation of forests. In turn, a greater interest in reforestation arose to continue exploiting these resources. This repopulating process would be responsible to a certain degree for the tree recovery observed in the studied cores.

7. In Miengo, Zumaia and Axpe, the increase in *Pinus pinaster*, especially after the 1940s, was due to the entry into force of the "Plan Nacional de Repoblaciones" (National Reforestation Plan). This plan gave priority to taxa such as *Pinus pinaster* over the typically autochthonous (deciduous *Quercus*).

8. However, the identification of high percentages of *Pinus pinaster* may be the result of the National Plan of the 1940s to promote reforestation with allochthonous taxa such as *Pinus radiata*, which is difficult to differentiate taxonomically from its type taxon (*Pinus pinaster*).

9. The record of *Eucalyptus* sp. (allochthonous taxon) in our sedimentary cores would be a consequence of the plantations carried out with this taxon, especially from the 20th century onwards.

10. The increased presence of *Pinus pinaster* and the presence of *Eucalyptus* sp. in the Anthropocene sedimentary records respond to economic purposes. These taxa have shorter logging shifts and faster growth than the autochthonous species on the Cantabrian Coast.

11. The increase in allochthonous taxa or the favoring of others with faster growth rates means the loss of territory for the autochthonous species of the Cantabrian Coast and, therefore, directly affects the characteristic deciduous-mixed type of forest.

12. The presence of high percentage values of Poaceae sp., especially from the 20th century onwards, could be due to the introduction of *Cortaderia seollana*. The degradation of coastal environments after industrialization led to the uncontrolled expansion of species introduced for purely ornamental interest, such as this Poaceae, whose invasive capacity has become one of the most important ecological problems in the Iberian Peninsula today.

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