# Vegetation-(Bio-)diversity by Pollen analysis: A comparative Approach Across the Central and Southern Balkan Regions

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# Abbreviations

| | |
|---|---|
| Anth-Indic | Anthropogenic Indicators |
| AP/NAP | Arboreal and Non arboreal |
| BCE | Before the Common Era |
| CE | Common Era |
| EH | Early Holocene |
| Far | Farming Indicators |
| FInVeg | Fire Induced Vegetation |
| IRSL | Infrared stimulated Luminescence dating |
| KOH | Potassium Hydroxide |
| LG | Last Glacial |
| LGM | Last Glacial Maximum |
| LV | Local Vegetation |
| LSA | Late Stone Age |
| MDecBro | Mixed Deciduous Broadleaved |
| MPZ | Mohoş Pollen Zone |
| MPinMaq | Mediterranean Pine woodlands, Maquis |
| MTDs | Mass Transport Deposits |
| NE | North Eastern |
| NMDS | Non-metric multidimensional scaling |
| PEas | Pollen-Equivalent assemblages |
| PROTEST | Procrustes statistic |
| PTas | Pollen Type assemblages |
| PAZ | Pollen Assemblage zones |
| RSAP | Relevant source area of pollen |
| SD | Standard Deviation |
| SDMs | Species distribution models |
| SZA | St. Ana pollen zones |
| YD | Younger Dryas |

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# I Introduction

## 1.1 Biodiversity

Biodiversity is defined as “the variety of life, encompassing variation at all levels, from the genes within a species to biologically created habitat within ecosystems” (Duffy et al. 2013). Biodiversity is considered to be the backbone of any ecosystem to function smoothly and seamlessly (Cardinale et al. 2012). The field of biodiversity is particularly attractive for conservation biologists and ecologists because of its significant role in maintaining the stability, productivity, and functioning of an ecosystem. The factors that influence biodiversity include climate, heterogeneity of habitats, predation and competition, and availability of energy sources (Currie et al. 2004). However, the exact mechanisms by which these factors influence biodiversity in a region are unclear and the underlying causes for the ever-changing biodiversity are unknown. Efforts have been made to obtain information from plant and animal fossils regarding biodiversity in the past; however, these have failed to provide contiguous, clear, and precise information (Benton 2000).

An ecosystem is largely influenced by the diversity of species pertaining in it, especially for shorter timescales. In case of larger timescales and ecosystems that do not change over time, it is difficult to assess the impact of biodiversity on the characteristic features of the ecosystem. In such scenarios, analysis of pollen provides a comprehensive investigation tool to study the different types of vegetation in a region and relate that to the surrounding ecosystem (Matthias et al. 2015). Fossil pollen obtained from sediment samples can provide valuable insights regarding plant species diversity, and studies have analyzed both pollen number as well as species in available samples (Bush and Colinvaux 1990).

## 1.2 Use of Pollen to study Biodiversity

Pollen analysis is a valuable tool for studying biodiversity. It involves examining differences in pollen production and dispersal among plant species, which can lead to variations in species abundance in both vegetation and pollen samples. When interpreting pollen data as percentages, it's essential to consider that a decline in one taxon may correspond to an increase in others, though these changes may not accurately reflect shifts in the actual vegetation (Srivastava et al. 2021). Moreover, over time, the composition of pollen in samples can change, and statistical analysis of these variations can provide insights into environmental changes (Birks and Line 1992).

For example, a higher number of pollen types in a sample may indicate long-standing human use of the land for cultivating various plants and crops. The concentration of pollen from autogamous cereal species in waste heaps near human settlements is well-documented in studies such as Trobls-Smith (1955), Welten (1967), and Schütrumpf (1968), particularly in the vicinity of Neolithic lake-shore dwellings. Within the habitation site at Brugäschisee-sud, cereal pollen reached 114%, while only 0.8% was recorded in a contemporaneous sample taken just outside the settlement (Welten 1967).

Similar fluctuations were noted by Schutrumpf (1968), with cereal pollen concentrations varying significantly between different cultural layers at the Ehrenstein excavation, emphasizing the historical patterns of cereal cultivation. It could also indicate recent changes in the landscape, high floristic richness especially where flowering plants lack species diversity, and presence of higher taxa of plant types in the region (Mazaris et al. 2010). Diversity indices have also been formulated based on two important characteristic features of pollen – richness and abundance.

Reitalu et. al. (2019) confirm that pollen data can provide valuable insights into past changes in plant richness in northern Europe. By carefully considering pollen-production differences and the spatial scale represented, researchers can use pollen data to investigate vegetation diversity trends over extended periods, even in the face of changing climatic and habitat conditions. Notably, the highest correlations are observed between pollen data and the richness of trees and shrubs, as well as wind-pollinated taxa (Reitalu et al. 2019). The significance of these correlations varies depending on the region under investigation and the diversity of the studied vegetation.

Various indices are available for assessing the significance of pollen richness and abundance, tailored to the region and the diversity of the vegetation being examined. Among the commonly used indices are the Shannon-Wiener index, Simpson's diversity index, Margalef's richness index, Menhinick's richness index, Pielou's evenness index, and Berger-Parker dominance index (Birks & Birks, 1980). In addition to these general indices, there are specialized measures for pollen richness and abundance analysis. For instance, the Pollen Richness Index quantifies the number of different pollen types in an assemblage, while the Pollen Abundance Index quantifies the total amount of pollen within an assemblage. Other factors that might influence the formulation of these diversity indices include productivity of pollen, ability of pollen to get dispersed easily, and accumulation rate in sediments, as these factors can introduce biases in species representation and abundance (Birks & Birks, 1980).

It is well established that plant richness in Europe follows the major temperature gradient (Whittaker et al. 2007). However, pollen richness can be influenced by temperature in two ways: indirectly through its impact on plant richness and directly through its effect on pollen production. Landscape diversity and openness are known to influence plant diversity (Reitalu et al. 2014), and these factors also directly affect pollen dispersal patterns (Odgaard, 1999). For instance, open areas tend to have a larger pollen-source area, leading to higher richness estimates due to the broader 'sampling' area (Sugita et al. 1999). In mountainous regions at high elevations, pollen has been observed to be transported from the lowlands (Bajpai & Kar, 2018), which may have implications for the relationship between pollen and plant richness.

Despite these complexities, the combination of pollen data and species diversity can yield valuable insights into the past vegetation of a region (Purvis and Hector 2000). For example, when pollen analysis indicates a high abundance of pollen grains from a particular plant species in a region at a specific time in the past, yet the current species

diversity in that region is low, it suggests a decline in species diversity over time. This decline may be attributed to factors such as climate change, habitat loss, or other environmental influences.

### 1.3 Use of Pollen to study Climate

The geographical distribution of various vegetation types is intricately shaped by a host of environmental factors. Scientists and ecologists employ multiple indicators to comprehend and categorize these vegetation types based on their specific geographical settings. One of the most natural influential determinants of the geographical distribution of vegetation, alongside soil type, water availability, and topography, is climate. This is because each plant species possesses unique requirements and tolerances for a range of climatic factors, including extreme temperatures, precipitation, humidity and sunlight. Temperature, as a fundamental climatic element, exerts a profound influence on plant distribution. It not only dictates the freezing tolerance of plants but also defines their optimal growth conditions. Consequently, tropical vegetation thrives in warmth and adapts differently to colder climates (Nievola et al., 2017). The patterns of precipitation play a pivotal role in shaping plant ecosystems. High levels of rainfall nurture lush forests, while arid regions give rise to deserts and grasslands, thus underscoring the direct influence of water availability on plant distribution (Zhang et al., 2023). Humidity levels in an environment exert a significant influence on transpiration rates and lead to adaptive changes in leaf characteristics. In humid regions, plants tend to have broad leaves, while arid areas foster water-conserving features (Qaderi et al., 2019). Sunlight intensity and day length are influential factors that determine the types of vegetation that flourish in a given area. These elements govern whether shade-loving plants dominate forest understories or sun-loving species predominate in open landscapes (Dormann et al., 2020). Altitude introduces temperature variations, resulting in the creation of distinct altitudinal zones on mountains, thus supporting specific plant communities at different elevations (Måsviken et al., 2020).

Given the undeniable influence of climatic changes in the past on the growth and distribution of terrestrial plants, comprehensive analyses of these changes are possible by delving into fossil pollen records. These records, primarily sourced from peat bogs, lake sediments, and middens, provide a deep understanding of historical and pre-historical plant distribution. However, it's crucial to acknowledge that the reliability of fossil pollen records may not always be foolproof. This is because the formation, dispersion, and preservation of pollen can vary significantly between different plant species (Chevalier et al. 2020). To enhance the clarity of the relationship between climatic variations and plant distribution, one approach involves the reconstruction of information from modern pollen, which can then be correlated with contemporary climatic variations. The insights gained from this method can be extrapolated to interpret fossil pollen records (Brewer et al. 2013; Guiot et al., 1993, Schäbitz et al. 2013).

Modern pollen analogs have played a pivotal role in paleoecological reconstructions, with paleo-records being calibrated using the relationship between pollen trap data and vegetation (Huntley et al. 2011). These quantitative studies have allowed for accurate relationships to be drawn between pollen, altitudes, and climatic conditions for the examination of regional vegetation. For instance, in tropical regions like Africa, extensive pollen-rain studies have been conducted to differentiate vegetation types along latitudinal and altitudinal gradients (Watrin et al. 2007). The results of such studies have highlighted the unique nature of pollen spectra within specific vegetation zones, distinct from spectra obtained from other zones. This suggests that pollen spectra are characteristic of individual vegetation zones, and reconstructing vegetation profiles in one region may not provide insights into vegetation profiles in other global regions (Gajewski et al. 2002).

### 1.4 Challenges in using Pollen to understand Biodiversity

In an ideal scenario, the comprehensive detection and accurate identification of all pollen varieties would provide a direct and reliable indication of plant diversity within a region (Weng et al. 2006). However, utilizing pollen to gain insights into and analyze regional vegetation presents numerous challenges. Taxonomically, the precise classification of plant types remains a hurdle, complicating our understanding of species diversity in specific areas. Moreover, pollen from distinct plant species exhibits variations in formation and dispersal, rendering results from one plant species inapplicable to others (Giesecke et al. 2014).

The diversity of pollen does not consistently correlate with plant diversity due to several factors. Firstly, not all species of pollen have been meticulously documented. Additionally, many plants belonging to the entomophilous taxa, which rely on animal vectors for pollen transport, remain "silent" in pollen spectra. This means that they are underrepresented, as their relatively large and heavy pollen grains are less likely to be wind-dispersed over long distances. Furthermore, these plants produce sticky or clumped pollen that adheres to visiting insects, making them predominantly prevalent in sites of close proximity, such as forest-hollows, but virtually absent in lake sediments. As a consequence, pollen diversity may either overemphasize or underestimate plant diversity, necessitating a comprehensive understanding of these challenges to accurately interpret pollen spectra (Faegri and Iversen 1989).

## 2 Modern Pollen Analysis

In the field of paleoecology, the study of fossil pollen and spores is instrumental in unraveling plant biodiversity and vegetation changes driven by climatic variations in a given region. To harness the full potential of fossil pollen, it's imperative to grasp how accurately it reflects the diversity of plant species.

Modern pollen analysis employs contemporary analog techniques, involving a comparative examination between fossil pollen samples and their modern counterparts. This approach helps us trace changes in landscapes, climates, and vegetation over time (Barboni et al. 2004). Additionally, it provides valuable insights into the productivity of pollen from different plant species, enriching our interpretation of fossil pollen spectra (Soepboer et al. 2007). It also empowers scientists to reconstruct past environments and ecosystems by scrutinizing pollen assemblages. Furthermore, it is widely employed to deepen our understanding of pollen productivity among various species or plant communities, a vital aid in the interpretation of fossil pollen spectra (Newsome, 1999).

## 2.1 Importance of Modern Pollen Analysis for understanding Pollen Vegetation Relationship

Until recently, fossil pollen samples were used to reconstruct mainly Quarternary environments, understand the distribution patterns of past vegetation, and consequentially gain insights into past climatic variations. However, it has become increasingly apparent that modern pollen analysis is essential to interpret the results of fossil pollen analysis by analyzing the composition of modern pollen-rain samples. Today, ecologists compare fossil pollen data with pollen data acquired from local vegetation in order to understand the growth patterns of vegetation in the past. The investigations may be either qualitative or quantitative or both, and variations in pollen spectra are used to draw conclusions regarding variations of vegetation diversity in the past (Jackson et al. 1995).

An important reason for studying pollen-vegetation relationships is to predict future changes in vegetation in response to climatic variations. Modern pollen analysis helps ecologists develop vegetation-climate models that can be compared with known data and used for predictions of future vegetation distribution (Ni et al. 2000). Despite the fact that fossil pollen records provide direct correlation with past vegetation distribution patterns, modern pollen analysis helps in accurate interpretation of fossil pollen data. Not only this, but analysis of modern pollen samples helps extrapolate data to a continental level and shorter or longer time ranges. Several studies have reported the use of modern pollen analysis for large-scale reconstructions of past vegetation (Marchant et al. 2001; Paez et al. 2001).

## 2.2 Representation of Human impact activities in Pollen Spectra

Pollen analysis, a vital field of palynology, offers a detailed record of human impacts on Earth's ecosystems. By scrutinizing these minuscule particles, scientists can decipher meaningful patterns that reflect human interactions with the environment. For example, when people engage in agricultural activities, specific imprints appear in the pollen spectra. Grains and cultivated plant pollen reveal farming practices, while the presence of weed pollen indicates agricultural activities and land cultivation (Alenius et al., 2020). The process of deforestation and land clearance leaves its mark as well. It results in a decrease in tree pollen and an increase in herbaceous plant pollen, signaling the

transformation of forests into farmlands or urban areas. Meanwhile, globalisation and industrialization introduce new species, and industrial pollutants change the local plant composition, all of which become evident through shifts in pollen spectra (Ortiz et al., 2021).

Moreover, various cultural and agricultural practices, such as shifting cultivation or terraced farming, leave distinctive signatures. Invasive species and human-mediated plant movements also leave their mark through the introduction of non-native plant pollen (Hall et al., 2013). Pollen spectra can even unveil shifts in crop types due to climate change and human responses to these environmental transformations. These subtle changes in pollen composition provide invaluable insights into the intricate interplay between human societies and natural ecosystems, offering a glimpse into the complex environmental history of a region. Because of the profound and widespread impacts of destructive human activities on local ecosystems, it has become crucial to comprehend the extent of these impacts across various temporal and spatial scales.

Investigations of this kind are instrumental in understanding the ecological hierarchy, ecosystems, and their evolution under human influence (Franco-Gaviria et al., 2018). Pollen analysis is a key method for exploring the intricate relationship between humans and the environment, enabling scientists to reconstruct ancient vegetation patterns and uncover historical land use, agricultural practices, and deforestation. By studying pollen spectra preserved in sedimentary layers, researchers gain insights into past plant distributions and their transformation over time.

This paleoecological perspective, combined with contemporary observations of plant growth patterns, provides a comprehensive understanding of how human activities have shaped the natural world. Pollen analysis also reveals cultivated plants, shedding light on the evolution of farming, domestication, and their impact on landscapes. Declines in tree pollen and increases in herbaceous pollen during certain periods indicate large-scale deforestation, emphasizing significant human intervention. These findings, aligned with current observations of reduced forests and shifting vegetation, underscore the lasting consequences of human-induced environmental changes (Delcourt and Delcourt, 1991).

## 3 Comparison of vegetation diversity in Last Glacial Maximum and Holocene

The time span encompassing the Last Glacial Maximum (LGM), occurring around 20,000 years ago, and the early Holocene, approximately 11,700 years ago, signifies a pivotal phase in Earth's climatic and environmental evolution. This period of rapid and extensive climate variations, often referred to as deglaciation, initiated the transformation from glacial to interglacial conditions, leaving a profound imprint on the planet's physical and ecological landscape (Jones et al. 2017). Given that this represented the most recent major natural climatic shift experienced by the Earth, comprehending these climatic transitions and their impacts on biodiversity is crucial for comprehending our present circumstances and anticipating forthcoming alterations to the landscape (Orombelli and Ravazzi 1996),

especially considering human activities' significant role in the contemporary environment.

Biodiversity is consistently influenced by changes in both global and regional climatic conditions, and numerous patterns in vegetation distribution have emerged as responses to these climatic transformations over time (Svenning et al. 2015).

### 3.1 The Last Glacial Period

Approximately 20,000 years ago, during the coldest phase of the last glacial period known as the Last Glacial Maximum (LGM), the Earth experienced a significant cooling event lasting about 2,000 years. This period was characterized by globally similar climatic conditions and extensive ice coverage on the planet. Carbon dioxide concentrations in the atmosphere were notably low, and aridity was at its peak (Ray and Adams 2001). These conditions were consistent with findings in tropical regions (Schäbitz et. al. 2021).

The frigid temperatures and the vast ice sheets had a profound impact on the distribution of plant life. During the LGM, a substantial portion of the Earth's surface was covered by tundra, featuring low-growing plant species adapted to the cold and harsh environmental conditions. Fossil pollen analysis of samples collected from various regions in Europe during this period revealed a prevalence of steppe tundra, shrub tundra, and polar deserts. In regions where forests were present, they existed in small pockets located in relatively sheltered areas. Coniferous tree species such as spruce and pine demonstrated better adaptability to the cold climate and therefore dominated the limited forested regions. Analysis of pollen samples from central and southern Europe indicated the presence of coniferous trees and open park tundra. Meanwhile, pollen samples from the Mediterranean region showed evidence of deciduous woodlands. In general, deciduous trees were primarily confined to forested areas, mostly concentrated in the southern and southeastern regions of Europe (Birks and Willis 2008).

### 3.2 The Holocene

The Holocene, the current geological period, represents a pivotal period in Earth's history, characterized by significant climatic and environmental changes. This chapter delves into the dynamic relationship between climate and vegetation in the context of the European Holocene, drawing upon a range of scientific studies and findings.

The Holocene has witnessed variations in climate, from the early post-glacial warming to the subsequent Holocene Climatic Optimum (HCO). This climatic variability has profoundly influenced vegetation patterns across Europe. According to Wanner et al. (2008), the HCO, which occurred around 9,000 to 5,000 years ago, was a period of elevated temperatures, leading to the expansion of forests and a shift in vegetation composition. During the HCO, oak and beech trees became dominant in many parts of Europe (Davis, 2003).

The influence of climate on vegetation dynamics is a central theme in the study of the

Holocene. Pausas et al. (2015) emphasize that temperature and precipitation changes during the Holocene have driven shifts in plant species composition and distribution.

The warming temperatures of the HCO were associated with the spread of temperate deciduous forests across Europe, while cooler, moister conditions during the Neoglacial period led to a resurgence of coniferous forests (Birks and Birks, 2000).

In this period, the interaction between climate and vegetation was further compounded by human activities. The transition from hunter-gatherer societies to agricultural communities had a profound impact on land use and vegetation patterns. The establishment of Neolithic farming communities in Europe introduced crops and domesticated animals, altering the landscape and vegetation. According to Roberts (2007), the spread of agriculture influenced the prevalence of certain plant species and led to the cultivation of crop plants, such as wheat, barley, and flax.

The era also coincided with the emergence of early European civilizations. The climate of this period played a significant role in shaping human societies and cultures. The Mediterranean region, for instance, experienced Mediterranean climate conditions that influenced agricultural practices and the development of ancient civilizations like the Minoans and Mycenaeans (Finné et al., 2011).
In the later part of the Holocene, the impact of human activities on the climate and environment began to intensify. The modern era has witnessed unprecedented changes in climate due to factors like industrialization, deforestation, and increased greenhouse gas emissions. These changes have raised concerns about global warming and its implications for vegetation and ecosystems in Europe and beyond (IPCC, 2018).

### 3.3 Short Term climatic conditions covering late LGM and Holocene

Between the LGM and the Holocene, Europe experienced a series of shorter-term climatic changes, each leaving distinctive imprints on landscapes and ecosystems (Roberts et al., 2018). These variations offer valuable insights into the region's dynamic climate during this transition (Ebbesen et al., 2007). Key fluctuations include:

**Older Dryas (~15,000 BP)**: A brief cold period during the LGM deglaciation, characterized by a return to colder and drier conditions, which delayed the northward expansion of vegetation and influenced species distribution patterns.

**Bølling-Allerød (14,700–12,700 BP)**: A relatively warm, moist interval marked by a 5°C temperature increase compared to the LGM, enabling forests and grasslands to expand northward.

**Younger Dryas (12,700–11,700 BP)**: An abrupt return to cold and arid conditions, with temperatures dropping by as much as 10°C. This period caused significant ecological disruptions, forcing plant and human communities to retreat southward (Lotter et al., 2000).

**Preboreal (11,700–9,700 BP)**: Gradual warming (5°C increase) facilitated the re-expansion of forests and human recolonization of northern Europe.

**Boreal (9,700–7,700 BP)**: Relatively warm, dry conditions with a 2°C temperature rise compared to the Preboreal supported forest growth and the beginnings of agriculture.

**Atlantic (7,700–5,500 BP)**: The warmest and wettest Holocene phase, with a 1°C temperature increase compared to the Boreal. Forests dominated the continent, and agriculture thrived.

**Subboreal (5,500–2,600 BP)**: Gradual cooling and drying trends led to forest retreat and challenges for agriculture.

**Subatlantic (2,600 BP–Present)**: Cooler and wetter conditions further reduced forests, prompting agricultural shifts toward cereal crops (Roberts et al., 2018).

These shorter-term climatic fluctuations reveal the intricate interplay between climate, vegetation, and human societies, offering critical insights into Europe's environmental responses during this pivotal transition (Davis, 2003). Understanding these dynamics provides valuable lessons for addressing contemporary climate challenges.

## 4. Conclusions

To achieve a clear and concise idea of all concepts discussed above, a comparative analysis between modern pollen and fossil pollen can give tremendous insights into the distribution patterns of vegetation in different parts of the world. These distribution patterns vary with changes in climatic conditions of our planet which in turn is impacted by human activities that cause harmful effects to the environment. As the past two decades have seen huge variations in temperature, the pattern of growth and migration of plant species has also undergone major alterations, some of them even going extinct. Studying the changes in plant distribution patterns of the past is significant as it can help us understand the underlying causes for which plant species become extinct and predict future changes in vegetation distribution in response to climatic changes. There are several limitations to pollen analysis, one of them being that it can only provide information about the taxa and not about the plant species. Despite these limitations, it is the best available method currently to study patterns of vegetation distribution and diversity and activities that impact these aspects.

## 5. Aim and Objectives of the Thesis

This thesis aims to comprehensively investigate the patterns of vegetation distribution and biodiversity in different Balkan regions and additionally focuses on the transitions between the Last Glacial period and the Holocene period. It encompasses modern pollen analysis, fossil pollen data, climatic variations, and the impacts of human activities on the

environment. By analyzing these factors, this Thesis aims to provide insights into the ecological and climatic history of various regions, forming the basis for understanding the dynamics of plant migration, speciation, and environmental change by answering the following scientific questions.

*Main Scientific Questions:*

Pollen Representation and Biodiversity:

- How accurately do pollen assemblages represent the composition of the surrounding vegetation in two different biogeographical regions of southeastern Europe?
- Can pollen assemblages effectively capture the diversity of plant species found in the nearby vegetation in these regions?
- To what extent can pollen data reveal ecological gradients and environmental characteristics of the surrounding vegetation?

Human-Landscape Interactions in Halkidiki, Greece:

- How have human activities influenced the landscape of Halkidiki in northern Greece over the past 3.5 millennia?
- What information can be derived from palynological (pollen) records about historical changes in vegetation and land use in the region?
- How do archaeological and historical archives complement the palynological data in understanding the long-term human-landscape interactions in Halkidiki?
- Can the integration of palynological, archaeological, and historical data provide insights into the sustainability and resilience of past human societies in this region?

Mohoş Peat Bog Investigation:

- How do the dense tephra and ash deposits in the sediment layers of the Mohoş peat bog affect our ability to access and understand the deeper layers of the bog's history?
- Can this investigation shed light on vegetation development in the region before the latest eruptions of the Ciomadul volcano, and does it have the potential to provide insights into the deeper past through comparison with data from the nearby St Ana lake sediment core?

## 6. Outline of the Thesis

This thesis is presented in six chapters. The focal points of each chapter are presented below.

In the *Chapter 1*, a general introduction and theoretical background about Pollen and its importance in studying the biodiversity. In addition, the objective and the design of the study are presented in this chapter.

*Chapter 2* focuses on the description of the study area. A brief description of geographical setting, geology of the area, review of regional recent climate, human settlement history, flora and fauna of the study sites are discussed to get an overall understanding of the nature and climatic conditions.

In *Chapter 3*, comparation of pollen assemblages from moss samples in two southeastern European forests with the surrounding vegetation to investigate their compositional similarity, the association between their diversity characteristics in both terms of richness and evenness, and the correspondence of the main ecological gradients that can be revealed by them is discussed.

*Chapter 4*, presents the palynological data and highlights the strong correlation to archaeological and historical sources mainly of the Sithonia peninsula and the NE parts of Halkidiki. An attempt is made to compare pollen signal of this coastal site with that of a marine core collected outside the coast of Athos.

In *Chapter 5*, 42 core sections of a continuous sequence, retrieved from the Mohoş peat bog (Sediment core MOH-1 and 2) using a hydraulic hammer piston corer, are presented and discussed with the aim of investigating vegetation development in a period prior to the latest eruptive events of Ciomadul volcano.

Lastly, *Chapter 6* states conclusion and a comprehensive overview of pollen-vegetation relationships and their significance in reconstructing past environmental dynamics and vegetation changes.

## 7. References

Alenius, T., Marquer, L., Molinari, C., Heikkilä, M., & Ojala, A. (2020). The environment they lived in: anthropogenic changes in local and regional vegetation composition in eastern Fennoscandia during the Neolithic. Vegetation History and Archaeobotany, 30(4), 489–506.

Barboni, D., Harrison, S.P., Bartlein, P.J., Jalut, G., New, M., Prentice, I.C., Werner, C., Brewer, S., Brewer, C., Friedlingstein, P., Harrison-Prentice, T.I., Inoue, J., Izumi, K., Marlon, J.R., Mooney, S., Monks, A., Mooney, H.A., Pälike, H., Tarasov, P., Valdes, P.J., Zhang, Y., & von Grafenstein, U. (2004). Modern pollen rain, vegetation, and climate relationships in the Mediterranean region. Plant Ecology, 163(2), 105-121.

Bajpai, R., & Kar, R. (2018). Modern pollen deposition in glacial settings in the Himalaya (India): Abundance of Pinus pollen and its significance. Palynology, 42, 475–482.

Benton, M.J. (2000). Biodiversity on land and in the sea. Geology, 28(11), 1023-1026.

Birks, H. J. B. & Birks, H. H. (1980). Quaternary palaeoecology. Edward Arnold, London.

Birks, H. H., & Birks, H. J. (2000). Future uses of pollen analysis must include plant macrofossils. Journal of Biogeography, 27(1), 31-35.

Birks, H. J. B., & Line, J. M. (1992). The use of rarefaction analysis for estimating palynological richness from Quaternary pollen-analytical data. Holocene, 2(1), 1-10.

Birks, H. J. B., & Willis, K. J. (2008). Alpines, trees, and refugia in Europe. Plant Ecology & Diversity, 1(2), 147-160.

Borzenkova, I., Zorita, E., Borisova, O., Kalniņa, L., Kisielienė, D., Koff, T., Kuznetsov, D., Lemdahl, G., Sapelko, T., Stančikaitė, M., & Subetto, D. (2015). Climate Change During the Holocene (Past 12,000 Years). Regional Climate Studies, 25–49.

Brewer S, Guiot J, Barboni D. (2013). Pollen methods and studies | use of pollen as climate proxies. In Encyclopedia of Quaternary Science, 2nd edn, SA Elias, CJ Mock (eds). Elsevier: Amsterdam; 805–815.

Bush, M.B., & Colinvaux, P.A. (1990). A 12,000-year pollen record from the Amazon lowlands, Ecuador. Vegetatio, 89(1), 25-32.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. Nature, 486(7401), 59-67.

Chevalier, M., Davis, B. A., Heiri, O., Seppä, H., Chase, B. M., Gajewski, K., Lacourse, T., Telford, R. J., Finsinger, W., Guiot, J., Kuhl, N., Maezumi, S. Y., Tipton, J. R., Carter, V. A., Brussel, T., Phelps, L. N., Dawson, A., Zanon, M., Vallé, F., Nolan C., Mauri A., de Vernal A., Izumi K., Holmstrom L., Marsicek J., Goring S., Sommer P.S., Chaput M., & Kupriyanov, D. (2020). Pollen-based climate reconstruction techniques

for late Quaternary studies. Earth-Science Reviews, 210, 103384.

Currie, D.J., G.G. Mittelbach, H.V. Cornell, R. Field, J.-F. Guegan, B.A. Hawkins, J.T. Kerr, T. Oberdorff, E. O'Brien, & J.R.G. Turner (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters, 7(12), 1121-1134.

Davis, M. B. (2003). The Holocene in the Eastern United States. In M. R. Waters & D. L. Keene (Eds.), Quaternary Geochronology, Methods and Applications (pp. 297 -318). Geological Society of America.

Delcourt, H. R., & Delcourt, P. A. (1991). Quaternary paleoecology of the southern Appalachian mountains. Springer Science & Business Media.

Dormann, C. F., Bagnara, M., Boch, S., Hinderling, J., Janeiro-Otero, A., Schäfer, D., Schall, P., & Hartig, F. (2020). Plant species richness increases with light availability, but not variability, in temperate forests understorey. BMC Ecology, 20(1).

Duffy, J. E., Amaral-Zettler, L. A., Fautin, D. G., Paulay, G., Rynearson, T. A., Sosik, H. M., & Stachowicz, J. J. (2013). Envisioning a Marine Biodiversity Observation Network. BioScience, 63(5), 350–361.

Ebbesen, H., Hald, M., & Eplet, T. H. (2007). Lateglacial and early Holocene climatic oscillations on the western Svalbard margin, European Arctic. Quaternary Science Reviews, 26(15–16), 1999–2011.

Franco-Gaviria, F., Sarmiento, A. M., Correa-Metrio, A., Díaz-Molina, O., & Restrepo, J. C. (2018). Ecological impacts of pre-Columbian and modern land use in the savannas of the Llanos de Mojos in the Bolivian Amazon. Journal of Quaternary Science, 33(4), 481-492.

Faegri, K., Iversen, J. (1989). Textbook of Pollen Analysis. John Wiley & Sons, Chichester. 328.

Finné, M., Holmgren, K., Sundqvist, H. S., Weiberg, E., Lindblom, M., Eriksson, O., and Jankovska, V. (2011). "Climate in the eastern Mediterranean, and adjacent regions, during the past 6000 years—a review." Journal of Archaeological Science, 38(12), 3153-3173.

Gajewski, K., Viau, A.E., Sawada, M.C., Atkinson, D.E., & Wilson, S.E. (2002). Modern pollen data from North America and Greenland for multi-scale paleoenvironmental applications. Quaternary Science Reviews, 21(4-6), 397-420.

Giesecke, T., Bennett, K. D., Birks, H. J., Bjune, A. E., Bozilova, E., Feurdean, A., Hickler, T., Finsinger, W., Froyd, C. A., Granoszewski, W., Grimm, E. C., Kuneš, P., Montoya, E., Rösch, M., Salonen, J. S., Stančikaitė, M., Tonkov, S., Veski, S. & Seppä, H. (2014). Potential bias in pollen-based plant diversity reconstructions. Global Ecology and Biogeography, 23(2), 229-238.

Giesecke, T., Brewer, S., Finsinger, W., Leydet, M., Bradshaw, R. H. W., & Thomas, P. A. (2019). Patterns and dynamics of European vegetation change over the last 15,000 years. Journal of Biogeography, 46(12), 2544-2556.

Giesecke, T., Wolters, S., van Leeuwen, J.F.N., van der Knaap, P.W.O., Leydet, M. & Brewer, S. (2019) Postglacial change of the floristic diversity gradient in Europe. 740 Nature Communications, 10, 5422.

Guiot, J., Harrison, S. P., & Prentice, I. C. (1993). Reconstruction of Holocene Precipitation Patterns in Europe Using Pollen and Lake-Level Data. Quaternary Research, 40(2), 139–149.

Hall, S. J., Trujillo, J., Nakase, D., Strawhacker, C., Kruse-Peeples, M., Schaafsma, H., & Briggs, J. (2013). Legacies of Prehistoric Agricultural Practices Within Plant and Soil Properties Across an Arid Ecosystem. Ecosystems, 16(7), 1273–1293.

Huntley, B., Birks, H. J., Bozilova, E., Chambers, F. M., Daniëls, F. J., Finsinger, W., Kühl, N., Poska, A., van der Knaap, W. O., Valsecchi, V., Ammann, B., van Leeuwen, J. F., Lotter, A. F., Marchant, R., Tinner, W., & Verhoeven, K. (2011). European vegetation history - state of the art. Quaternary Science Reviews, 30(17-18), 2019-2036.

IPCC. (2018). Global warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change.

Jackson, S. T., Webb, R. S., Anderson, K. H., Overpeck, J. T., & Webb III, T. (1995). Vegetation and environment in Eastern North America during the Last Glacial Maximum. Quaternary Science Reviews, 14(8), 723-749.

Jones, R. A., Williams, J. W., & Jackson, S. T. (2017). Vegetation history since the last glacial maximum in the Ozark highlands (USA): A new record from Cupola Pond, Missouri. Quaternary Science Reviews, 170, 174–187.

Lotter, A., Birks, H., Eicher, U., Hofmann, W., Schwander, J., & Wick, L. (2000). Younger Dryas and Allerød summer temperatures at Gerzensee (Switzerland) inferred from fossil pollen and cladoceran assemblages. Palaeogeography, Palaeoclimatology, Palaeoecology, 159(3–4), 349–361.

Marchant, R., Cleef, A., Harrison, S. P., Hooghiemstra, H., Markgraf, V., van Boxel, J., Ager, T., Almeida, L., Anderson, R., Baied, C., Behling, H., Berrio, J. C., Burbridge, R., Björck, S., Byrne, R., Bush, M., Duivenvoorden, J., Flenley, J., De Oliveira, P., van Geel, B., Graf, K., Gosling, W. D., Harbele, S., van der Hammen, T., Hansen, B., Horn, S., Kuhry, P., Ledru, M.-P., Mayle, F., Leyden, B., Lozano-García, S., Melief, A. M., Moreno, P., Moar, N. T., Prieto, A., van Reenen, G., Salgado-Labouriau, M., Schäbitz, F., Schreve-Brinkman, E. J., & Wille, M. (2001). Pollen-based biome reconstructions for Latin America at 0, 6000 and 18,000 radiocarbon years ago. Climate Dynamics, 17(7-8), 725-739.

Matthias, I., Gilbert, M. T. P., & Bunting, M. J. (2015). The use of pollen analysis to investigate biodiversity. Ecology, 96(1), 86-97.

Måsviken, J., Dalerum, F., & Cousins, S. A. O. (2020). Contrasting altitudinal variation of alpine plant communities along the Swedish mountains. Ecology and Evolution, 10(11), 4838–4853.

Mazaris, A.D., Tsianou, M.A., Stathi, I., Lengyel, S., Sgardelis, S.P., & Kallimanis, A.S. (2010). Biodiversity, species ranges, and ecological processes in dynamic landscapes. Oikos, 119(9), 1293-1302.

Newsome, J.C. (1999): Pollen-vegetation relationships in semiarid southwestern Australia. – Rev. Palaeobot. Palynol. 106: 103 – 119.

Ni, J., Harrison, S. P., & Prentice, I. C. (2000). Investigating the sensitivity of terrestrial ecosystems to climatic variations and CO2 using land surface models. Tellus B: Chemical and Physical Meteorology, 52(5), 511-526.

Nievola, C. C., Carvalho, C. P., Carvalho, V., & Rodrigues, E. (2017). Rapid responses of plants to temperature changes. Temperature, 4(4), 371–405.

Odgaard, B. V. (1999). Fossil pollen as a record of past biodiversity. Journal of Biogeography, 26, 7–17.

Orombelli, G., & Ravazzi, C. (1996). The Last Glacial-Holocene transition in southern Europe. Quaternary International, 33, 77-84.

Ordonez, A., & Svenning, J. (2015). Geographic patterns in functional diversity deficits are linked to glacial-interglacial climate stability and accessibility. Global Ecology and Biogeography, 24(7), 826–837.

Ordonez, A., & Svenning, J. C. (2017). Consistent role of Quaternary climate change in shaping current plant functional diversity patterns across European plant orders. Scientific Reports, 7(1).

Ortiz, D. I., Piche-Ovares, M., Romero-Vega, L. M., Wagman, J., & Troyo, A. (2021). The Impact of Deforestation, Urbanization, and Changing Land Use Patterns on the Ecology of Mosquito and Tick-Borne Diseases in Central America. Insects, 13(1), 20.

Paez, M. M., Cortes, J., & Urrego, L. E. (2001). Vegetation change in the tropical Andes: evidence from southern Colombia. Quaternary Research, 56(3), 341-349.

Pausas, J. G., Pratt, R. B., Keeley, J. E., Jacobsen, A. L., Ramirez, A. R., Vilagrosa, A., Paula S., Kaneakua-Pia I. N., & Davis S.D. (2015). Towards understanding resprouting at the global scale. New Phytologist, 209, 945-954.

Purvis, A., & Hector, A. (2000). Getting the measure of biodiversity. Nature, 405(6783), 212-219.

Qaderi, M., Martel, A., & Dixon, S. (2019). Environmental Factors Influence Plant Vascular System and Water Regulation. Plants, 8(3), 65.

Ray, N., & Adams, J. M. (2001). A GIS-based Vegetation Map of the World at the Last Glacial Maximum (25,000–15,000 BP). Internet Archaeology, 11.

Reitalu, T., Helm, A., Pärtel, M., Bengtsson, K., Gerhold, P., Rosén, E. Takkis K., Znamenskiy S., & Prentice, H. C. (2014). Determinants of fine-scale plant diversity in dry calcareous grasslands within the Baltic Sea region. Agriculture, Ecosystems & Environment, 182, 59–68.

Reitalu, T., Bjune, A., Blaus, A., Giesecke, T., Helm, A., Matthias, I., Peglar, S., Salonen, J., Seppä, H., Väli, V., & Birks, H. (2019). Patterns of modern pollen and plant richness across northern Europe. Journal of Ecology, 107, 1662 - 1677.

Roberts, N. (2007). Holocene climate and vegetation change in the eastern Mediterranean. In Holocene climate and cultural evolution in late prehistoric-early historic West Asia (pp. 139-152). University of Pennsylvania Press.

Roberts, N., Fyfe, R. M., Woodbridge, J., Gaillard, M. J., Davis, B. A. S., Kaplan, J. O., Marquer, L., Mazier, F., Nielsen, A. B., Sugita, S., Trondman, A. K., & Leydet, M. (2018). Europe's lost forests: a pollen-based synthesis for the last 11,000 years. Scientific Reports, 8(1).

Schäbitz, F., Wille, M., Francois, J.P., Haberzettl, T., Quintana, F., Mayr, C., Lücke, A., Ohlendorf, C., Mancini, M.V., Paez, M.M., Prieto, A.R., & Zolitschka, B. (2013): Reconstruction of palaeoprecipitation based on pollen transfer functions – the record of the last 16 ka from Laguna Potrok Aike, southern Patagonia. Quaternary Science Reviews, Special Iss. PASADO, V.71: 175-190.

Schütrumpf, R. (1968). Die neolithischen Siedlungen von Ehrenstein bei Ulm, Aichbühl und Riedschachen im Federseemoor im Lichte moderner Pollenanalyse. Veröffentlichungen des Staatlichen Amtes für Denkmalpflege Stuttgart, A, 10/II, 79 – 104.

Srivastava, J., Manjunatha, B. R., Balakrishna, K., Prajith, A., Manjunatha, H., Jose, J., & Kumar, N. (2021). Quantitative pollen-based reconstruction of the vegetation diversity in response to the late-Holocene climate change near Karwar, south-west coast of India. Quaternary International, 599–600, 95–106.

Soepboer, W., Brinkkemper, O., & Van der Borg, K. (2007). The use of modern pollen rain in establishing land-use histories on Sumbawa, Indonesia. Vegetation History and Archaeobotany, 16(6), 479-493.

Sugita, S., Gaillard, M.-J., & Broström, A. (1999). Landscape openness and pollen records: A simulation approach. The Holocene, 9, 409–421.

Svenning, J. C., Eiserhardt, W. L., Normand, S., Ordonez, A., Sandel, B., & Violle, C. (2015). The influence of late Quaternary climate-change velocity on species endemism. Science, 334(6056), 660-664.

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F., De Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. Nature, 427(6970), 145-148.

Trobls-Smith, J. (1955), Pollenanalytische Untersuchungen zu einigen schweizerischen Pfahlbauproblemen. Das Pfahlbauproblemen; Monogr. Ur- und Fruhgesh. D. Schweiz, 11, 11-58.

Wanner, H., Beer, J., Bütikofer, J., Crowley, T. J., Cubasch, U., Flückiger, J., Goose H., Grosjean M., Joos F., Kaplan J.O., Küttel M., Müller S.A., Prentice I.C., Solomina O., Stocker T.F. Tarasov P., Wagner M.& Widmann M. (2008). Mid-to late Holocene climate change: an overview. Quaternary Science Reviews, 27(19-20), 1791-1828.

Watrin, J., Elenga, H., Le Thomas, A., & Vincens, A. (2007). Vegetation mapping in equatorial Africa: an overview. Quaternary International, 167-168, 28-37.

Weng, C., Tarasov, P.E., & Wagner, M. (2006). Assessing pollen percentages to improve the analysis of present-day vegetation. Review of Palaeobotany and Palynology, 141(1-2), 1-28.

Welten, M. (1967). Bemerkungen zur paläobotanischen Untersuchung von vorgeschichtlichen Feuchtbodenwohnplätzen und Ergänzungen zur pollenanalytischen Untersuchung von Burgäschisee-Sud. Acta Bernensia, 2, 9-20.

Whittaker, R. J., Nogués-Bravo, D., & Araújo, M. B. (2007). Geographical gradients of species richness: a test of the water-energy conjecture of Hawkins et al. (2003) using European data for five taxa. Global Ecology and Biogeography, 16, 76–89.

Zhang, Y., Song, Y. G., Zhang, C. Y., Wang, T. R., Su, T. H., Huang, P. H., Meng, H. H., & Li, J. (2022). Latitudinal Diversity Gradient in the Changing World: Retrospectives and Perspectives. Diversity, 14(5), 334.

Zhang, Z., Zhang, Z., Hautier, Y., Qing, H., Yang, J., Bao, T., Hajek, O. L., & Knapp, A. K. (2023). Effects of intra-annual precipitation patterns on grassland productivity moderated by the dominant species phenology. Frontiers in Plant Science, 14.

# II Study Area

## 2.1 Geographical Setting

The areas under study in this thesis are located in Southeast Europe, encompassing Northern Greece with the Halkidiki peninsula and Pieria mountains, and Central Romania with the southern Carpathians, specifically Ciomadul (Fig. 2.1).

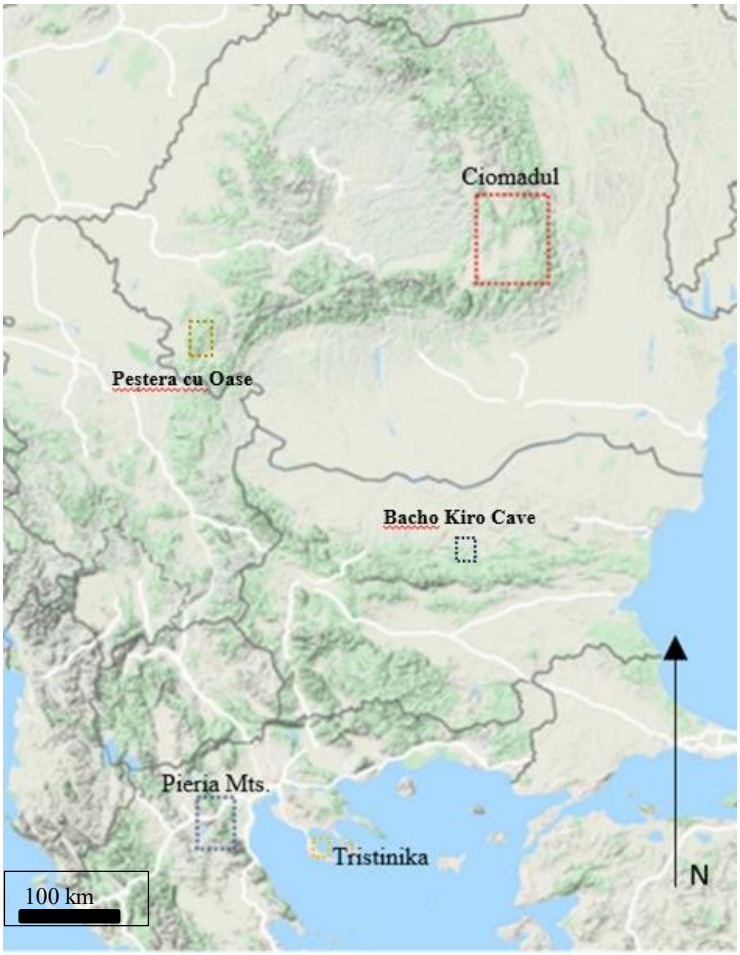


**Fig. 2.1:** Location of the two study areas. On right above, Ciomadul, Romania; right below, Pieria mountains and Tristinika, Greece (modified after Google maps). Additionally, the location of the archaeological sites of Peștera cu Oase (Romania) and Bacho Kiro Cave (Bulgaria).

### Northern Greece: Halkidiki and Pieria Mountains

The Pieria mountains, reaching up to 2,104 m, are located in northern central Greece, extending in a north-northeast to south-southwest direction with eastern and western slopes (Fig. 2.1). The region exhibits altitudinally stratified vegetation, including low-altitude thermophilous oak woodlands and scrub with *Quercus coccifera*, *Q. frainetto*, and *Q. pubescens*, mid-altitude semi-open beech forests, and high-altitude pine woodlands of *Pinus sylvestris* and *P. nigra*. Other species like *Carpinus orientalis*, *C. betulus*, *Ostrya carpinifolia, Corylus avellana*, and *Juniperus spp.* are also present. The eastern slopes face rain-bearing winds from the Aegean Sea,

with annual precipitation ranging from 900 mm in the lower to around 1,200 mm in the upper beech forests (Katsavouni et al., 2014). Halkidiki, located in North-Central Greece, boasts three prominent peninsulas—Kassandra, Sithonia, and Athos—surrounded by the Cholomontas mountain range, with Mount Athos reaching around 2030 m and Mount Itamos in Sithonia at approximately 800 m, adorned with ancient yew trees (*Taxus baccata*) (Fig. 2.2). This region encompasses diverse vegetation zones, reflecting the entirety of Greek inland biodiversity, excluding cold-tolerant conifers. Pavlidis (1976) notes that the intricate tapestry of vegetation is influenced by factors such as altitude, soil composition, climatic conditions, and human impact. Beech (*Fagus sylvatica*) graces high-altitude forests and stands, while sparse instances of *fi*r (*Abies borisii-Regis*) dot Mount Athos. Mid-altitude areas feature thermophilous oak (*Quercus frainetto*, *Q. pubescens*) forests and woodlands. Sithonia Peninsula, nestled between Kassandra and Mount Athos, showcases a rich mixture of pine woodlands (*Pinus halepensis*, *P. nigra*, *P. pinea*) and maquis with species like *Quercus coccifera*, *Olea europaea*, *Erica arborea*, *Arbutus unedo*, among others. Central Sithonia witnesses sparse deciduous oaks (*Q. frainetto, Q. pubescens*), while coastal areas feature nitrophilous, halophytic vegetation. Sithonia's climate, classified as Csa in Köppen's system, experiences Mediterranean conditions, marked by scorching summers exceeding 30°C (86°F) and mild, relatively wet winters. The climate, as described by Pavlidis (1976), significantly shapes the local flora and fauna, fostering the flourishing of olive trees, vineyards, drought-resistant plants, and adaptable wildlife.

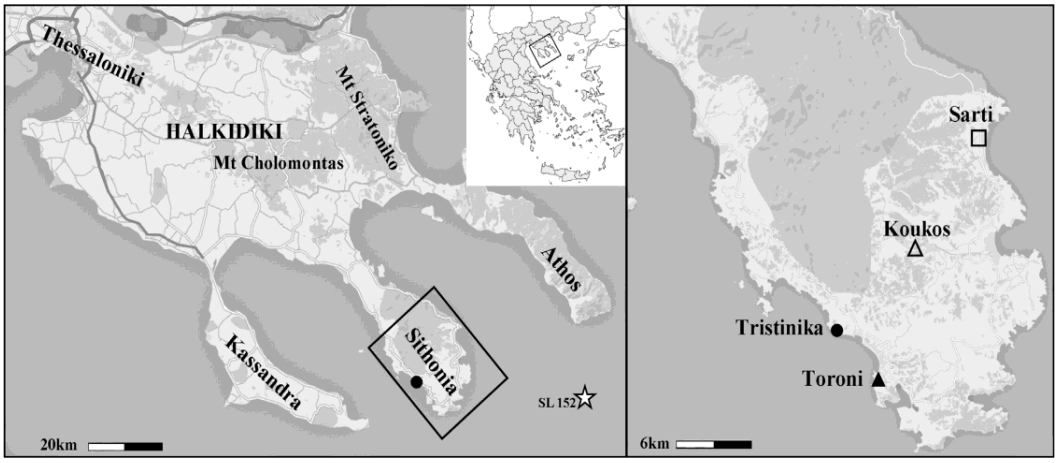


**Fig. 2.2:** Map of Halkidiki showing coring site (Tristinika), nearest marine core (SL 152, Kotthoff et al., 2008), and relevant archaeological sites.

### Central Romania: Ciomadul - Mohoş

The Ciomadul lava dome complex, rising to an elevation of up to 1,301 m in central Romania, stands as a prominent constituent of the Inner Carpathian volcanic chain and is enveloped by mature, dense *forests* primarily comprising *Fagus sylvatica* (beech) and *Picea abies* (spruce) (Fig. 2.3). Within this rich ecosystem, various trees and shrubs such as *Carpinus betulus*, *Betula pubescens*, *Corylus avellana*, *Alnus glutinosa*, *Abies alba*, and *Pinus sylvestris* thrive, contributing to the overall biodiversity of the region. The

zonal vegetation aligns with the Symphyto cordati-Fagetum vegetation association (Coldea 1991).

In contrast to the Pieria mountains, Ciomadul experiences a temperate-montane climate, characterized by annual precipitation exceeding 1,000 mm, with a peak during summer and a minimum in winter.

Ciomadul's distinctive features extend to a mixed forest with peat moss, creating a landscape predominantly covered by a marshy forest. The peat is dominated by mixed moss varieties, as evidenced by the vegetation type identified as a 'Vaccinio uliginosi – Pinetum ilvestri' plant vegetation association, while the zonal vegetation primarily aligns with a 'Symphyto cordati–Fagetum' association (Coldea; 1991). The fringe zone encircling the Mohoş peat bog showcases a *Picea abies* forest, and a thermal inversion in this area contributes to a reversal in the altitudinal distribution of vegetation zones. It's noteworthy that Mohoş is an integral part of Ciomadul, and this ecological diversity adds to the unique character of the region (https://harghitavalues.ro/lake-saint-anne-and-mohos-peat-bog/).

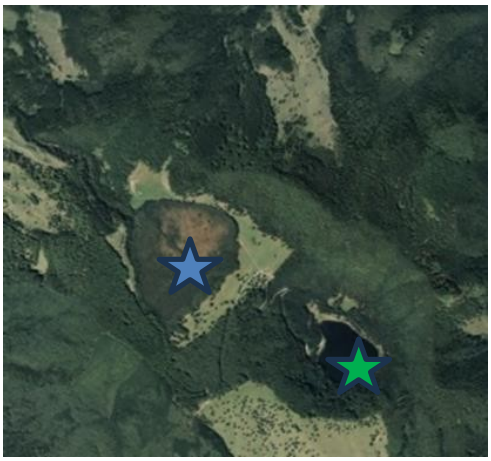

**Fig 2.3** Image of Mohoş peat bog and lake Santa Ana (Provided by Romanian Authorites) ★indicates the location of Mohoş peat bog and ★ indicates the location of lake Santa Ana

## 2.2 Human settlement history and land cover/land use of the Balkans

This section delves into the rich historical tapestry of human settlement and land utilization within the Balkan area, offering insights into the ancient origins of Southeastern Europe's populace. Two pivotal archaeological sites, Bacho Kiro Cave in Bulgaria and Peștera cu Oase in Romania, provide evidence of ancient habitation.

Peștera cu Oase (Romania)-

Peștera cu Oase, located in the Carpathian Mountains of Romania, offers another intriguing glimpse into the region's ancient past. The discovery of the Oase mandible, dating to approximately 40,000 years ago (ca. 40 ka cal BP), provides invaluable genetic and morphological data, showcasing a blend of modern and archaic features (Trinkhaus et al., 2003). These findings underscore the complexity of human evolution.

and interactions with Neanderthal populations, unraveling the intricate tapestry of Southeastern Europe's prehistoric inhabitants.

The Bronze Age (circa 3500–1100 BCE) marked a transformative period in Romania, characterized by significant cultural and technological advancements. Societies such as the Cotofeni, Glina, and Tei cultures emerged, distinguished by their mastery of metallurgy, particularly in crafting bronze tools, weapons, and ornaments. These communities also developed distinctive pottery styles and built fortified settlements, reflecting an increasingly organized social structure. The Carpathian region's abundant natural resources fostered vibrant trade networks and cultural exchanges, placing Romania at the crossroads of Southeastern European Bronze Age civilizations (Lazarovici & Merlini, 2005).

Bacho Kiro Cave (Bulgaria) –
Bacho Kiro Cave, situated in Bulgaria, constitutes a crucial archaeological site shedding light on the historical narrative of human settlement in Southeastern Europe. In a recent groundbreaking discovery led by Hublin et al. in 2020, the cave unveiled remarkable insights into our ancient past. The research, centered around human remains and artifacts, provides evidence of habitation dating back to the Upper Paleolithic period, approximately 45,000 years ago. One of the key findings was the identification of Homo sapiens fossils, showcasing a sophisticated interplay of modern and archaic features. Hublin et al.'s work at Bacho Kiro Cave contributes significantly to our understanding of the intricate mosaic of human evolution in the region, paralleling the discoveries at Peștera cu Oase in Romania. These archaeological sites collectively weave a tapestry of Southeastern Europe's ancient origins, highlighting the dynamic nature of human settlement and adaptation over millennia.

Sithonia's Settlement History (Greece)-
Sithonia has been inhabited since the Bronze Age (3000–1100 BCE), with significant settlements like Torone excavated from that period (Morris, 2009-2010). The Geometric (Iron Age) settlement Koukos, close to Tristinika marsh, is noteworthy for metallurgy related to copper and silver mines in the area. The collapse of the Mycenaean civilization in the 12th century BCE, influenced by a cold/dry spell (Drake, 2012), led to Greek colonization in Halkidiki, attracted by the region's metal and wood resources.

In the 8th century BCE, colonizers from Euboea established Torone on the ruins of a prehistoric settlement, transforming it into a major port (Tiverios, 2008). Historic sources mention the foundation of thirty cities in Sithonia around the same time. During the Classic/Hellenistic period, Torone became a significant trade center for wood, wine, and olive oil and a member of the Delian League. In the Roman climatic optimum of the 1st century BCE, coastal plains were allocated to Roman army veterans, leading to a revival of the agricultural economy, particularly in the Kassandra peninsula.

In the meso-Byzantine era (6th to 8th century CE), social upheaval and epidemics of plague led to a population reduction in Halkidiki, resulting in the abandonment of most ancient cities (Harbeck et al., 2013; Lefort, 2006).

By the end of the 9th century CE, with the establishment of the monastic state of Athos, peace was restored in the area. Byzantine rulers granted land to the monks of Athos and wealthy landowners of Thessaloniki, leading to the colonization of Sithonia by small villages, hamlets, and fortified estates of the monasteries. In the post-Byzantine era, Sithonia's landscape shifted to wine, olive, cereal, and charcoal production, with a mining revival in the 16th century contributing to the foundation of villages known as ‘Siderokavsia’ (meaning 'smelting iron' in Greek).

The Ottoman occupation in the mid-15th century saw the settlement of semi-nomadic pastoralists (Yüruks) in north Halkidiki.

This exploration of the study area sets the stage for understanding the environmental dynamics and historical context that shape the focus of the thesis. The next chapters will delve deeper into the climate, vegetation, and human impact on these diverse landscapes.

## 2.3 References

Coldea, G. (1991). Prodrome des associations végétales des Carpates du sudest (Carpates roumanies). Doc Phytosociol, 13:317–539.

Drake, B. L. (2012). The influence of climatic change on the Late Bronze Age Collapse and the Greek Dark Ages. Journal of Archaeological Science, 39(6), 1862–1870.

Harbeck, M., Seifert, L., Hänsch, S., Wagner, D. M., Birdsell, D., Parise, K. L., Wiechmann, I., Grupe, G., Thomas, A., Keim, P., Zöller, L., Bramanti, B., Riehm, J. M., & Scholz, H. C. (2013). Yersinia pestis DNA from Skeletal Remains from the 6th Century AD Reveals Insights into Justinianic Plague. PLoS Pathogens, 9(5), e1003349.

Hublin, J. J., Sirakov, N., Aldeias, V., Bailey, S., Bard, E., Delvigne, V., Endarova, E., Fagault, Y., Fewlass, H., Hajdinjak, M., Kromer, B., Krumov, I., Marreiros, J., Martisius, N. L., Paskulin, L., Sinet-Mathiot, V., Meyer, M., Pääbo, S., Popov, V., Rezek, Z., Sirakova, S., Skinner, M. M., Smith, G. M., Spasov, R., Talamo, S., Tuna, T., Wacker, L., Welker, F., Wilcke, A., Zahariev, N., McPherron, S. P., & Tsanova, T. (2020). Initial Upper Palaeolithic *Homo sapiens* from Bacho Kiro Cave, Bulgaria. Nature 581(7808), 1-4.

Katsavouni S, Doulgeris C, Papadimos D. (eds) (2014) Time series of meteorological data spatially distributed within the four pilot sites, 3rd edn. Thermi, Greek Biotope Wetland Centre (EKBY).

Lazarovici G., & Merlini M. (2005). The Archaeological Context of the Tărtăria Tablets. Documenta Praehistorica, 32, 25-47.

Lefort, J. (2006). Société rurale et histoire du paysage à Byzance. Association des Amis du Centre d'Histoire et Civilisation de Byzance, Paris.

Morris, S.P. (2009–2010). Prehistoric Torone: A Bronze Age Emporion in the Northern Aegean. Preliminary Report on the Lekythos Excavations 1986 and 1988 – 1990. Mediterranean Archaeology: Australian and New Zealand Journal for the Archaeology of the Mediterranean World, 22–23. 1–67.

Pavlidis, G. (1976). I chloris kai i vlastisis tis chersonisou Sithonias Halkidikis (Flora and Vegetation of the Sithonia Peninsula in Halkidiki). PhD thesis University of Thessaloniki, Aristotle, p. 300.

Tiverios, M. (2008). Greek colonisation of the Northern Aegean. In: Tsetskhladze, G. (Ed.), Greek Colonisation: An Account of Greek Colonies and Other Settlements Overseas 2, 1–154.

Trinkaus E., Moldovan O., Milota Ș., Bîlgăr A., Sarcina L., Athreya S., Bailey S. E., Rodrigo R., Mircea G., Higham T., Ramsey C. B., & van der Plicht J. (2003). An early modern human from the Peștera cu Oase, Romania. Proceedings of the National Academy of Sciences of the United States of America, 100 (20), 11231-11236.

# III Testing the potential of pollen assemblages to capture composition, diversity and ecological gradients of surrounding vegetation in two biogeographical regions of southeastern Europe


## Abstract

Due to the complex relationship between pollen and vegetation, it is not yet clear how pollen diagrams may be interpreted with respect to changes in floristic diversity and only a few studies have hitherto investigated this problem. We compare pollen assemblages from moss samples in two southeastern European forests with the surrounding vegetation to investigate (a) their compositional similarity, (b) the association between their diversity characteristics in both terms of richness and evenness, and (c) the correspondence of the main ecological gradients that can be revealed by them. Two biogeographical regions with different vegetation characteristics, the Pieria mountains (north central Greece) and the slopes of Ciomadul volcano (eastern Romania), were chosen as divergent examples of floristic regions, vegetation structure and landscape openness. Pollen assemblages are efficient in capturing the presence or absence, rather than the abundance in distribution of plants in the surrounding area and this bias increases along with landscape openness and vegetation diversity, which is higher in the Pieria mountains. Pollen assemblages and vegetation correlate better in terms of richness, that is, low order diversity indices. Relatively high correlation, in terms of evenness, could be potentially found in homogenous and species poor ecosystems as for Ciomadul. Composition and diversity of woody, rather than herb, vegetation is better reflected in pollen assemblages of both areas, especially for Pieria where a direct comparison of the two components was feasible, although this depends on the species-specific pollen production and dispersal, the openness of landscape and the overall diversity of vegetation. Gradients revealed by pollen assemblages are highly and significantly correlated with those existing in vegetation. Pollen assemblages may represent the vegetation well in terms of composition, diversity (mainly richness) and ecological gradients, but this potential depends on land use, vegetation structure, biogeographical factors and plant life forms.



**Keywords**: Diversity, Hill's numbers, Pollen assemblages, Vegetation, Richness, Evenness

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## 3.1 Introduction

Palaeoecological studies can offer insights into past changes of vegetation diversity driven by climate or human impact (Odgaard 1999; Berglund et al. 2008; Colombaroli and Tinner 2013; Giesecke et al. 2019). A recent review (Birks et al. 2016) strongly supports this view and discusses the need for exploring modern pollen-vegetation relationships in terms of diversity. Several studies (for example, Meltsov et al. 2011; Matthias et al. 2015; Felde et al. 2016; Reitalu et al. 2019) have provided evidence for statistically significant relationships between pollen and plant diversity; however, Odgaard (2008) cautions that attempts to reconstruct components of past plant diversity are potentially biased. These biases are well known and include taxon-specific pollen production and dispersion properties, low pollen taxonomic resolution and lack of a fixed pollen source area (Giesecke et al. 2014).

Studies comparing the modern relationship also need to consider biases introduced by sampling design and the data used in the analyses (Birks et al. 2016). Diversity is traditionally assessed through taxa richness (number of taxa) and evenness (abundance of taxa) (Gotelli and Chao 2013). Palynological richness, the number of pollen types encountered in a sample, increases with the number of pollen grains examined or counted (Rull 1987) and therefore it needs to be compared at a standardized sum (Birks and Line 1992). Odgaard (1999) demonstrated how the encounter of pollen types declines for samples with a standardized pollen sum, when the vegetation changes from low to high pollen producers. It should be theoretically possible to reduce this bias by adjusting for pollen production and dispersal.

However, Matthias et al. (2015) did not find an improvement with adjusted pollen proportions, while Felde et al. (2016) obtained a better fit between pollen and floristic plant richness when applying simple correction factors. Given a well dated sediment accumulation, which is usually the case for varved sediments, van der Knaap (2009) demonstrated that it is possible to circumvent the problem of differential pollen dispersal and deposition by estimating the number of different pollen types deposited per unit of sediment and time. Other biases, like low pollen taxonomic resolution, may not be resolved and Odgaard (2001, 2008) therefore suggested that investigating the dynamics of pollen and vegetation evenness might be more rewarding. Matthias et al. (2015) compared different diversity indices and found that the Shannon index compared best with the number of different vegetation types, while other studies found relationships for richness (Felde et al. 2016). The limited number of modern studies comparing pollen and vegetation diversity does not yet provide conclusive interpretations of pollen diversity, evenness and richness.

Hill's numbers (Hill 1973) constitute a useful approach to diversity partitioning as they can be calculated with different weights given to the richness and evenness components of diversity and they are very effective in comparing diversity between different assemblages (Ellison 2010; Birks et al. 2016). In addition to Hill's numbers, Birks et al. (2016) suggest that studies exploring modern diversity patterns of pollen and vegetation should also include multivariate approaches, such as co-correspondence analysis, that

allow the simultaneous assessment of the covariation of datasets derived from identical sampling sites.

Compositional similarity between pollen assemblages and surrounding vegetation constitutes a basic prerequisite for reliable interpretation of palaeoecological data (Birks and Birks 1980). Many studies investigated the similarity between pollen assemblages and floristic composition of surrounding vegetation types (for example, Hjelle 1999; Felde et al. 2014). In most cases, such studies showed that pollen assemblages can reveal different vegetation types, although the pollen biases mentioned above may blur this potential. Appropriate sampling design as far as scale, sampled area and measurement methods are concerned, is essential to acquire reliable data and reveal meaningful relationships (Felde et al. 2016; Birks et al. 2016). Ordination analysis can further help to assess whether modern pollen assemblages correspond to the main vegetation gradients (Legendre and Birks 2012).

There is a lack of integrated studies of compositional similarity and diversity of pollen and surrounding vegetation for south-east Europe, where most of the palaeoecological studies have been carried out in mountainous areas such as the Pieria mountains (Gerasimidis and Panajiotidis 2010) and Mohoş (Tanţău et al. 2003). Feurdean et al. (2013), in a com- parative study of cores collected in the Romanian Carpathians, point out that land use and landscape openness influence the elevational patterns of palynological richness. Moreover, the site Mohoş (Ciomadul, Romanian eastern Carpathians), situated in closed beech forests of low vegetation diversity, showed low palynological richness, a feature prominent over the last century due to the intensification of land use (mainly forestry plantations) on a regional scale.

In this study, we compare pollen assemblages with vegetation plots collected from two areas, the Pieria mountains in north-central Greece and the Ciomadul lava-dome complex in the Romanian Eastern Carpathians. The former is a semi-open forested mountain in the Mediterranean region, with high landscape diversity that leads to a greater floristic richness, while the latter is an extensive dense Fagus dominated forest with a species poor understory vegetation in the continental biogeographical region. In Ciomadul dense forests are surrounded by large forestry plantations and open grazed meadows. In the Pieria mountains farming is restricted to low altitudes, with grazing in scrub. Beech forests are subjected to felling, with variously opened stands. We sampled the modern vegetation of vascular taxa within the altitudinal range of beech forests in both areas, in circles of 10 and 100 m radius around moss cushions from which the modern pollen deposition was analysed. In this comparison, we focused on the following features:

(a) compositional similarity, to assess the degree in which vegetation composition is represented by pollen assemblages;

(b) similarity of diversity (both richness and evenness components), by exploring different orders of Hill's numbers, and the potential of pollen assemblages to capture vegetation diversity; and

(c) correspondence of gradients revealed by pollen and vegetation data.

Specifically, we address the following questions:

- To what extent the herb and woody components of pollen assemblages in moss cushions resemble corresponding components in the surrounding vegetation sampled at different spatial scales of 10 and 100 m radii?
- Does the pollen type diversity represent species diversity in the vegetation, and which component of diversity (richness or evenness) exhibits the strongest relationship between pollen assemblages and vegetation?
- Is there any correspondence between the main gradients revealed by pollen assemblages and vegetation?

Differences in terms of landscape openness, land use and vegetation structure between the two regions are considered in an attempt to interpret compositional similarity and diversity correlation results.

## 3.2 Methods

### 3.2.1 Study Regions

The Pieria mountains (up to 2,104 m) are situated in northern central Greece, extending in a north-northeast to south- southwest direction, thus having eastern and western slopes (Fig. 3.1). There is an altitudinally stratified vegetation composed of low-altitude thermophilous oak woodlands and scrub with *Quercus coccifera, Q. frainetto and Q. pubescens*, mid-altitude (800–1,700 m) semi-open beech forests with *Abies borisii-regis* stands and high altitude pine woodlands of *Pinus sylvestris and P. nigra*. Apart from the major vegetation types mentioned above, small stands of *Carpinus orientalis, C. betulus, Ostrya carpinifolia, Corylus avellana and Juniperus spp.* are encountered (Gerasimidis et al. 2006). The eastern slopes of the massif are exposed to rainbearing winds from the Aegean Sea. Annual precipitation ranges between 900 mm in the lower and ca. 1,200 mm in the upper beech forests, with its maximum during winter and its minimum in summer (Katsavouni et al. 2014).

The Ciomadul lava dome complex (up to 1,301 m), situated in central Romania, belongs to the Inner Carpathian volcanic chain, and is covered mainly by mature, dense forest of *Fagus sylvatica* (beech) and *Picea abies* (spruce) (Fig. 3.1). However, trees and shrubs such as *Carpinus betulus, Betula pubescens, Corylus avellana, Alnus glutinosa, Abies alba and Pinus sylvestris* are also found in the area. The zonal vegetation of the area belongs to the *Symphyto cordati-Fagetum* vegetation association (Coldea 1991). The climate is temperate-montane with an annual precipitation reaching above 1,000 mm and presenting, in contrast to the Pieria mountains, a maximum during summer and a minimum in winter.

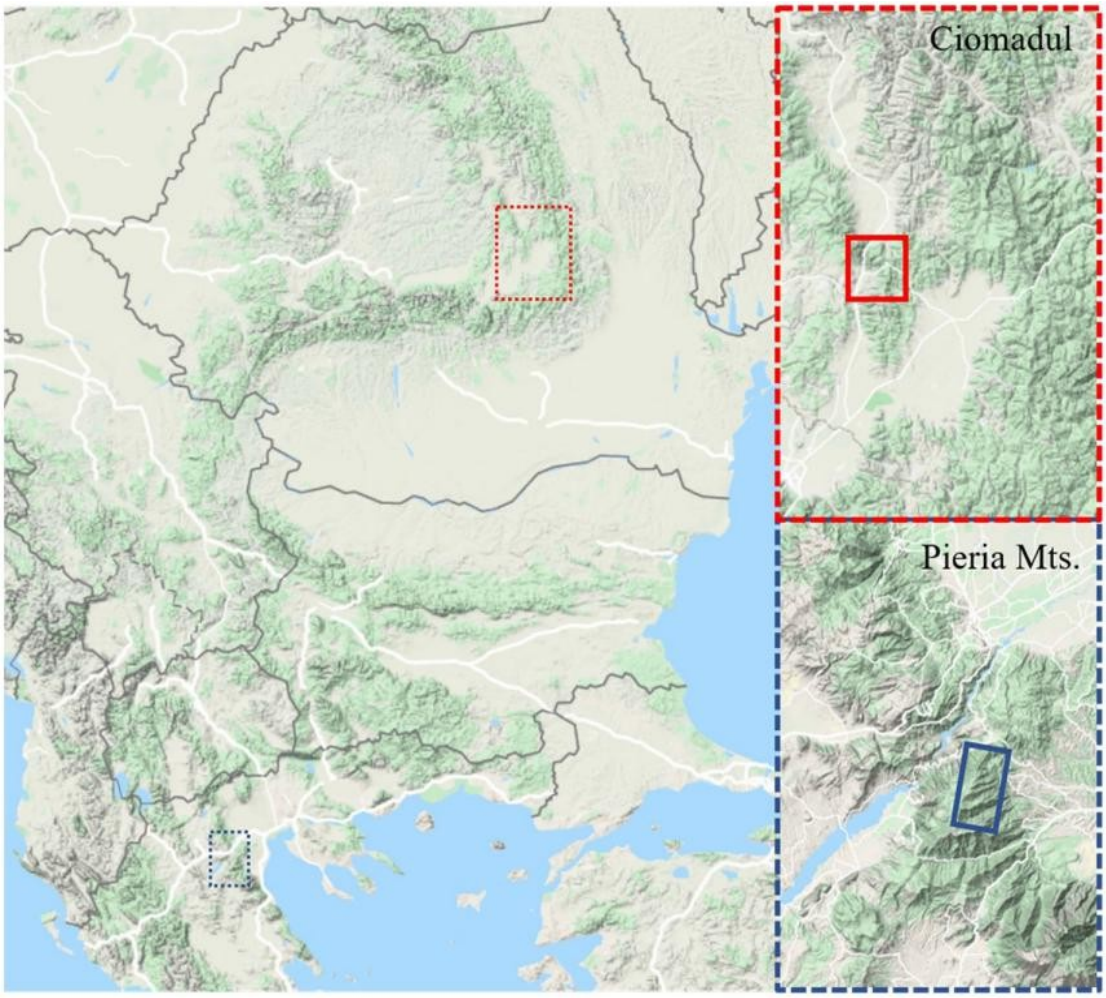


**Figure 3.1:** Location of the two study areas. On right above, Ciomadul, Romania; right below, Pieria mountains, Greece (modified after Google maps)

### 3.2.2 Moss Cushion Sampling

Moss cushions were sampled during the summers of 2011 (Pieria mountains, 22°13‘00“ to 22°16‘30“E and 40°13‘30“ to 40°21‘30“N) and 2014 (Ciomadul, 25°51‘00“ to 25°56‘00“E and 46°05‘00“ to 46°10‘00“N). Aerial photos with a scale 1:10,000 were used to select the sampling points. To capture most of the landscape diversity in the Pieria mountains, sampling sites were selected in the oak woodland/beech forest and beech/pine forest transition zones, including sites with mixed beech/fir stands. Within the beech matrix at Ciomadul, sites with differing abundances of major trees (*Fagus, Picea, Betula, Alnus, Pinus*) were chosen in order to capture most of the landscape diversity. A 5 cm diameter circular moss cushion was collected from each vegetation sampling location. Moss cushions were collected from an altitudinal range of ca. 850-1,600 m in Pieria and 700-1,310 m in Ciomadul. Fourteen sampling sites were selected in Pieria and 18 in Ciomadul (Fig. 3.2).

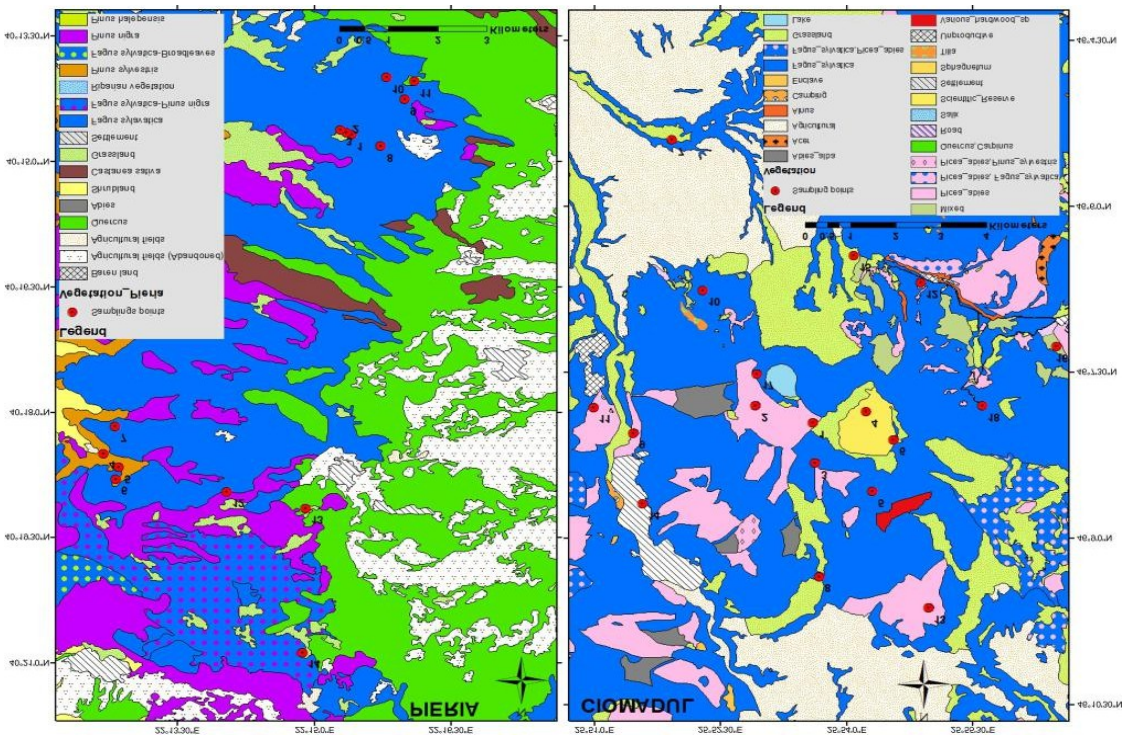


**Figure 3.2:** Vegetation units and sampling points. Left, Pieria mountains; right, Ciomadul. Circles represent the 10 and 100 m radius sampled vegetation areas

### 3.2.3 Vegetation Sampling and Mapping

In both areas the protocol of Bunting et al. (2013) was adopted, with some modification for the recording of herb vegetation in the Pieria mountains to help capture the higher heterogeneity that characterizes mountainous Mediterranean vegetation. The protocol combines different approaches for the various vegetation layers (tree/ shrub and herb). The floristic composition of the vascular plants in the herb layer was recorded within a 10m radius around each sampling point. This distance is considered representative of the relevant pollen source area of many herbaceous taxa (Hjelle 1997; Bunting 2003; Bunting et al. 2013), but it may vary in size depending on the pollen taxon (Shaw and Whyte 2020). The herb cover was estimated by using 33 quadrats of 0.25 $m^2$ in the Pieria mountains and 21 quadrats of 1 $m^2$ in Ciomadul. The quadrats in both study areas were placed within the 10 m radius in eight different directions, north, northeast, east etc., and at different distances from the sampled moss cushion. The canopy cover of woody taxa, which are generally high pollen producers, was estimated in 10 m concentric rings within the range 10–100 m from each moss cushion. Similarly, the canopy cover of woody taxa present in the 0–10 m radius was estimated in concentric rings of 1 m. In Pieria, open tree canopy within 10 m radius was more than 50% of the respective total area in half the sampling points, with minimum and maximum values of 6.6 and 100% of total area respectively. In Ciomadul open canopy within a 10 m radius was less than 10% of the total area in two thirds of the sampling points, while minimum and maximum values reached 1 and 76% respectively.

### 3.2.4 Pollen Analysis and Data Preparation

The moss polsters were processed following Hicks et al. (1996), washing the contents of the moss sample into a cellulose filter paper that is then acetolysed. Samples from the Pieria mountains were prepared at the laboratory of Forest Botany-Geobotany at the Aristotle University of Thessaloniki, Greece, while those of Ciomadul at the laboratory of the Institute of Geography and Education, University of Cologne, Germany. A light microscope with 400× magnification was used to identify the pollen and spores. Pollen and spore identification was based on published keys and atlases (Reille 1992, 1995; Chester and Raine 2001; Beug 2004) as well as on reference material held at both laboratories. A minimum of 500 arboreal pollen grains were counted for each sample (Hicks et al. 1996). Throughout the text the term 'herbs' refers to both pollen of angiosperms and spores of vascular cryptogams.

Vascular plant taxa were identified to species or sub-species level following Flora Europaea (Tutin et al. 1968, 1993). Identified taxa were transformed to pollen and spore equivalents with taxa belonging to the same pollen/spore type, based on Beug (2004) and their cover abundances were merged to the corresponding pollen equivalent assemblages (Tichý et al. 2011). To explore different components of the pollen signal we created different subsets of Pollen Type assemblages (PTas) and Pollen-Equivalent assemblages (PEas) using two sampling distances (10 and 100 m) as well as different combinations of plant life form (herbs; trees + shrubs; all terrestrial vascular plants) as constraints. Herb data sets for Ciomadul were not analysed, as some of the PTas had very low herb pollen counts with less than 20 pollen grains (ESM 1 Table 6). Thus, four different combinations were evaluated:

allPV: all pollen and spore PEas of vegetation (allV) vs. pollen and spore PTas (allP), only for the 10 m radius plots where all plant life forms were recorded;

herbPV: herb PEas of vegetation plots (herbV) within 10 m radius vs. herb PTas (herbP);

woodPV: woody PEas of vegetation (wooV) within 10 m radius vs. woody PTas (wooP);

woodPV-100: woody PEas of vegetation (wooV-100) within 100 m radius vs. woody PTas (wooP).

### 3.2.5 Data Analysis

To eliminate the bias introduced by the different sizes of the pollen counts within each data set, we resampled each PTa to the minimum pollen count recorded in each site, following Felde et al. (2016), although for each PTa we resampled 100 times, since pollen count size differences were relatively small. Bray-Curtis coefficients were calculated for each PEa and all the 100 corresponding PTas resulting from resampling. The average and standard deviations were calculated. Similarly, for each Pta, an average value of diversity for each order of diversity (Hill's numbers), was calculated from all the 100 pollen samples derived from resampling (Hill 1973; Chao et al. 2014). Hill's numbers were also calculated for each PEa.

The advantage of Hill's numbers is that they produce different indices that represent both species richness and evenness by giving different weights to the two components (Hill 1973; Chao et al. 2014). The weight of the above- mentioned components of diversity is tuned by a parameter, called the "order" of diversity and is symbolized by the letter q (Jost 2006). We used the following q values: 0, 0.25, 0.5,

1, 2, 4, 8, 16, 32, 64 and ∞.

Calculating the dissimilarity, we explored how well each PTa set represented the corresponding PEa set. Three calculations of Bray-Curtis similarity coefficient were made using the following data: 1, presence or absence of pollen types/pollen equivalents; 2, untransformed percentage cover (pollen equivalents)/frequencies (pollen types); and 3, square root transformed and normalized percentages of pollen types or pollen equivalents. We compared the Hill's numbers between each combination of vegetation and pollen datasets using Spearman's rank correlation coefficient (Spearman 1904). For each PTa and its Hill's numbers of a specific order, q correlations were calculated with Hill's numbers of its corresponding PEa set for the same and all other selected orders of q. This pattern of calculations was applied to all Hill's numbers derived from the selected q orders for each PTa set. Hill's numbers of different q values are expected to present weaker and perhaps insignificant correlations, because of the different weight given through the different q values to abundances and to common and rare taxa (Jost 2006). However, a different trend cannot be precluded, considering that Hill's numbers were calculated for different entities, the species for the vegetation samples, and pollen types for the pollen assemblages. Moreover, presence of pollen types in a sample, contrary to their vegetation equivalents, is a much more biased and stochastic procedure in terms of abundance and richness, a fact that merits exploration for potential correlational patterns between diversities of different orders.

To further explore the similarity between pollen assemblages and vegetation plots, we performed non-metric multidimensional scaling (NMDS) using the different data sets. Percentages of pollen types and equivalents were square root transformed and normalized before NMDS analysis. Bray-Curtis distance between vegetation plots or pollen assemblages was used as a distance measure. In order to investigate the correlation between the ordination diagrams of corresponding PEa/PTa sets, we applied a permutation test based on a Procrustes statistic (PROTEST) (Jackson 1994; Peres-Neto and Jackson 2001). PROTEST compares two ordinations using symmetric Procrustes analysis (Oksanen 2015) and it results in the correlation r between the two ordinations, its significance on the basis of a permutation test and the symmetric Procrustes residual between configurations after optimal fit ($m^2$), which is low when there is a close match between ordinations (Peres-Neto and Jackson 2001).

Bray-Curtis similarity coefficients, Hill's numbers, NMDS and PROTEST were done with vegan v. 2.2.1 (Oksanen et al. 2013) in R v. 3.1.2 (R Core Team 2014). Spearman's correlation coefficients were calculated using SPSS (IBM 2012). Diagrams were drawn using Origin Pro v. 7.5 SR6 (OriginLab 1991–2006).

## 3.3 Results

### 3.3.1 Plant Taxa and Pollen Types recorded in Vegetation and Moss Cushions

In the Pieria mountains, 264 plant taxa were identified in the sampling plots around the moss cushions, a very high number considering that the total sampled area was about 40% of that sampled in Ciomadul. These taxa were assigned to 111 pollen and spore equivalents, of which 95 were herbaceous (85.6%), 14 woody plants (12.6%) and two ferns. A total of 102 pollen and spore types were recorded in the corresponding pollen assemblages of which 65 belong to herbaceous taxa (63.7%), 31 to woody taxa (30.4%) and six to ferns. A total of 50 pollen types (45%), of which 26 herbaceous (40% of all herbs) and 20 woody types (64.5% of all trees and shrubs), were not recorded in the sampled vegetation.

In Ciomadul only 134 plant taxa were identified in the vegetation plots. These were assigned to 82 pollen and spore equivalents, of which 66 were herbaceous (80.5%), 13 woody taxa (15.9%) and three ferns (3.7%). A total of 37 pollen and spore types were recorded in the corresponding pollen assemblages of which 19 belong to herbaceous taxa (51.4%), 15 to woody (40.5%) and three to ferns (8.1%). A total of 12 types (32.4%), comprising seven herbaceous (36.8% of all herbs) and four woody types (26.7% of all trees and shrubs), were not recorded in the sampled vegetation.

For the Pieria mountains, about 41% (39/95) of the herb equivalents present in the plots were also recorded in the pollen assemblages, but on the contrary, for Ciomadul only 18.2% (12/66) of the herbaceous equivalents were also recorded. In both areas, nearly all woody equivalents present in the sampled vegetation were also recorded in the pollen assemblages, 13 out of 14 or 92.85% for Pieria and 11 out of 13 or 84.6% for Ciomadul. Most pollen samples from Pieria are characterised by very low pollen counts of Fagus and more than half of the samples have values around or less than 5% (ESM 1 Table 3), while for Ciomadul the situation is reversed and more than half of the samples have values over 20% (ESM 1 Table 6).

### 3.3.2 Similarity between Vegetation Plots and Pollen Assemblages

Presence/absence based similarity coefficients were always higher (more similar) than those based on abundance of pollen types and pollen equivalents (Table 3.1). Similarity coefficients of the square root transformed percentage data were intermediate or closer to those of presence/absence data (Table 3.1). For both areas, the Bray-Curtis similarity coefficients of presence/absence and frequency data of PEas and their corresponding PTas are highly variable for most cases (Fig. 3.3). The largest bias, in terms of similarity, between presence/absence and frequency data sets is observed for Pieria (Fig. 3.3). For both areas, PTas and PEas representing woody components within 100 m were the most similar. For Pieria, the woody PTa/PEa sets were less similar than the corresponding sets of total floristic composition for the 10 m plots. In contrast, for Ciomadul the pollen assemblages and presence/absence records of the woody

component from the vegetation plots within 10 m were much more similar than the corresponding total floristic composition sets. For Pieria, the herb data sets yielded similarity values approximately equal to those of the 10 m woody and total component sets.

| Data set | Pieria Mts. | | Ciomadul | |
|---|---|---|---|---|
| | Median | SD | Median | SD |
| allPV[a] | 0.294 | 0.066 | 0.310 | 0.084 |
| allPV[b] | 0.245 | 0.056 | 0.324 | 0.066 |
| allPV[c] | 0.14 | 0.073 | 0.269 | 0.066 |
| wooPV[a] | 0.255 | 0.114 | 0.524 | 0.181 |
| wooPV[b] | 0.225 | 0.105 | 0.397 | 0.101 |
| wooPV[c] | 0.097 | 0.09 | 0.283 | 0.075 |
| wooPV-100[a] | 0.433 | 0.057 | 0.626 | 0.134 |
| wooPV-100[b] | 0.352 | 0.075 | 0.482 | 0.082 |
| wooPV-100[c] | 0.167 | 0.055 | 0.331 | 0.037 |
| herbPV[a] | 0.264 | 0.082 | | |
| herbPV[b] | 0.176 | 0.066 | | |
| herbPV[c] | 0.091 | 0.055 | | |

**Table 3.1:** Median and standard deviation of the Bray-Curtis similarity coefficient values between different vegetation PEas and their corresponding Ptas for Pieria and Ciomadul. allPV, 10 m total component; wooPV, 10 m woody component; wooPV-100, 100 m woody component; herbPV, 10 m herb component

a. Based on presence-absence data

b. Based on the untransformed cover values (for vegetation plots) and pollen frequencies

c. Based on power transformed cover values

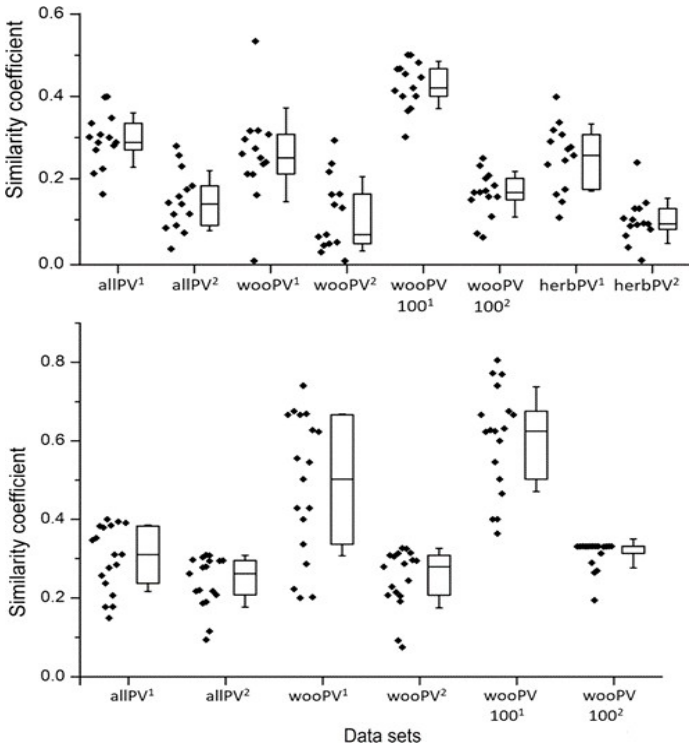


**Fig. 3.3** Box and whiskers plots of the Bray-Curtis similarity coefficients between the vegetation plots and their corresponding pollen assemblages, and for different data sets. Upper diagram, Pieria; lower diagram, Ciomadul. Boxes represent the 25th and 75th percentiles and whiskers (lines) one standard deviation.
Diamonds show the similarity values of the plots for each data set. allPV, 10 m total component; wooPV, 10 m wood component; wooPV-100, 100 m woody component; herbPV, 10 m herb component; (1), presence/absence data of untransformed cover values of vegetation plots; (2) pollen frequency data.

### 3.3.3 Correlational patterns of Diversity

For the Pieria mountains statistically significant ($p \leq 0.05$) correlations for the comparison between pollen and vegetation diversity were found for the full untransformed datasets. Only low order diversity with q values between 0 and 1 of PTas and PEas for the whole vegetation showed statistically significant correlations (Fig. 3.4a). Evenness components of PTas were weakly correlated to richness component of PEas, but almost negatively to their PEas counterpart (Fig. 3.4a; ESM 2 App. 1). Evenness components of PTas were better correlated to richness components of PEas for the herb and the within 100 m woody components, but they were weakly negatively correlated to their counterpart for the latter and faintly positive to their counterpart of the former (Fig. 3.4c, d; ESM 2 App. 3 and 4). In most cases, the strongest correlations were found between the richness component of vegetation diversity ($q = 0$) and Hill's numbers for pollen diversity.

All data sets, with the exception of the 10 m woody component, show a rather similar correlation pattern for the different orders of diversity. A decrease in correlation values between the corresponding pollen and vegetation data sets is observed as the order of diversity increases for the vegetation component. In the 10 m woody data set the strongest correlations were encountered when comparing low orders of vegetation diversity ($q = 0$ to 1) with high orders of pollen diversity (32 to $\infty$).

For Ciomadul only one combination of pollen and vegetation, the 100 m woody data set for $q = 0$, yielded a statistically significant correlation (Fig. 3.5c; ESM 2 App. 2). In general, evenness ($q \geq 2$) rather than richness components of woody PTas were better correlated with all orders of diversity of the corresponding 10 and 100 m vegetation data sets (Fig. 3.5 b, c; ESM 2 Apps. 6 and 7). Unlike the Pieria data, a positive though weak correlation is observed between evenness components of PTas and PEas for the 100 m woody vegetation data set (Fig. 3.5 b). Remarkably low correlations were recorded between the 10 m data sets of vegetation (with and without the herb component) and corresponding PTas for all combinations of diversity orders (Fig. 3.5a, b; ESM 2 Apps. 5 and 6).

### 3.3.4 Similarity of Gradients between Vegetation plots and Pollen Assemblages

For the Pieria data the first NMDS axis of the diagrams, where the woody component is included (Fig. 3.6a–c, right column), represents a gradient related to altitude and the transition from thermophilous broadleaved forest of *Quercus* and *Ostrya* to the forests in cooler areas of *Fagus sylvatica, Abies borisii-regis and Pinus sylvestris*. The second axis contributes to the discrimination of certain plots in the diagrams, but does not seem to represent a specific ecological gradient. In the diagram showing the herbaceous taxa data set from Pieria (Fig. 3.6d), the first axis mainly discriminates the plots sampled near Pinus sylvestris forests. The second axis, also in the case of the data set of herbaceous taxa, does not reflect a specific ecological gradient.

For Ciomadul, the first axis in the NMDS diagrams in Fig. 3.7 (a–c, right column) represents a transition gradient from the *Abies alba-Fagus sylvatica-Picea abies* mixed stands to the pure or mixed stands of the latter two taxa, *F. sylvatica and P. abies*. It may also represent a moisture gradient of *Abies-Fagus-Picea* mixed stands, indicated by higher frequency and abundance of ferns. The second NMDS axis mainly indicates the differentiation of the two *Pinus sylvestris* forest plots from the plots of pure or mixed *Abies, Fagus and Picea* stands.

The Procrustes tests indicate statistically significant correlations between all ordinations of pollen versus vegetation datasets (Table 3.2). For Pieria, the correlations found between the

ordination diagrams were higher than those for Ciomadul. The higher resemblance between the ordination plots of PTas and PEas for the Pieria data sets in comparison with Ciomadul can be discerned already from the ordination plots (Figs. 3.6a–d and 3.7a–c). The highest correlation between the Pieria data sets was found for the total floristic composition. The second highest correlation was recorded for the 100 m woody component. The latter data set was also the one that resulted in the highest correlation among the three data sets from Ciomadul.

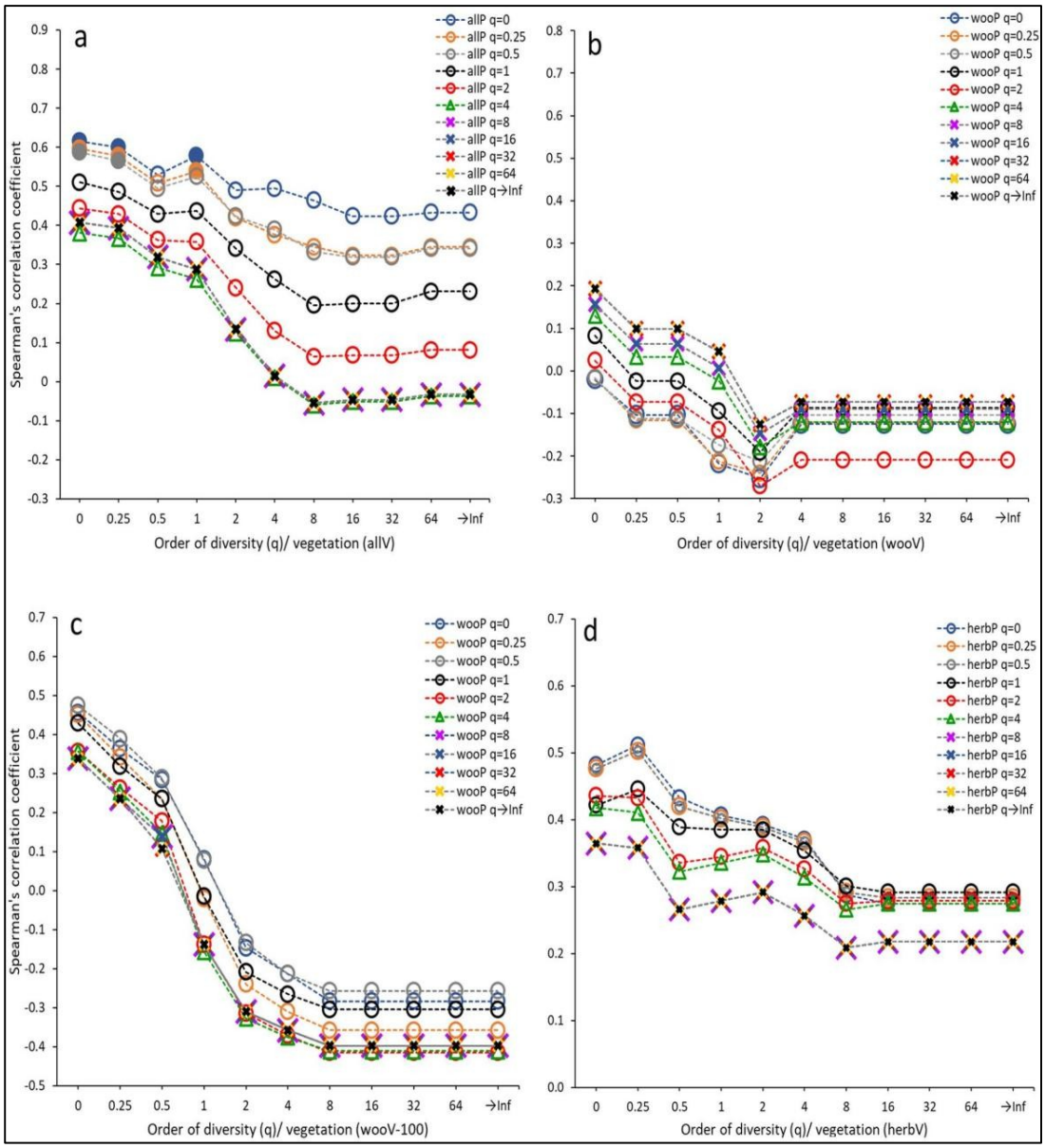


**Figure 3.4:** Patterns of correlation coefficients between Hill's numbers of PTas and PEas for Pieria. Symbols on lines represent correlation coefficients calculated between Hill's numbers of a specific order q of PTas and Hill's numbers of the same and all other selected orders of q of PEas. Filled symbols indicate significant correlations.
**a,** data set of all taxa (allPV);
**b,** woody taxa (wooPV);
**c,** woody taxa and vegetation plots of 100 m radius (wooPV-100);
**d,** herbaceous taxa (herbPV)

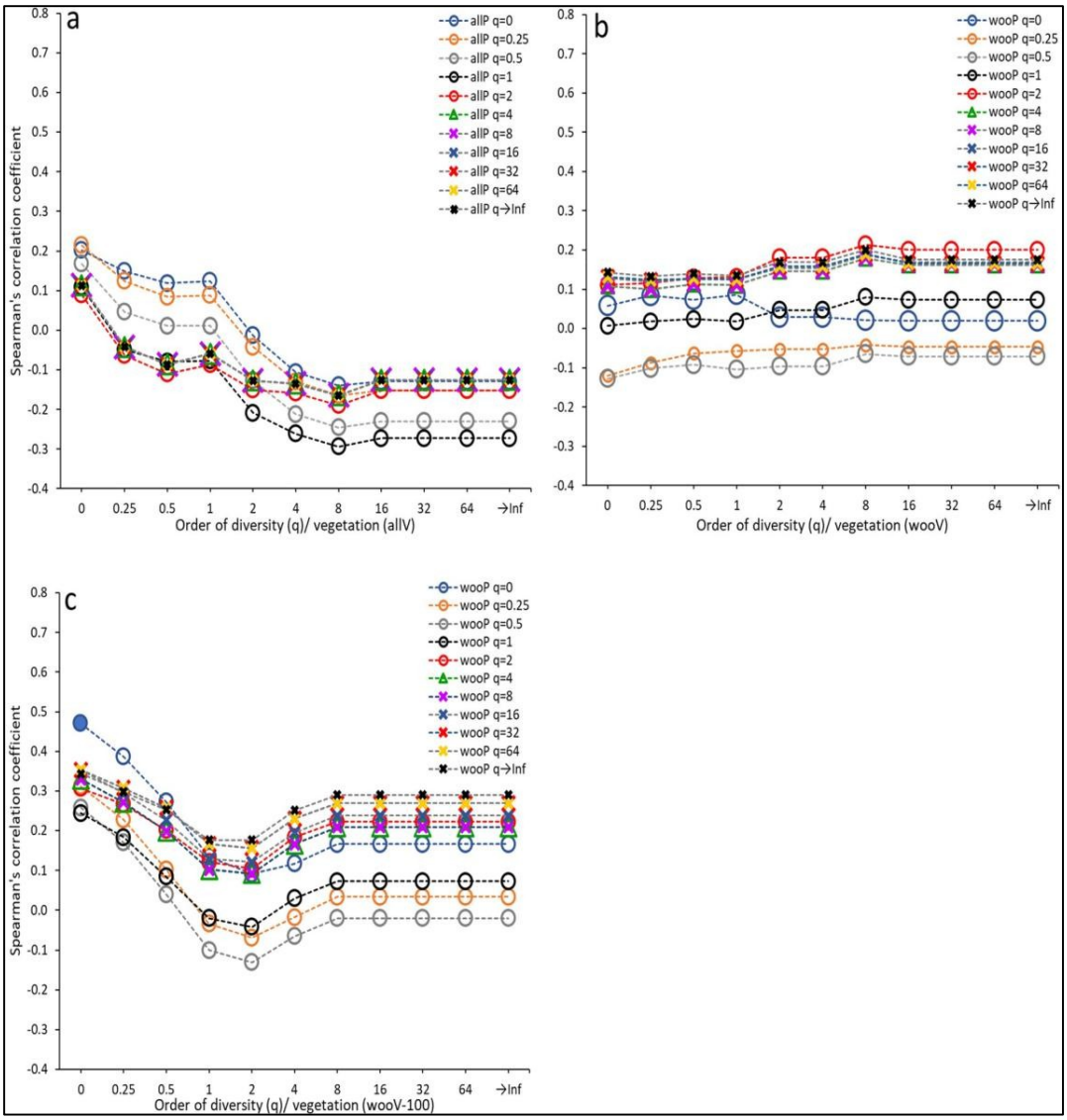


**Figure 3.5:** Patterns of correlation coefficients between Hill's numbers of PTas and PEas for Ciomadul. Symbols on lines represent correlation coefficients calculated between Hill's numbers of a specific order q of PTas and Hill's numbers of the same and all other selected orders of q of PEas. Filled symbols indicate significant correlations; a, data set of all taxa; b, woody taxa; c, woody taxa and 100 m radius vegetation plots

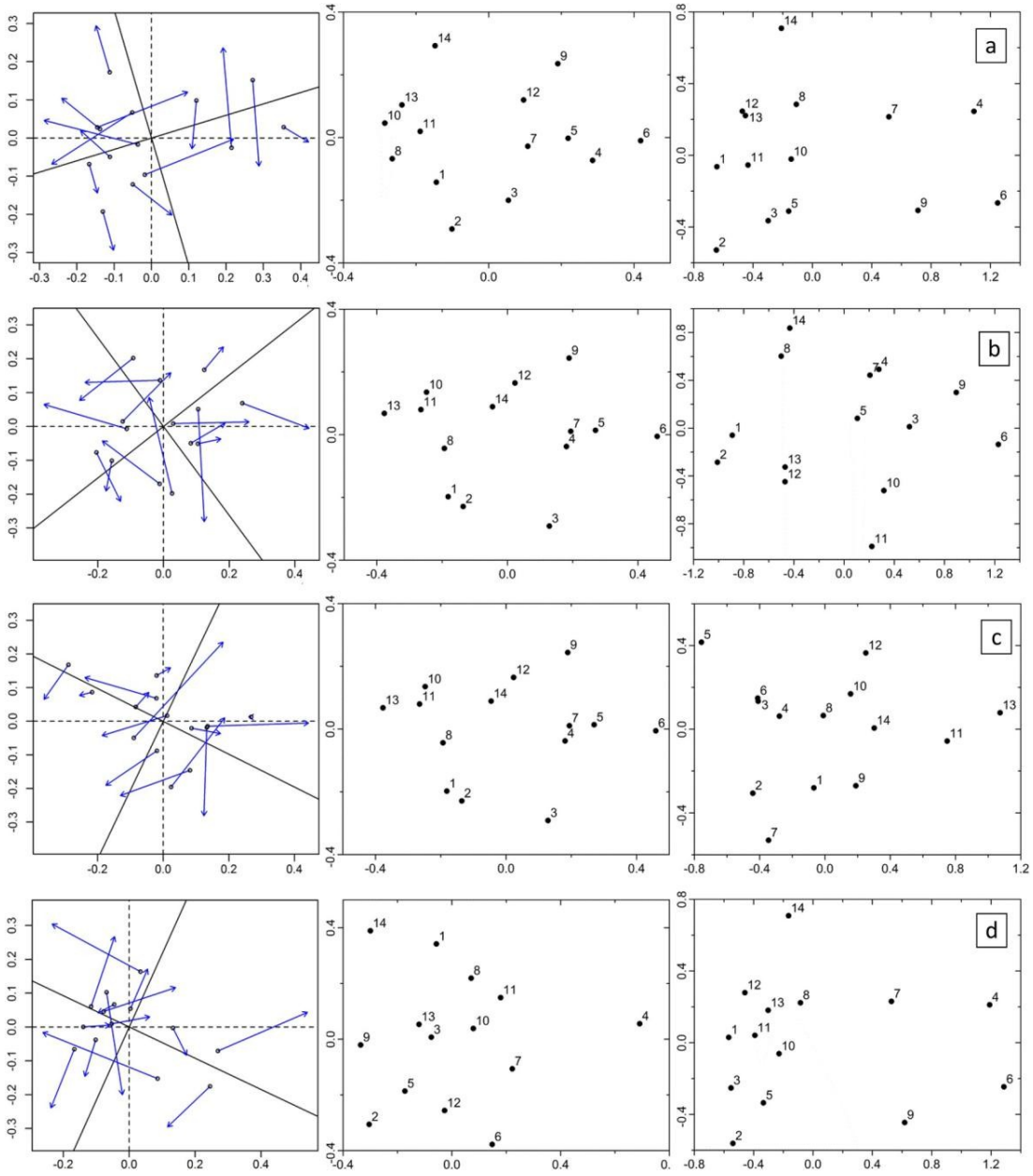


**Figure 3.6:** Pieria; left column, plots of the Procrustes analysis error in the first two dimensions; middle column, ordination plots of site scores along the two first axes of NMDS for the pollen assemblages; right column, vegetation plots. The rows from the top downwards correspond to the data sets of
**a,** the total composition (1st row);
**b,** the 10 m woody component;
**c,** the 100 m woody component;
**d,** the herb component

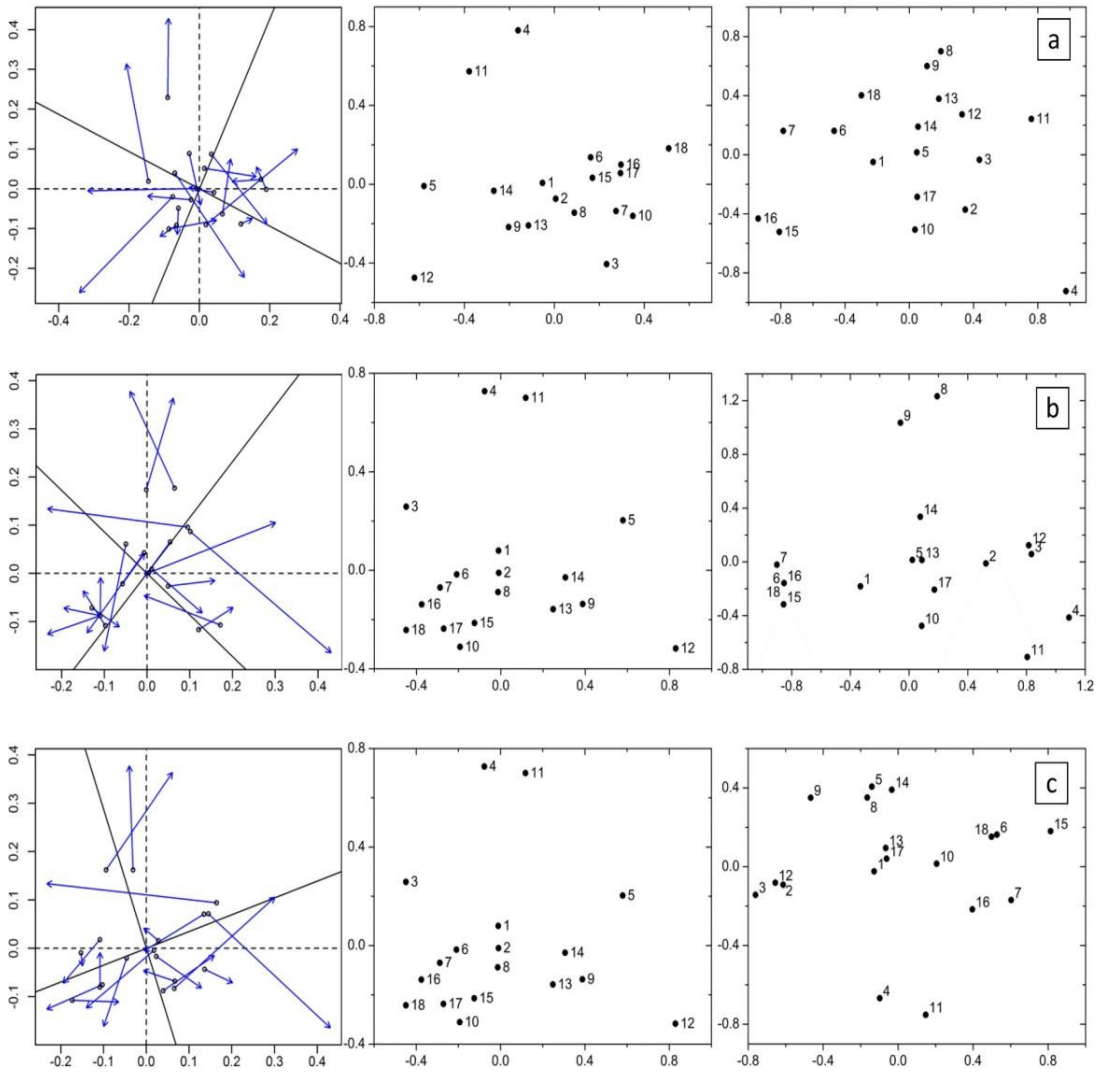


**Figure 3.7:** Ciomadul; left column, plots of the Procrustes analysis errors in the first two dimensions; middle column, ordination plots of site scores along the two first axes of NMDS (non metric multidimensional scaling) for the pollen assemblages; right column, vegetation plots. The rows from top to bottom correspond to the data sets of **a,** the total composition; **b,** the 10 m component; **c,** the 100 m woody component

| | Ineria Mts. | | | Ciomadul | | |
|---|---|---|---|---|---|---|
| | $m^2$ | r | p | $m^2$ | r | p |
| allPV | 0.4858 | 0.7171 | 0.001 | 0.7396 | 0.5102 | 0.018 |
| wooPV | 0.6096 | 0.6248 | 0.008 | 0.705 | 0.5432 | 0.006 |
| wooPV-100 | 0.5991 | 0.6331 | 0.001 | 0.686 | 0.5603 | 0.005 |
| herbPV | 0.6392 | 0.6006 | 0.007 | | | |

**Table 3.2:** Symmetric Procrustes residuals between configurations after optimal fit ($m^2$), correlations (r) between them and their significance on the basis of permutation tests for the different data sets analysed in the two study areas; NMDS ordination has been run for all the data sets

## 3.4 Discussion

### 3.4.1 Similarity between Pollen Assemblages and Vegetation

In terms of compositional similarity, a generally poor correspondence between pollen and vegetation datasets, scattering around a value of 0.3, was found (Fig.3.3). Although pollen analysis is generally not regarded as a tool to evaluate presence or absence of a plant in the surrounding vegetation, the index reveals closer correspondence for presence/absence compared to abundances. This is due to the differences between taxa in their pollen productivity and dispersal (Davis and Goodlett 1960; Andersen 1970; Prentice 1985; Schäbitz 1989). It is worth noticing that in Pieria, Fagus was poorly represented in pollen assemblages (ESM 1 Table 3), although dominant in the sampled vegetation (Tables 3.1,3.2). Very low pollen representation of Fagus has also been observed at high altitudes (Markgraf 1980) or in immature forests (Kvavadze and Stuchlik 2002) which in our case, may have been further decreased by coppicing (Waller et al. 2012). In contrast, a prolific pollen producer like Pinus, which in the Pieria mountains forms a continuous vegetation belt, dominates all pollen assemblages irrespectively of its presence in the sampled vegetation (ESM 1 Tables 2, 3). The application of correction factors such as Andersen (1970) or models of pollen dispersal with relative pollen productivity estimates such as Sugita (1994) could improve abundance-based similarities between pollen and vegetation and thus their diversity (Felde et al. 2016), but no such means are available for the studied areas. In addition, attempts to adjust for the pollen production of herbaceous taxa introduce additional large uncertainties and may not in all cases improve the relationship (Matthias et al. 2015). In both study regions, the best correspondence between pollen and vegetation was found for the presence or absence comparison of woody taxa within the 100 m radius. The higher similarity in Ciomadul, also for the smaller radius of 10 m, is most probably because the pollen samples were collected from small openings in the tree canopy (ESM 1 Table 4)—hollows in the sense of Calcote (1995)—in a region characterised by a smaller pool of woody taxa and a regional component (mainly from plantations) is essentially absent from the pollen assemblages (Feurdean et al. 2013). The percentage of woody taxa present as pollen but absent from the vegetation is much higher for Pieria at 64.5% (20/31) compared to 26.7% (4/15) in Ciomadul. The relatively good correspondence between pollen and vegetation for the woody taxa in Ciomadul is much reduced when herbaceous pollen is added, due to the large representation bias of herb equivalents in pollen assemblages. We did not make an explicit comparison of the herbaceous taxa for Ciomadul because several moss samples yielded remarkably low herb pollen counts (ESM 1 Table 4), which may be due to *Fagus* and *Picea* pollen swamping these samples in below-canopy situations (compare Matthias et al. 2012).

### 3.4.2 Similarity of diversity patterns between Pollen Assemblages and Vegetation

Comparing the two regions, there is a strong overall relationship between the floristic richness and the number of pollen types standardized to the lowest pollen sum, with 264 plant taxa and 102 pollen and spore types from Pieria versus 134 plants and 82 pollen and spore types from Ciomadul. The richness and evenness relationships of samples within either region are either not very strong or non-existent. The strongest relationship was found in Pieria for herb and total floristic and palynological richness within 10 m of the sample site. Here the local herbaceous flora richness seems to determine total palynological richness if we consider that the ratio of herbaceous taxa present in both PTas and PEas is much higher than that of the woody taxa. When the herbaceous vegetation is singled out, the relationship is weaker and not significant, using Spearman's rank correlation coefficient (Fig. 3.4b, ESM 2 App. 2,), as at least two thirds of the woody pollen types are not present in the vegetation within the 10 m radius. The overall low presence/absence but mostly abundance similarities for the herb dataset indicate poor correspondence between pollen types and equivalents for the taxa found in both pollen and vegetation. Indeed, only eight out of 39 taxa for which both pollen and plant were recorded are well represented in both sets, namely *Crepis*, *Filipendula*, Juncaceae, *Matricaria*, *Potentilla*, *Ranunculus acris*, *Sanguisorba minor* and *Trifolium repens*. Thus, although there is a correlation between palynological and floristic richness for the herbaceous types, this is weakly connected to the local vegetation. The reason for this mismatch is likely the sampling of different canopy openings, which sometimes covered the entire ground surface (100 m radius) of the sampled vegetation (ESM 1 Tables 1, 2). Large openings support a rich herbaceous flora and reduce the size of the gravity component from the nearest trees which swamp the sample with their pollen, as discussed above. Therefore, in addition to the component of the local flora, a larger number of pollen types from the long-distance component are found in these samples at a standard pollen count. Moreover, a thorough vegetation sampling around moss cushions (Shaw and Whyte 2020) indicated that for several pollen taxa the relevant source area of pollen may be larger than the 10 m circle adopted in this study. In the case of Pieria, such vegetation sampling, on the entire surface of the 10 m radius, would have been extremely difficult to do. Meltsov et al. (2011) found higher palynological richness in surface sediment samples from lakes in more open environments, which, although on a different scale, agrees with this interpretation. Woody equivalents and pollen types within the 100 m radius show the strongest correlation for richness ($q = 0$), as also shown in other studies (Meltsov et al. 2011; Felde et al. 2016; Reitalu et al. 2019). Trees are generally prolific pollen producers, so that the pollen types of common trees will be found in all samples regardless of whether the parent tree grows in the close surroundings. This correlation is most likely due to the occurrence of rare woody taxa in the sample plots and their good correspondence in the pollen samples as seen particularly for Ciomadul (ESM 1 Tables 5, 6), where richness correlation was found to be significant. In a similar study, in terms of pollen and vegetation sampling, Blaus et al. (2020) found no significant or high correlation between pollen and woody vegetation

richness, attributing this result partly to the small area sampled. Furthermore, the Ciomadul data also show a relationship between the richness of woody taxa in the vegetation plots and a stronger contribution of the evenness component in the pollen type diversity ($q > 1$). This positive correlation, though not statistically significant, indicates a positive relationship between the richness of high pollen producing plants near a sample site and the evenness of pollen abundances as pointed out by Odgaard (2001). Also, Matthias et al. (2015) found that pollen type evenness rather than richness is most strongly correlated with the richness of vegetation types within 1 km of a lake.

The vegetation sampling for this study used a standardized protocol for studies aiming at a comparison between pollen and vegetation (Bunting et al. 2013). This differs from other investigations aiming to compare floristic and palynological diversity (Meltsov et al. 2011; Felde et al. 2014). In the case of Pieria, it would have been beneficial for the comparison to work with floristic diversity of a wider area and although tree stands were also mapped for the 100 m radius, a separate floristic survey was not done. For Ciomadul, however, the large bias in the representation of herb equivalents in pollen assemblages indicates that further sampling was unnecessary. Another problem when comparing herbaceous vegetation types with pollen is that this component may change drastically between years. At Pieria we addressed this problem by collecting the moss samples at the end of the flowering season, while recording the flora during the flowering season. However, this was not possible for Ciomadul and may have some influence on the results. In terms of woody taxa, most pollen samples from Ciomadul were collected in forest hollows for which RSAP (relevant source area of pollen) is confined within 50-100 m (Calcote 1995). For Pieria, the RSAP for most of the pollen samples is considerably larger, at 300–400 m (Mazier et al. 2008), still we feel that even at this scale of sampling, representation of woody taxa would have shown the mismatches derived from pollen production biases and the fact that a considerable number of wind pollinated woody taxa would grow outside the sampling area.

### 3.4.3 Gradient similarities between Pollen assemblages and Vegetation

The significantly correlated ordinations of corresponding PEa and PTa sets in this study show the ability of pollen assemblages to reflect vegetation composition (Blaus et al. 2020) and the ecological gradients existing in vegetation as also shown by other studies (Hjelle 1999; Felde et al. 2014). Ecological gradients in vegetation plots are the outcome of differences in commonality of local plant equivalents, while gradients in pollen assemblages are much influenced by differences in commonality of extra-local/regional pollen types and differences in pollen production of woody taxa. This is especially the case for Pieria, where a large number of woody pollen types originate from outside the sampled areas and are found in nearly all pollen assemblages, such as *Quercus ilex*-type, *Platanus*, *Corylus*, *Olea* and *Juglans*, which coupled with biases in pollen production for major woody taxa caused in many cases no great similarity or correlation of diversity between PTas and PEas. We tested this idea by deleting taxa from PTas not recorded in vegetation plots (data not presented here) and found a reduction of

PROTEST correlations between the ordinations of PTas and PEas.

## 3.5 Conclusions

Our results add to the still small number of studies investigating the relationship between palynological and floristic diversity, showing that this relationship is complex within regions. At terrestrial pollen sums between 500 and 600 grains, the correspondences between presence or absence of taxa in the pollen assemblage compared with the vegetation were stronger than abundance relationships. Palynological richness, rather than pollen type diversity or evenness, responded most strongly to vegetation richness and diversity. The size of the canopy opening may have determined the local floristic diversity and enhanced the importance of regional pollen type richness, thus causing a correlation between the two components in Pieria. Comparing the floristic and pollen composition shows at best a weak direct correspondence for the herbaceous taxa in Pieria, but a strong correspondence for the woody taxa in Ciomadul. These differences in the results between the two study areas indicate the influence of landscape heterogeneity, canopy openness and vegetation structure, which should be kept constant to ensure comparability.

## 3.6 References

Andersen, S. T. (1970). The Relative Pollen Productivity and Pollen Representation of North European Trees, and Correction Factors for Tree Pollen Spectra. Determined by Surface Pollen Analyses from Forests. *Danmarks Geologiske Undersøgelse II. Række*, *96*, 1–99.

Berglund, B. E., Gaillard, M. J., Björkman, L., & Persson, T. (2008). Long-term changes in floristic diversity in southern Sweden: palynological richness, vegetation dynamics and land-use. *Vegetation History and Archaeobotany*, *17*(5), 573–583.

Beug, H-J. (2004). Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete. Pfeil, München.

Birks, HJB., Birks, H.H. (1980). Quaternary palaeoecology. Edward Arnold, London.

Birks, H. J., & Line, J. M. (1992). The use of Rarefaction Analysis for Estimating Palynological Richness from Quaternary Pollen-Analytical Data. *The Holocene*, *2*(1), 1–10.

Birks, H. J. B., Felde, V. A., Bjune, A. E., Grytnes, J. A., Seppä, H., & Giesecke, T. (2016). Does pollen-assemblage richness reflect floristic richness? A review of recent developments and future challenges. *Review of Palaeobotany and Palynology*, *228*, 1–25.

Blaus, A., Reitalu, T., Gerhold, P., Hiiesalu, I., Massante, J. C., & Veski, S. (2020). Modern Pollen–Plant Diversity Relationships Inform Palaeoecological Reconstructions of Functional and Phylogenetic Diversity in Calcareous Fens. *Frontiers in Ecology and Evolution*, *8*.

Bunting, M. (2003). Pollen–vegetation relationships in non-arboreal moorland taxa. *Review of Palaeobotany and Palynology*, *125*(3–4), 285–298.

Bunting, M., Farrell, M., Broström, A., Hjelle, K., Mazier, F., Middleton, R., Nielsen, A., Rushton, E., Shaw, H., & Twiddle, C. (2013). Palynological perspectives on vegetation survey: a critical step for model-based reconstruction of Quaternary land cover. *Quaternary Science Reviews*, *82*, 41–55.

Calcote, R. (1995). Pollen Source Area and Pollen Productivity: Evidence from Forest Hollows. *The Journal of Ecology*, *83*(4), 591.

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*, *84*(1), 45–67.

Chester, P. I., & Raine, J. I. (2001). Pollen and spore keys for Quaternary deposits in the northern Pindos Mountains, Greece. *Grana*, *40*(6), 299–387.

Coldea, G. (1991). Prodrome des associations végétales des Carpates du sudest (Carpates roumanies). Doc Phytosociol, 13:317–539

Colombaroli, D., & Tinner, W. (2013). Determining the long-term changes in biodiversity and provisioning services along a transect from Central Europe to the Mediterranean. *The Holocene*, *23*(11), 1625–1634.

Davis, M. B., & Goodlett, J. C. (1960). Comparison of the Present Vegetation with Pollen-Spectra in Surface Samples from Brownington Pond, Vermont. *Ecology*, *41*(2), 346–357.

Ellison, A. M. (2010). Partitioning diversity1. *Ecology*, *91*(7), 1962–1963.

Fall, P. L. (2012). Modern vegetation, pollen and climate relationships on the Mediterranean island of Cyprus. *Review of Palaeobotany and Palynology*, *185*, 79–92.

Felde, V. A., Peglar, S. M., Bjune, A. E., Grytnes, J. A., & Birks, H. J. B. (2014). The relationship between vegetation composition, vegetation zones and modern pollen assemblages in Setesdal, southern Norway. *The Holocene*, *24*(8), 985–1001.

Felde, V. A., Peglar, S. M., Bjune, A. E., Grytnes, J. A., & Birks, H. J. B. (2015). Modern pollen–plant richness and diversity relationships exist along a vegetational gradient in southern Norway. *The Holocene*, *26*(2), 163–175.

Feurdean, A., Parr, C. L., Tanţău, I., Fărcaş, S., Marinova, E., & Perşoiu, I. (2013). Biodiversity variability across elevations in the Carpathians: Parallel change with landscape openness and land use. *The Holocene*, *23*(6), 869–881.

Gerasimidis, A., & Panajiotidis, S. (2010). 9. Flambouro, Pieria Mountains (northern Greece). *Grana*, *49*(1), 76–78.

Gerasimidis, A., Panajiotidis, S., Hicks, S., & Athanasiadis, N. (2006). An eight-year record of pollen deposition in the Pieria mountains (N. Greece) and its significance for interpreting fossil pollen assemblages. *Review of Palaeobotany and Palynology*, *141*(3–4), 231–243.

Giesecke, T., Ammann, B., & Brande, A. (2014). Palynological richness and evenness: insights from the taxa accumulation curve. *Vegetation History and Archaeobotany*, *23*(3), 217–228.

Giesecke, T., Wolters, S., van Leeuwen, J. F. N., van der Knaap, P. W. O., Leydet, M., & Brewer, S. (2019). Postglacial change of the floristic diversity gradient in Europe. *Nature Communications*, *10*(1).

Gotelli, NJ., Chao, A. (2013). Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. In: Levin SA (ed) Encyclopedia of biodiversity vol 5, 2nd edn. Elsevier, Amsterdam, 195-211.

Hicks, S., Amman, B., Latałowa, M., Pardoe, H., Tinsley, H. (1996). Europaean Pollen Monitoring Programme. Oulu University Press, Oulu, Project Description and Guidelines.

Hill, M. O. (1973). Diversity and Evenness: A Unifying Notation and Its Consequences. *Ecology*, *54*(2), 427–432.

Hjelle, K. L. (1997). Relationships between pollen and plants in human-influenced vegetation types using presence-absence data in western Norway. *Review of Palaeobotany and Palynology*, *99*(1), 1–16.

Hjelle, K. L. (1999). Modern pollen assemblages from mown and grazed vegetation types in western Norway. *Review of Palaeobotany and Palynology*, *107*(1–2), 55–81.

IBM Corporation Released (2012) IBM SPSS statistics for windows, Version 21.0. IBM corporation, Armonk, NY

Jackson, ST. (1994). Pollen and spores in Quaternary lake sediments as sensors of vegetation composition: theoretical models and empirical evidence. In: Traverse A (ed) Sedimentation of organic particles. Cambridge University Press, Cambridge, 253–286

Jost, L. (2006). Entropy and diversity. *Oikos*, *113*(2), 363–375.

Katsavouni, S., Doulgeris, C., Papadimos, D. (eds) (2014). Time series of meteorological data spatially distributed within the four pilot sites, 3rd edn. Thermi, Greek Biotope Wetland Centre (EKBY).

Kvavadze, E.V., Stuchlik, L. (2002). Relationship between biodiversity of recent pollen spectra and vegetation of beech forests in Caucasus and Carpathian Mountains. *Acta Paleobotany*, 42:63–92.

Legendre, P., Birks, HJB. (2012). From classical to canonical ordination. In: Birks HJB, Lotter AF, Juggins S, Smol JP (eds) Tracking envi- ronmental change using lake sediments, vol 5. Data handling and numerical techniques. Springer, Dordrecht, 201–248.

Markgraf, V. (1980). Pollen Dispersal in a Mountain Area. *Grana*, *19*(2), 127–146.

Matthias, I., Nielsen, A. B., & Giesecke, T. (2012). Evaluating the effect of flowering age and forest structure on pollen productivity estimates. *Vegetation History and Archaeobotany*, *21*(6), 471–484.

Matthias, I., Semmler, M. S. S., & Giesecke, T. (2015). Pollen diversity captures landscape structure and diversity. *Journal of Ecology*, *103*(4), 880–890.

Mazier, F., Broström, A., Gaillard, M. J., Sugita, S., Vittoz, P., & Buttler, A. (2008). Pollen productivity estimates and relevant source area of pollen for selected plant taxa in a pasture woodland landscape of the Jura Mountains (Switzerland). *Vegetation*

*History and Archaeobotany*, *17*(5), 479–495.

Meltsov, V., Poska, A., Odgaard, B. V., Sammul, M., & Kull, T. (2011). Palynological richness and pollen sample evenness in relation to local floristic diversity in southern Estonia. *Review of Palaeobotany and Palynology*, *166*(3–4), 344–351.

Odgaard, B. V. (1999). Fossil pollen as a record of past biodiversity. *Journal of Biogeography*, *26*(1), 7–17.

Odgaard, B. V. (2001). Palaeoecological perspectives on pattern and process in plant diversity and distribution adjustments: a comment on recent developments*. *Diversity and Distributions*, *7*(4), 197–201.

Odgaard, B. V. (2008). Species richness of the past is elusive-evenness may not be. Terra Nostra 2:209

Oksanen J (2015) Multivariate analysis of ecological communities in R: vegan tutorial. http://cc.oulu.fi/~jarioksa/opetus/metodi/vegan tutor.pdf

Oksanen J, Blanchet FG, Kindt R et al (2013) Vegan: Community Ecology Package. R package version 2.0-9. http://CRAN.R-proje ct.org/package=vegan

OriginLab Corporation (1991-2006) OriginPro, version 7.5 SR6.OriginLab Corporation, Northampton, MA

Peres-Neto, P. R., & Jackson, D. A. (2001). How well do multivariate data sets match? The advantages of a Procrustean superimposition approach over the Mantel test. *Oecologia*, *129*(2), 169–178.

Prentice, I. (1985). Pollen Representation, Source Area, and Basin Size: Toward a Unified Theory of Pollen Analysis. *Quaternary Research*, *23*(1), 76–86.

R Core Team (2014) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/

Reille. M. (1992). Pollen et Spores d' Europe et d' Afrique du Nord. Laboratoire de Botanique Historique et Palynologie, Marseille.

Reille, M. (1995). Pollen et Spores d' Europe et d' Afrique du Nord. Laboratoire de Botanique Historique et Palynologie, Marseille.

Reitalu, T., Bjune, A. E., Blaus, A., Giesecke, T., Helm, A., Matthias, I., Peglar, S. M., Salonen, J. S., Seppä, H., Väli, V., & Birks, H. J. B. (2019). Patterns of modern pollen and plant richness across northern Europe. *Journal of Ecology*, *107*(4), 1662–1677.

Rull, V. (1987). A note on pollen counting in palaeoecology. *Pollen Spores*, 29:471–480.

Schäbitz, F. (1989). Untersuchungen zum aktuellen Pollenniederschlag und zur holozänen Klimaund Vegetationsentwicklung in den Anden Nord-Neuquéns, Argentinien. Bamberger geographische Schriften 8, Universität Bamberg, Bamberg.

Shaw, H., & Whyte, I. (2020). Interpretation of the herbaceous pollen spectra in paleoecological reconstructions: A spatial extension of Indices of Association and determination of individual pollen source areas from binary data. *Review of Palaeobotany and Palynology*, *279*, 104238.

Spearman, C. (1904). The Proof and Measurement of Association between Two Things. *The American Journal of Psychology*, *15*(1), 72.

Sugita, S. (1994). Pollen Representation of Vegetation in Quaternary Sediments: Theory and Method in Patchy Vegetation. *The Journal of Ecology*, *82*(4), 881.

Tantau, I., Reille, M., de Beaulieu, J. L., Farcas, S., Goslar, T., & Paterne, M. (2003). Vegetation history in the Eastern Romanian Carpathians: pollen analysis of two sequences from the Moho? crater. *Vegetation History and Archaeobotany*, *12*(2), 113–125.

Tichý, L., Holt, J., Nejezchlebová, M. (2011). Juice, Program for management analysis and classification of ecological data, 2nd edn of the program manual. Masaryk University Brno, Czech Republic, Vegetation Science Group.

Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M., Webb, D.A. (ed) (1968, 1972, 1976, 1980) Flora Europaea, Vol. 2-5. Cambridge University Press, Cambridge.

Tutin, T.G., Burges, N.A., Chater, A.O. et al (1993) Flora Europaea, Vol 1: Psilotaceae to Platanaceae, 2nd edn. Cambridge University Press, Cambridge.

van der Knaap, W. (2009). Estimating pollen diversity from pollen accumulation rates: a method to assess taxonomic richness in the landscape. *The Holocene*, *19*(1), 159–163.

Waller, M., Grant, M. J., & Bunting, M. J. (2012). Modern pollen studies from coppiced woodlands and their implications for the detection of woodland management in Holocene pollen records. *Review of Palaeobotany and Palynology*, *187*, 11–28.

# IV Human-landscape interactions in Halkidiki (NC Greece) over the last 3.5 millennia, revealed through Palynological, and Archaeological-historical archives


## Abstract

The palynological investigation of a sediment core from the Tristinika coastal marsh reveals the strong correlation between vegetation development and human settlement in Halkidiki and provides the first complete record of vegetation transformations over the last 3.5 millennia. Taking into consideration the climatic variability of this period, the correlation of pollen data to the rich archaeological and historic archives elucidates the interactive human-environment relationship, in the vicinity of Torone an important ancient harbour of Halkidiki and Mount Athos with its great monastic history. The pollen record shows distinct landscape changes in which an impressive dominance of *Erica* heaths is succeeded by the expansion of Mediterranean pine woodlands and other maquis vegetation and different land uses (olive, cereal cultivation) show alternating phases of expansion and contraction. Signs of *Olea* and cereal cultivation appear in the Mycenaean era. Extensive *Olea* cultivation marks the Archaic/mid-Roman era and post-Byzantine/modern era. Systematic cereal cultivation starts in the Archaic but peaks in late-Roman/early-Byzantine era, it returns in the post-Byzantine era and peaks in Ottoman/Modern Times. Animal husbandry is the most regular human activity in the area and the cause of the great expansion of heaths. The most impressive phase of the diagram coincides with the period of the plague of Justinian (6th–8th century CE) that leads to a collapse of human activity in the area and to an abrupt expansion of Mediterranean pine and oak woodlands due to favorable climatic conditions and the lack of grazing pressure.



**Keywords**: Paleoecology, Pollen analysis, Halkidiki, Antiquity, Roman, Byzantine, Ottoman, Justinian plague


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## 4.1 Introduction

Understanding past climatic Coastal sites in the Mediterranean are suitable places for the study of past vegetation changes and the assessment of the major factors that drives them i.e., anthropogenic impact and climate change (Athanasiadis, 1975; Caroli and Caldara, 2007; Kouli, 2012). Archaeological excavations and historical sources on coastal or near-coast human settlements usually reveal a versatile human activity (animal husbandry, farming, trading). Palynological data from coastal deposits which are close to such human settlements can be compiled with the above mentioned sources and offer new insights to the interactions that shaped the human/natural environment (Marinova and Atanassova, 2006; Pavlopoulos et al., 2010; Triantaphyllou et al., 2010; Kouli, 2012).

Halkidiki which is located in NC Greece (Fig. 4.1) is an iconic place of Greece due to its morphology and especially its three long projecting peninsulas (Kassandra, Sithonia and Athos). In the frame of a multi-disciplinary project launched in 2014 a group of researchers who specialize mainly on Ancient, Roman, Byzantine and Ottoman era compiled data from archaeological excavations and historic archives to produce an environmental history of Halkidiki. In the frame of the same project a palynological research, the first in the coastland of Halkidiki, was undertaken in the Tristinika marsh near Torone (Sithonia). Out of the 7 m long core recovered from the marsh, the first 4.5 m which correspond to the period from Antiquity to Modern Times were analysed. This paper presents these palynological data and highlights their strong correlation to archaeological and historical sources mainly of the Sithonia peninsula and the NE parts of Halkidiki. Finally, a first attempt is made to compare pollen signal of this coastal site with that of a marine core collected outside the coast of Athos (SL 152, Kotthoff et al., 2008).

## 4.2 Study Area

### 4.2.1 Geographic Setting

The prefecture of Halkidiki lies in the central part of north Greece (Fig. 4.1). In the North Halkidiki borders with Thessaloniki prefecture, while in all other aspects is surrounded by the Aegean Sea. The southern part of Halkidiki ends in three narrow and long peninsulas, the ‘hilly’ Kassandra, the ‘semi-mountainous’ Sithonia (or Longos) and the ‘mountainous’ Athos (or Akti). Its largest mountain range Cholomontas occupies the central part and is succeeded in the east by mount Stratoniko. The highest top of Halkidiki reaching ca 2030 m. lies on Mount Athos. Mount Itamos (ca 800 m), named after the few old yew trees (Itamos is the Greek name of Taxus baccata) growing in the area, occupies the central part of the Sithonia peninsula. Geologically, Sithonia is dominated by granites and granodiorites (Christofides et al., 2007).

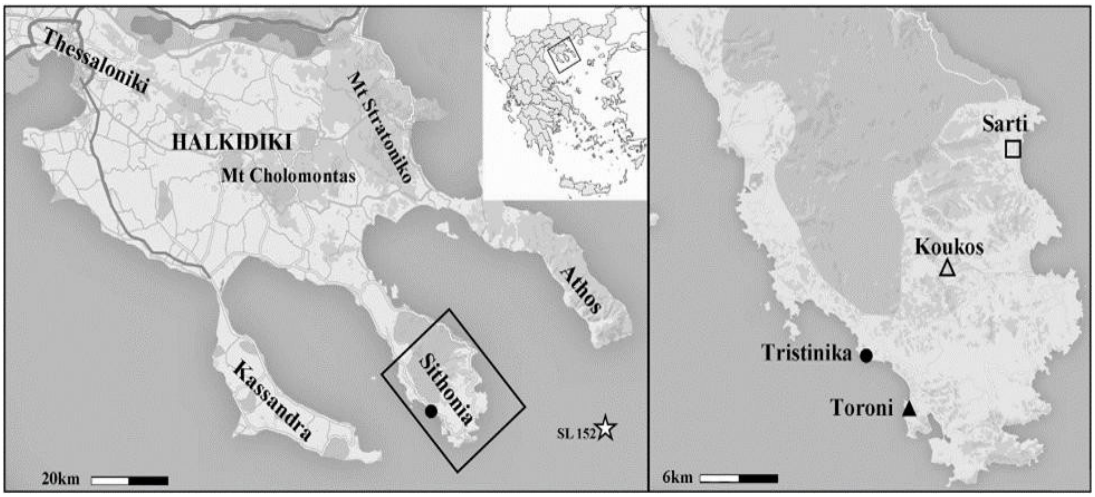


**Fig. 4.1.** Map of Halkidiki showing coring site (Tristinika), nearest marine core (SL 152, Kotthoff et al., 2008) and relevant archaeological sites.

### 4.2.2 Historic Setting

Sithonia has been inhabited from the Bronze Age (3000–1100 BCE) onwards. A major settlement of that period was excavated in Torone (Morris, 2009-2010). Another important settlement of the Geometric (Iron Age) Koukos is very close to Tristinika marsh. Signs of metallurgy related to copper and silver mines of the area came into light. The collapse of the Mycenaean civilization (end of 12th century BCE), due to a cold/dry spell (Drake, 2012) led to the first waves of Greek colonizers in Halkidiki, a place known to them as a source of metal and wood. In the 8th century BCE colonizers from Euboea found Torone on the ruins of a previous prehistoric settlement and transformed it to a major port of antiquity (Tiverios, 2008). Historic sources mention the foundation of thirty cities in Sithonia around the same time although only few sites have been excavated (Tiverios, 2008; Tsigarida and Xydopoulos, 2015). From that era on settlements became sedentary. The area thrived in the following periods especially in Classic/Hellenistic times when Torone became an important trade centre of wood, wine and olive oil and an important member of the Delian League. People lived in the countryside around Torone, as in other cities of Halkidiki, engaging in agriculture and trade. During the Roman climatic optimum culminated in the 1st century BCE (Reale and Dirmeyer, 2000), coastal plains were granted to Roman army veterans and a new revival of agricultural economy was recorded about the end of that era mainly in the Kassandra peninsula.

In the meso-Byzantine era (6th to 8th century CE) sociaupheaval (raids of Slavs and Arabs) but mostly epidemics of plague (Harbeck et al., 2013) led to a reduction of the population in Halkidiki and the abandonment of most ancient cities (Lefort, 2006). By the end of the 9th century CE, when the monastic state of Athos is established, the Byzantine rulers restored peace in the area and granted pieces of land to the monks of

Athos and the wealthy landowners of Thessaloniki. In the post Byzantine era Sithonia like the rest of Halkidiki is 'colonized' by small villages of a few dozens of households, hamlets and 'metochia', fortified estates of the monasteries of Athos (Lefort, 2006). Peasants are usually employed in these estates and/or retain small private pieces of land and very few domesticated animals e.g., pigs, cows, oxen, sheep, goats (Laiou-Thomadakis, 1977). Peasants are engaged in the exploitation of woodlands while the monasteries let large parts of land as winter pastures. All these settlements and estates shifted to wine, olive, cereal and charcoal production, which were traded with major cities like Thessaloniki (Laiou, 1995). A revival of the mining activity in the 16th century (Merle, 2001), which continued in the following centuries took place in north-east Halkidiki, leading to the foundation of villages (Kolovos and Kotzageorgis, 2015); collectively known as 'Siderokavsia' (Siderokavsia means 'smelting iron' in Greek). By mid 15th century CE, at the beginning of the Ottoman occupation, semi-nomadic pastoralists (Yüruks) settled in north Halkidiki (Necipoğlu, 2009). In the following centuries they will use the abandoned fields, dry and wet meadows and maquis of Sithonia as winter pastures.

### 4.2.3 Vegetation/Climate

All vegetation zones of the Greek inland (Athanasiadis, 1985), with the exception of cold-tolerant conifers (boreal forest), are encountered in Halkidiki. This vegetation diversity is determined by altitude, soil and climatic conditions and a long history of human impact (Pavlidis, 1976). The information about the vegetation of Halkidiki given below was retrieved from the "Natura 2000" network, and studies of Mount Cholomontas (Theodoropoulos, 1991), Mount Athos (Athanasiadis et al., 1998) and the Sithonia peninsula (Pavlidis, 1976).

Woodlands or stands of beech (Fagus sylvatica s.l.) are found in high altitude forests, e.g., in Cholomontas, Stratoniko and Athos mountains. Sparse stands and individuals of fir (*Abies borisii-Regis Mattf.*) are found on Mount Athos. Mid-altitudes are occupied mainly by thermophilous oak (*Quercus frainetto Ten., Q. pubescens Willd*.) forests and woodlands (e.g., Cholomondas, Stratoniko, Athos mounts).

The vegetation of Sithonia peninsula is a diverse mixture of pine woodlands (*Pinus halepensis Mill., P. nigra J. F. Arnold and P. pinea L.*), maquis composed of species like *Quercus coccifera L., Olea europaea L., Erica arborea L., E. manipuliflora Salisb., Arbutus unedo L., A. adrachne L., Phillyrea latifolia L., P. media, Pistacia lentiscus L., phrygana* e.g., *Cistus monspeliensis L., Cistus salviifolius L., C. creticus L., Sarcopoterium spinosum (L.) Spach*. Mediterranean pine woodlands (*P. halepensis*) are accompanied by an understorey of maquis which is often dominated by Erica spp. Nowadays only sparse trees and minor stands of deciduous oaks (*Q. frainetto, Q. pubescens*) are encountered in the central part of Sithonia. Nitrophilous, halophytic vegetation (mainly members of Chenopodiaceae family), grazed wet and dry meadows, cultivated fields, and olive groves hosting a variety of ruderals and weeds occupy the

less extended, relatively to the Kassandra peninsula, flat coastal areas and lowlands of Sithonia. The climate of Sithonia according to Köppen's classification belongs to the Csa type (Mediterranean type) and is characterised by long dry and hot periods and low precipitation (Pavlidis, 1976).

Near the tip of the Sithonia peninsula, 6 km north of the village Torone, at about sea level lays the Tristinika marsh (Fig. 4.1). According to an inventory of Greek wetlands the total area of the permanently flooded brackish water marsh of Tristinika (wetland code: 127083000) is 35 ha. However, the total area of the marsh covered by a water body fluctuates between dry and wet seasons (Zalidis and Mantzavelas, 1994).

Though Pavlidis (1976) mentions the impressive thick pockets of reeds (Phragmites communis Trin. and to a lesser extend *Typha latifolia* L.) that are found in the periphery and the centre of the marsh, in our field observations we encountered no *T. latifolia*. Cushions of sedges (*Scirpus maritimus L.)* and rushes (*Juncus maritimus Lam.)* are encountered at the edges of this formation. Present day vegetation around the marsh comprises olive groves, halophytic vegetation, pine stand on the north hillside planted in 1979, thick maquis and grazed meadows.

## 4.3 Methods

A seven-metre long sequence was recovered, using a hand driven chamber corer (Eijkelkamp, 04.09), close to the centre of the Tristinika marsh in June 2014. Five bulk samples were extracted from various depths, including the deepest part of the core and were sent to the CHRONOS laboratory of the University of Belfast for dating with AMS 14C (Table 4.1). Dates were calibrated using Calib 7.0 software (Stuiver and Reimer, 1993). The age-depth model based on all five 14C dates (Fig. 4.2) was constructed with the use of the Clam package (Blaauw, 2010) for R (R Development Core Team, 2010). A smooth spline curve was fitted between the original dated depths (Fig. 4.2). A total of 56 samples, each with a volume of 2 $cm^3$, were extracted ca. every 8 cm from the top 4.5 m of the core. Samples were treated according to a standard scheme of preparation (Faegri and Iversen, 1989).

Identification of pollen grains and spores was based on a key adapted to the Greek flora (Chester and Raine, 2001), routine keys (Moore and Webb, 1978; Beug, 2004), photographic material (Reille, 1992, 1995) and the use of reference material stored in the Laboratory of Forest Botany-Geobotany.

At least 400 pollen grains, with the exception of very few samples, and an independent number of fern spores and charcoals were counted in each slide. Counts of charcoals refer to the number of charcoal particles (Tinner and Sheng Hu, 2003) and the total count of both charcoals and the exotic marker, Lycopodium, was larger than 200–300 particles per slide (Finsinger and Tinner, 2005). Two size classes were recorded: 10–200 μm and N 200 μm. All black opaque, angular particles larger than 10 μm were recognised as charcoals (Whitlock and Larsen, 2002).

| Lab. code | Depth (cm) | Material | $^{14}$C year (BP) | Cal. year (BCE/CE) |
|---|---|---|---|---|
| UBA-28837 | 60 | Bulk organic | 211 ± 31 | CE 1644–1950 |
| UBA-28836 | 160 | « | 1094 ± 23 | CE 892–1010 |
| UBA-28835 | 310 | « | 2660 ± 25 | 893–796 BCE |
| UBA-28834 | 460 | « | 3272 ± 31 | 1624–1460 BCE |
| UBA-28833 | 698 | « | 5138 ± 31 | 4036–3805 BCE |

**Table 4.1:** Age control for core Tristinika based on AMS 14C. Ages calibrated with CALIB 7.0 (Stuiver and Reimer, 1993).

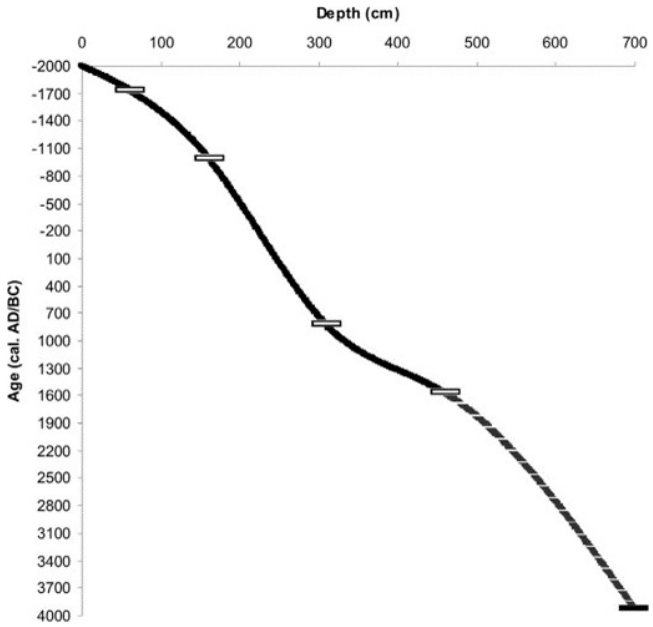


**Fig. 4.2.** Age-depth curve for the entire Tristinika core. Solid line represents ages assigned to the pollen diagram of Fig. 4.3.

### 4.3.1 Remarks on Pollen Identification

Though pollen identification was made to the lowest possible level some pollen types were amalgamated due to their very low presence in the pollen counts e.g., Plantago-type apart from the dominant *Plantago lanceolata*-type comprises also *Plantago coronopus* and *Plantago major*, *Cistus*-type includes *C. monspeliensis*-type and *C. salviifolius*-type, *Centaurea*-type is formed by the combination of *Centaurea cyanus*-type and *Centaurea jacea*-type (Chester and Raine, 2001). Poaceae pollen includes all pollen of wild grasses. In our samples the majority of the Poaceae pollen belongs probably to *Phragmites*-type even though a number of pollen grains were somewhat larger (b 30 μm) than the size barrier (b 26 μm) used by Faegri and Iversen (1989).

### 4.3.2 Remarks on Pollen Indicators-Pollen Representation

In interpreting human impact on the landscape we adopt widely used pollen taxa (Behre, 1981, 1990; Bottema and Woldring, 1990; Mazier et al., 2009) as indicators of arboriculture, agriculture and animal husbandry. Pollen of *Erica, Cistaceae and Sarcopoterium* are considered strong indicators of fire-induced vegetation (Kouli, 2012).
Among the evergreen broad-leaved taxa, *Q. coccifera* and *Erica spp*. are very well represented in pollen spectra, while taxa like *Arbutus spp., Phillyrea, Pistacia spp.* are poorly represented. A few pollen grains of the latter three taxa signal occurrence in the vicinity of the coring site. *Cistaceae* have also a low representation in pollen rain and *Sarcopoterium* an even lower (Bottema, 1974).
The Tristinika marsh lies at the side of a "strip" of hilly land and is actually engulfed in water for several kilometres, which literally means no vegetation. This "peculiarity" allows us to identify the pollen signal of some taxa like Fagus, Abies, as solely background (sensu Sugita, 1994), originating from the Athos peninsula and north, north-east Halkidiki, as indicated by the wind patterns (Kotthoff et. al., 2008). Other pollen taxa that constitute background pollen are *Tilia, Corylus, Carpinus betulus, Ostrya/Carpinus orientalis*.

### 4.3.3 Pollen Diagram

The pollen percentage diagram was based on the sum of all upland taxa (trees, shrubs and herbs). We have placed Poaceae in local vegetation (*Typha, Cyperaceae, Juncaceae*) to avoid the large pollen input of Phragmites that would have suppressed the signal of vegetation that lies further away. Pollen percentage values of local vegetation, spores of ferns and charcoals were calculated based on a larger sum that included pollen of local vegetation and spores of ferns as well. All calculations and graph depictions were performed with TILIA software (Grimm, 1992-2011).

## 4.4 Results

The pollen diagram (Fig. 4.3) comprises a selection of the total of pollen and spore taxa that were identified. Selected taxa are considered good representatives of the different vegetation types encountered in the area and useful tools in interpreting different types of land-use.
Seven pollen assemblage zones (PAZ) indicated with the prefix Trist and numbered from the bottom to the top of the sequence were identified (Fig. 4.3). The zones are described based on qualitative and quantitative changes of major terrestrial taxa. The median and maximum pollen percentage values for abundant taxa are given in all seven zones. Description of the changes in pollen zones is grouped according to major vegetation types.

**Trist-1** (abundant *Erica* heaths, restricted Mediterranean pine woodlands-mixed deciduous forests, signs of *Olea*-*Vitis*-cereal cultivation, grazing and fire pressure).

The zone is characterised by the overall low presence of *Pinus* (median: 8.8%, max: 11.5%). Fire-induced vegetation prevails with *Erica* being the dominant type (heaths, 50.5%, 65.6%) followed by *Cistus* (3.2%, 7.1%) while *Sarcopoterium* is constantly present in most of the zone. Maquis are represented by relatively low fluctuating values which are contributed mainly by evergreen *Quercus* (*Q. coccifera*-type, 6.5%, 12.2%) while *Phillyrea* is constantly present but with very low values. Deciduous oaks (*Quercus pubescens*-type, 8.9%, 13.3%) fluctuate showing distinct low values in the middle of the zone. Their counterpart, *Ostrya*/*Carpinus orientalis* (2.4%, 3.6%) fluctuates, showing two distinct peaks before the middle and near the end of the zone while *Corylus* (1.4%) has a discontinuous curve. The curve of *Fagus* (2%, 3.6%) fluctuates through the whole zone. *C. betulus* is steadily present with very low values (1%, 1.4%). The zone is characterised by signs of *Olea* (1.4%) and *Vitis* (0.6%) cultivation. Signs of cereal (*Triticum*/*Secale*) cultivation are found in the middle and the upper boundaries of the zone. A wide range of pollen indicators of grazing and abandoned fields, and weeds growing in cultivated land are encountered. Asteraceae (5%), Caryophyllaceae (3.3%), *Ranunculus acris*-type (1.7%) are those with the highest maximum values.

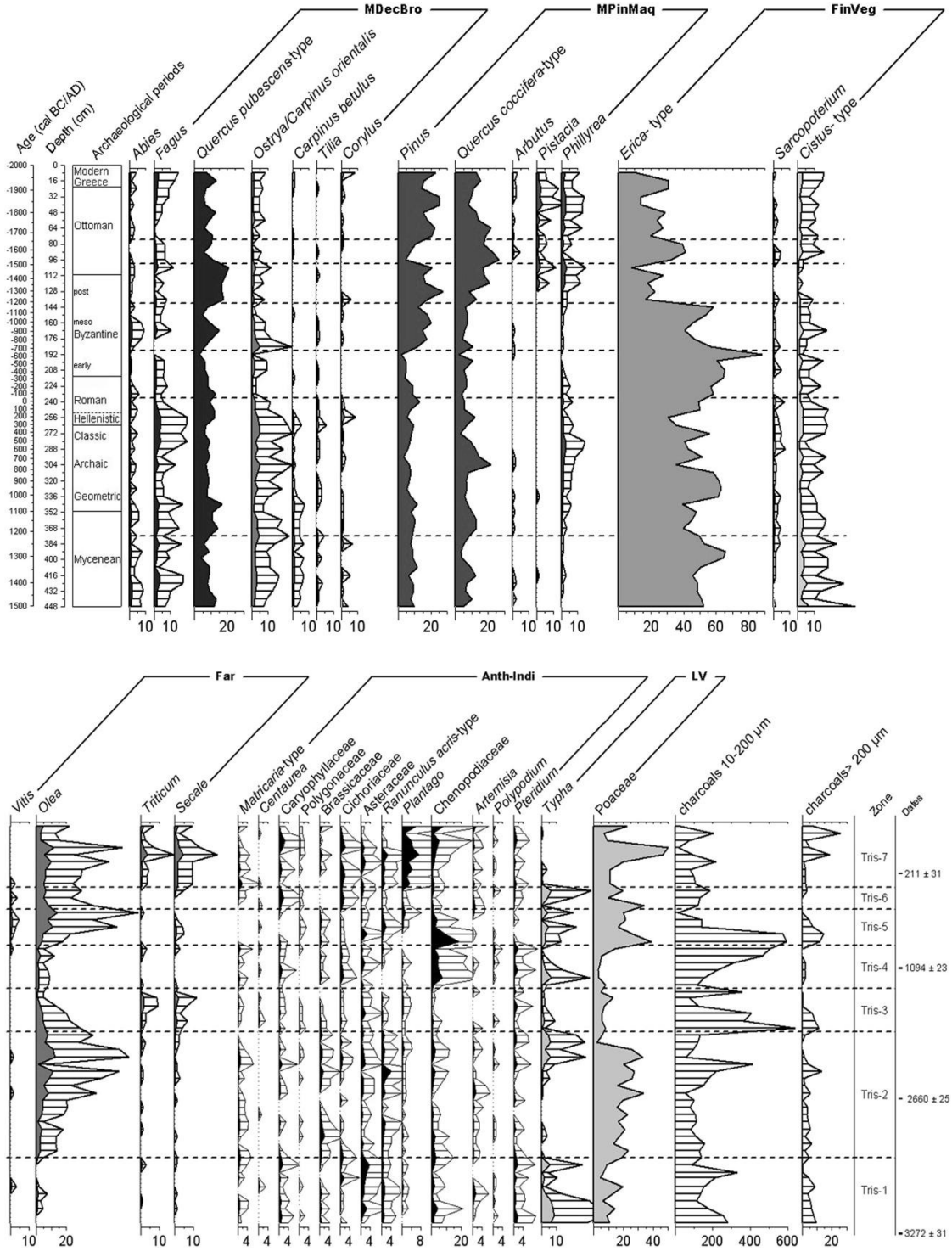


**Fig. 4.3.** Pollen percentage diagram of selected taxa of Tristinika marsh. MDecBro = Mixed Deciduous Broadleaved, MPinMaq = Mediterranean Pine woodlands, Maquis, FInVeg = Fire Induced Vegetation, Far = Farming Indicators, Anth-Indic = Anthropogenic Indicators, LV = Local Vegetation.

**Trist-2** (abundant *Erica* heaths, further reduction of pine woodlands, expansion of *Olea* cultivation, systematic cereal cultivation, grazing and fire pressure).

*Pinus* (7.4%, 12.9%) retreats further, but recovers at the end of the zone with values similar to the start of the zone. Fire-induced vegetation continues as the prevalent type, represented by *Erica* heaths (47.8%, 62.8%) while *Cistus* (2.4%, 3.7%) and *Sarcopoterium* (0.6%, 1.5%) show smaller differences in their pollen values. Maquis are represented by evergreen *Quercus* (8%, 21.8%) which fluctuates intensely though *Phillyrea* (1.2%, 2.9%) becomes also an important element of this type of vegetation. The curve of deciduous *Quercus* (9%, 16.9%) remains steady for a large part of the zone, showing peaks at the first and last quarter of the zone. The curve of *Ostrya*/*Carpinus orientalis* (3.1%, 5%) is fluctuating, while its maximum values usually alternate with those of deciduous *Quercus*. A discontinuous curve characterises the *Corylus* (0.3%, 1.8%) occurrence. *Fagus* (2.4%, 4.1%) retreats in the middle of the zone only to recover in its largest presence for the entire diagram. The trend of the curve of *Carpinus betulus* (0.3%, 1.5%), as in the previous zone, is similar to that of *Fagus*, though its values are lower. The zone is characterised by the intense cultivation of *Olea* (4.2%, 12.4%). Signs of *Vitis* (0.4%) cultivation are traced on the upper middle part of the zone. Cereal cultivation (0.3%, 1%) becomes evident in the entire zone but more systematic in its upper part. *R. acris*-type (4.4%), Caryophyllaceae (3.6%), Asteraceae (3.3%), are the pollen indicators with the highest maximum values. The curve of *Matricaria*-type as in the previous zone follows that of cereals.

**Trist-3** (abundant *Erica* heaths, decline of mixed deciduous and Mediterranean pine woodlands, peak of cereal cultivation, gradual decline of *Olea* cultivation).

This zone is characterised by the lowest values of *Pinus* (4.3%, 8.7%) for the entire sequence. Fire-induced vegetation is represented solely by *Erica* (64.5%, 87.9%) which at the end of the zone becomes the single dominant type in the pollen diagram, while *Cistus* (1.4%, 3.1%) retreats and *Sarcopoterium* appears only on the upper part of the diagram. Maquis are badly represented as pollen values of evergreen *Quercus* (6.4%, 10.7%) are the lowest of the sequence, showing at the end of the zone a drop similar to that of *Pinus*, *Ostrya*/*Carpinus orientalis* and deciduous *Quercus*. *Phillyrea* retreats to low values before disappearing at the end of the zone. The curve of deciduous *Quercus* (6.6%, 8.1%) retreats continuously, showing largest and minimum values at the boundaries of the zone. From this zone onwards the curve of *Fagus* (1.3%, 1.7%) shows low values and gains values as high as those of the previous zones only at the top of the sequence. From this zone onwards, *Ostrya*/*Carpinus orientalis* (0.6%, 1.9%) retreats, although its values increase at the end of the zone. A sporadic occurrence characterizes *C. betulus* not only for the specific zone but also those that follow. A gradual withdrawal of *Olea* cultivation (2.7%, 4.5%) is observed,

while cereal cultivation (2%, 4.3%) expands sharply and falls the same way at the end of the zone. Asteraceae (2.6%) and Caryophyllaceae (1.2%) are the pollen indicators with the highest maximum values.

**Trist-4** (retreat of *Erica* heaths, expansion of oak and Meditteranean pine woodlands, collapse of human activity, fallow lands).

The abrupt expansion of *Pinus* (16.1%, 20%), started at the end of the previous zone, marks this zone. On the contrary, fire-induced vegetation retreats as *Erica* (50.2%, 57.9%) follows a sharp declining course which is only temporarily suspended at the end of the zone. *Cistus* (1.3%, 3.6%) and *Sarcopoterium* show no differentiation in relation to the previous zone. Maquis show no distinct changes as evergreen *Quercus* (6.8%, 10.7%) seem to expand but this trend becomes clear at the end of the zone and *Phillyrea* is weakly represented. A sharp rise and fall characterise the curve of deciduous *Quercus* (8.4%, 14.9%), with the maximum value reached at the middle of the zone. At the start of the zone, *Ostrya*/*Carpinus orientalis* (1.6%, 4.8%) reaches for the last time such a size of maximum value. *Fagus* (0.9%, 2.1%) is absent at the beginning of the zone but continuously present in the rest of the zone. *Olea* cultivation (1.6%, 2.4%) is literally abandoned and the same holds true for cereals (1.2%). Signs of *Vitis* (0.3%) cultivation are traced at the upper end of the zone. Chenopodiaceae (7.3%), Asteraceae (2.6%), Caryophyllaceae (2.3%) and Cichoriaceae (1.5%) are the pollen indicators with the highest maximum values.

**Trist-5** (expansion of deciduous and evergreen oak and pine woodlands, further withdraw of *Erica* heaths, *Olea* cultivation expands, cereal cultivation firm, fallow lands).

The expansion of *Pinus* (17.9%, 27.2%) continues in the current zone with two maxima at the boundaries of the zone. Fire-induced vegetation retreats further as the fluctuating curve of *Erica* (17.7%, 27.1%) reaches the lowest recorded value for the whole sequence at the end of the zone while *Cistus* (0.6%, 1.9%) and *Sarcopoterium* (0.8%) are literally absent. Maquis increase as the curve of evergreen *Quercus* (16.7%, 20.9%) starts a fluctuating but rather steep rise, reaching its maximum value at the middle of the zone. *Phillyrea* (1.8%, 3%) returns to levels similar to those of zone Trist-2. *Pistacia* (2.3%) appears for the first time around the middle of the zone, with a continuous occurrence. The zone is characterised by the highest occurrence of deciduous *Quercus* (17.9%, 20.7%) recorded in the sequence while its counterpart *Ostrya*/ *Carpinus orientalis* (1.5%, 2.3%) continues with a low presence. *Fagus* (1.2%, 2.3%) show no change in its representation. *Olea* cultivation (7.6%, 13.7%) is intensified, reaching values that are the highest for the whole sequence. Cereal cultivation (1.1%) continues with the same intensity as in the previous zone. *Vitis* cultivation (0.9%) is traced in the entire zone. Chenopodiaceae, with an astonishing 18.6%, Asteraceae (4.9%), *R. acris*-type (2%) and *Plantago* (1.7%) are the pollen indicators with the highest maximum values.

**Trist-6** (*Erica* heaths expand, pine and deciduous oak woodlands decline, evergreen oak peak, fire and grazing pressure).

Pinus (6.9%, 10.2%) sharp drop started in the previous zone is completely reversed on the upper end of this zone. Fire-induced vegetation expands as *Erica* recovers (39.4%, 41%) but not to the levels of the first four zones. *Cistus* (1.9%, 3.2%) increase in relation to the previous zone while Sarcopoterium is only present with low values. *Maquis* expand due to evergreen *Quercus* (16.7%, 20.9%) which continues its rather steep rise and diversify as indicated by the simultaneous presence of *Phillyrea* (1.3%, 1.4%), *Pistacia* (1.1%, 1.3%) and *Arbutus*. Deciduous *Quercus* (10.2%, 11%) retreat abruptly at the start of the zone and partially recover by the end. Fagus (1.4%, 1.4%) has a steady but low presence. *Olea* cultivation (6%, 7.8%) remains intense though the maximum pollen value is lower than the previous zone. A short abandonment of cereal cultivation (1%) is succeeded by a noticeable expand. Vitis cultivation (0.6%) continues to be present. *Caryophyllaceae* (2.3%), *Asteraceae* (2.2%), *Cichoriaceae* (1.6%), are the pollen indicators with highest maximum values.

**Trist-7** (Mediterranean pine woodlands expand, diversified maquis, versatile human activity: *Olea* cultivation, intense cereal cultivation, animal husbandry).

Pinus (20.5%, 25.5%) curve shows characteristic peaks in the boundaries and the middle of the zone. *Erica* (23.7%, 30.6%) pollen values alternate with those of Pinus, showing a peak around the end of the zone. Pollen values of *Cistus* (2.3%, 3.2%) are stabilised in relation to the previous zone, while Sarcopoterium (0.6%) is only discontinuously present. The curve of evergreen *Quercus* (12.7%, 21.9%) drops gradually towards the middle of the zone and then rises in the same way. *Phillyrea* (2.2%, 2.8%) and *Pistacia* (1.3%, 3.6%), accompanied by Arbutus, show the same trend in their curves, characterised by fluctuations and higher values than in the previous zone. Presence of deciduous *Quercus* (7.3%, 13%) returns to levels seen in a large part of sequence. The same holds for the curve of *Ostrya/Carpinus* orientalis (1%, 1.7%), as its values reflect the trend of retreat shown in the upper half of the sequence. *Fagus* (1%, 3%) shows a steady increase all the way to the top of the zone. *Olea* cultivation (5%, 11.5%) is established as the main human activity. Cereal cultivation (2.7%, 8.2%) becomes almost equally important by the middle of this zone. The last signs of Vitis cultivation (0.6%) are encountered in the beginning of the zone. *Chenopodiaceae* (8.1%), *Plantago* (7.7%), *Caryophyllaceae, Asteraceae* (3.4%), *R. acris-type* (3.1%) and *Cichoriaceae* (2.3%) are the pollen indicators with the highest maximum values.

## 4.5 Discussion

The discussion of the results is divided in two parts. In the first we deal with the early period of the pollen diagram (Mycenean/Roman era, Trist1–mid Trist3) and in the second with Byzantine era/modern era (roughly mid Trist3–Trist7).

### 4.5.1 Mycenean/Roman era

The pollen diagram of that period reveals a continuous management of vegetation through a controlled fire management that favors secondary vegetation of phrygana (*Cistus* and *Sarcopoterium*) and heaths (*Erica*) a practice that renews food resources for goats mostly and sheep. Post-fire studies in maquis of Sithonia (Papanastasis, 1988) mark the short temporal expansion of phrygana and the succession by heaths that eventually dominate the maquis within a period of 10 years. The remarkable dominance of *Erica* in the pollen diagram points to a regular burning mainly of maquis patches throughout the entire period. In places intense overgrazing creates degraded dry heathlands, which are indicated by the presence of *Pteridium and Polypodium* (Behre, 1981). Wet meadows, indicated by e.g. *Plantago, R. acris-type, Asteraceae, Cichoriaceae, Caryophyllaceae* (Behre, 1981), are equally important pastures. Metallurgical works demand strong heat which can be provided by charcoal of evergreen and deciduous oak wood customarily produced at that time (Horne, 1982). However, exploitation of deciduous oak woodlands is rather patchy and not systematic as revealed by the mixed composition of deciduous broadleaved forests in this part of the pollen diagram. The noticeable maquis elements, mainly kermes oak (Q. coccifera) and to a less extend *Phillyrea*, are well adapted to both fire and grazing, though intensive exploitation subjects them from time to time to strong suppression. The cold/dry spell (Drake, 2012) in the end of the Mycenean (end of Trist-1) is indicated by the sharp reduction of *T. latifolia* a plant species known for its aggressive invasion in saline marshes when the latter are flooded with freshwater (Apfelbaum, 1985). Reduction in humidity is also indicated by the recession of *Fagus* (Geometric to Archaic), though with a time lag, in relation to *Typha*. Both taxa reemerge in the Classic to early Roman era (upper part of Trist-2) a period assumed to have relatively warmer/wetter conditions (Reale and Dirmeyer, 2000). Under continuous grazing pressure and the exploitation for their wood and resin Mediterranean pine woodlands remain suppressed despite the favorable climatic conditions. This is evident especially in the relatively dry period of the Geometric/Hellenistic times (Trist-2). Signs of olive cultivation are traced in the lowest part of the diagram (Tris-7) corresponding to the Mycenean period particularly around 14th century BCE. Signs going back around this period have also been traced in the diagram of Bottema from Giannitsa (Athanasiadis et al., 1993a). Systematic cultivation, as in southern Greece (Kouli, 2012), starts in the Geometric period and culminates in the Archaic to early Roman era. The least-resistant to grazing native *O. europaea var. sylvestris*, an important palatable element of maquis, acquires a significantly random and scarce distribution with intense grazing (Alados et al., 2004).

It is apparent in the pollen diagram that the gradual rise of Olea pollen values is the result of its systematic cultivation. Signs of cereal (*Triticum*/*Secale*) cultivation, like olive cultivation, are traced back to Mycenaean but it becomes a firm human activity when more sedentary settlements are established in the area (from Archaic onwards) and culminates at the end of Roman era/early Byzantine period (end of Trist-3) when it partly replaces olive groves. The signs of *Vitis* cultivation are sparse and insignificant despite the fact that the trade of wine was a major activity in Antiquity. Pollen of *Vitis* is hardly dispersed outside a vineyard (Athanasiadis et al., 1993b) meaning that only occasionally the area around Tristinika was used for such cultivation.

### 4.5.2 Byzantine/Modern Era

#### 4.5.2.1 Decline of Human Activity - 'Plague of Justinian'

Perhaps the most intrinsic part of the diagram is the transition zone of PAZs Trist-3 and Trist-4. Reconstruction of past climate from a marine sediment collected about 30 km outside Tristinika (Ehrmann et al., 2007) indicates an intense dry period between 3rd–10th century CE (mid Trist3–mid Trist4) culminating around the 7th century CE. This drought event is justified in the pollen diagram by the total or near absence of Fagus pollen. Despite the drought, Mediterranean pine woodlands are nearly diminished by the end of early Byzantine period probably due to severe exploitation but 'shortly' afterwards burst reaching the area of Tristinika marsh. Oak woodlands also expand in a relatively same mode. Pavlidis (1976) observed that abandoned arable fields and cereal fields, after harvesting, are colonized heavily by members of the Chenopodiaceae. In the diagram the extended cereal fields of the early Byzantine times, probably located around Tristinika marsh, turn to fields occupied by Chenopodiaceae which show for the first time such high pollen values. Olea pollen values drop to the lowest levels for the entire diagram. These relatively short term changes in vegetation point to an expansion of the natural woody vegetation in a landscape where human activity has literally collapsed. This collapse takes place within a period when the 'plague of Justinian' plundered the Mediterranean world from mid 6th to mid 8th century CE (Harbeck et al., 2013). The proximity of Tristinika to the port of Torone further supports the hypothesis that the local population was devastated by the plague, a disease which spread by sea-born trade.

#### 4.5.2.2 Comparison of Tristinika with Marine Core SL 152

We attempt here a short comparison of our pollen record with that of the marine core SL 152 (Kotthoff et al., 2008) which covers the last 20,000 years and was collected about 20 km outside the coast of Athos (Fig 4.1). The core is the nearest to Tristinika marsh and is provided with a robust age-depth model. Pollen assemblages of SL 152 originate from a wider region (mainly coasts of N. Greece) but it is likely that Sithonia and Athos, due to their proximity, are important 'sources' of the recorded pollen assemblages.

Our pollen diagram falls with the upper half-part of the middle to late Holocene zone of SL 152 (Fig 4.3). The most striking feature of that part of SL 152 is the curve of Erica pollen which reaches values of 10% while it is virtually absent from the rest of the diagram. Considering the relevant distances of Tristinika and SL 152 cores from the Erica heathlands of Sithonia the high Erica values of the former are well substantiated. In both diagrams Quercus (deciduous and evergreen) pollen is the most important element of broadleaved vegetation. Quercus pollen values are lower in the Tristinika diagram but it is anticipated as human influence upon the vegetation is strong. Both diagrams are characterised by an almost continuous curve of Ostrya/Carpinus orientalis pollen, moreover this trend occurs only in this part of the SL 152 diagram.

## 4.6 Conclusion

Palynological studies correlated with archaeological data and historic archives could become valuable tools in understanding past vegetation changes and the role of humans and climate on these changes. Coastal sites having a long history of settlements are ideal for detecting and investigating the past human and natural landscape. The presented pollen diagram from the Tristinika marsh of Sithonia, Halkidiki, reveals the human/landscape interactions over the last 3.5 millennia. An aggressive grazing pressure and exploitation of the Mediterranean pine forests and maquis is observed throughout Antiquity. Changes in animal husbandry practices and introduction of a variety of animals could have a significant impact in the shape of natural vegetation as seen by the reduction of secondary fire-induced vegetation (heaths, phrygana). Cultivation of *Olea* shows two distinct periods of expansion Geometric/late Roman occupation and post Byzantine/Modern Times. The pattern is repeated with the cultivation of cereals but for somewhat different time periods (Archaic/early Byzantine and Ottoman occupation/Modern Times). The Tristinika pollen diagram is the first among a series of pollen diagrams from northern Greece which provides strong evidence of the plague of Justinian (Izdebski et al., 2015) and gives a clear picture of the effect which the sudden absence of man has on the restoration of natural vegetation.

## 4.7 References

Alados, C. L., ElAich, A., Papanastasis, V. P., Ozbek, H., Navarro, T., Freitas, H., Vrahnakis, M., Larrosi, D., & Cabezudo, B. (2004). Change in plant spatial patterns and diversity along the successional gradient of Mediterranean grazing ecosystems. *Ecological Modelling*, *180*(4), 523–535.

Apfelbaum, I.S. (1985). Cattail (Typha spp.) management. Natural Areas Journal. 5 (3), 9–17.

Athanasiadis, N. (1975). Zur postglazialen Vegetationsentwicklung von Litochoro Katerinis und Pertouli Trikalon (Griechenland). *Flora*, *164*(1), 99–132.

Athanasiadis, N. (1986). Forest phytosociology. *Giachoudi–Giapouli, Thessaloniki (in Greek)*.

Athanasiadis, N., Gerasimidis, A., Panajotidis, S. (1993a). I elia sta diagrammata gyris kai i simasia tis apo istorikoarchaeologiki apopsi (The Olive Tree in the Pollen Diagrams and its Significance from a Historical and Archaeological Point of View). Politistiko Technologiko Idryma ETBA, Athens.78–91.

Athanasiadis, N., Gerasimidis, A., Panajotidis, S. (1993b). I ampelos sta diagrammata gyris tis Voreias Elladas kai i simasia tis apo istorikoarchaeologiki apopsi (The Vineyard in the Pollen Diagrams of Northern Greece and its Significance From a Historical and Archaeological Point of View). Politistiko Technologiko Idryma ETBA, Idryma Fani Boutari, Athens. 170–178.

Athanasiadis, N., Theodoropoulos, K., Gerasimidis, A., Eleftheriadou, E., Tsiripidis, I., & Korakis, G. (1998). Monades vlastisis, tis zonis, ton aeifyllon platyfyllon tou Agiou Orous (Vegetation Units of the Evergreen Broadleaved Zone of the Holly Mountain). *Eidiki Ekdosi Thessaloniki Politistiki Protevousa tis Evropis: Thessaloniki, Greece*, 87.

Behre, K.-E. (1981). The Interpretation of anthropogenic indicators in pollen diagrams. *Pollen Spores*, 23, 225–245.

Behre, K. E. (1990). Some reflections on anthropogenic indicators and the record of prehistoric occupation phases in pollen diagrams from the Near East. *Balkema*. 219-231.

Beug, J.H. (2004). Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete. Verlag Dr. Friedrich Pfeil, Munich. 542.

Blaauw, M. (2010). Methods and code for 'classical' age-modelling of radiocarbon sequences. Quaternary Geochronology, 5(5), 512–518.

Bottema, S. (1974). Late Quaternary History of Northwestern Greece PhD thesis University of Gronigen. 190.

Bottema, S. (1990). Anthropogenic indicators in the pollen record of the Eastern Mediterranean. *Man's role in the shaping of the Eastern Mediterranean landscape*, 231-264.

Caroli, I., & Caldara, M. (2006). Vegetation history of Lago Battaglia (eastern Gargano coast, Apulia, Italy) during the middle-late Holocene. Vegetation History and Archaeobotany, 16(4), 317–327.

Chester, P. I., & Raine, J. I. (2001). Pollen and spore keys for Quaternary deposits in the northern Pindos Mountains, Greece. Grana, 40(6), 299–387.

Christofides, G., Perugini, D., Koroneos, A., Soldatos, T., Poli, G., Eleftheriadis, G., Del Moro, A., & Neiva, A. (2007). Interplay between geochemistry and magma dynamics during magma interaction: An example from the Sithonia Plutonic Complex (NE Greece). Lithos, 95(3–4), 243–266.

Drake, B. L. (2012). The influence of climatic change on the Late Bronze Age Collapse and the Greek Dark Ages. Journal of Archaeological Science, 39(6), 1862–1870.

Ehrmann, W., Schmiedl, G., Hamann, Y., Kuhnt, T., Hemleben, C., & Siebel, W. (2007). Clay minerals in late glacial and Holocene sediments of the northern and southern Aegean Sea. Palaeogeography, Palaeoclimatology, Palaeoecology, 249(1–2), 36–57.

Faegri, K., Iversen, J. (1989). Textbook of Pollen Analysis. John Wiley & Sons, Chichester. 328.

Finsinger, W., & Tinner, W. (2005). Minimum count sums for charcoal concentration estimates in pollen slides: accuracy and potential errors. The Holocene, 15(2), 293–297.

Grimm EC (1992/2004) TILIA, TILA.GRAPH, and TGView. Illinois State Museum, Research and Collections Center, Springfield, USA

Harbeck, M., Seifert, L., Hänsch, S., Wagner, D. M., Birdsell, D., Parise, K. L., Wiechmann, I., Grupe, G., Thomas, A., Keim, P., Zöller, L., Bramanti, B., Riehm, J. M., & Scholz, H. C. (2013). Yersinia pestis DNA from Skeletal Remains from the 6th Century AD Reveals Insights into Justinianic Plague. PLoS Pathogens, 9(5), e1003349.

Horne, L. (1982). Fuel for the metal worker: The role of charcoal and charcoal production in ancient metallurgy. Expedition 25(1): 6–13.

Izdebski, A., Koloch, G., & Słoczyński, T. (2015). Exploring Byzantine and Ottoman economic history with the use of palynological data: a quantitative approach (with one map and 32 figures). Jahrbuch Der Österreichischen Byzantinistik, 1, 67–110.

Kolovos, E., Kotzageorgis, P. (2015). Halkidiki in the early modern period: towards an environmental history. In: Gounaris, Basil C. (Ed.), Mines, Olives and Monasteries: Aspects of Halkidiki's Enviromental History. Epikentro Publishers, Pharos Books. 327.

Kotthoff, U., Müller, U. C., Pross, J., Schmiedl, G., Lawson, I. T., van de Schootbrugge, B., & Schulz, H. (2008). Lateglacial and Holocene vegetation dynamics in the Aegean region: an integrated view based on pollen data from marine and terrestrial archives. The Holocene, 18(7), 1019–1032.

Kouli, K. (2011). Vegetation development and human activities in Attiki (SE Greece) during the last 5,000 years. Vegetation History and Archaeobotany, 21(4–5), 267–278.

Laiou, E.A. (1995). The economy of Byzantine Macedonia in the Palaiologan period. In: Burke, John, Scott, Roger (Eds.), Byzantine Macedonia: Identity, Image, and History, Melbourne.

Laiou-Thomadakis, E.A. (1977). Peasant society in the late Byzantine Empire. A Social and Demographic Study. Princeton University Press, Princeton.

Lefort, J. (2006). Société rurale et histoire du paysage à Byzance. Association des Amis du Centre d'Histoire et Civilisation de Byzance, Paris.

Marinova, E., & Atanassova, J. (2006). Anthropogenic impact on vegetation and environment during the Bronze Age in the area of Lake Durankulak, NE Bulgaria: Pollen, microscopic charcoal, non-pollen palynomorphs and plant macrofossils. Review of Palaeobotany and Palynology, 141(1–2), 165–178.

Mazier, F., Galop, D., Gaillard, M., Rendu, C., Cugny, C., Legaz, A., Peyron, O., & Buttler, A. (2009). Multidisciplinary approach to reconstructing local pastoral activities: an example from the Pyrenean Mountains (Pays Basque). The Holocene, 19(2), 171–188.

Merle, A. (2001). Voyage au Levant (1553). Les observations de Pierre Belon du Mans, Paris, Chandeigne. 156–176.

Moore, P & Webb, J. (1978). An illustrated guide to pollen analysis, First edition. Hodder and Stoughton, Kent-London, 133- 133.

Morris, S.P. (2009–2010). Prehistoric Torone: A Bronze Age Emporion in the Northern Aegean. Preliminary Report on the Lekythos Excavations 1986 and 1988–1990. *Mediterranean Archaeology: Australian and New Zealand Journal for the Archaeology of the Mediterranean World*, 22–23. 1–67.

Necipoğlu, N. (2009). Byzantium Between the Ottomans and the Latins: Politics and Society in the Late Empire. Cambridge University Press, Cambridge. 99–100.

Papanastasis, V. (1988). Apokatastasi kai diaheirisi tis vlastisis meta apo pyrkagia se thamnones aeiphyllon platyfyllon (Rehabilitation and Management of Vegetation After Wildfires in Maquis-type Brushlands). Dasiki Erevna. 2. 77–90.

Pavlidis, G. (1976). I chloris kai i vlastisis tis chersonisou Sithonias Halkidikis (Flora and Vegetation of the Sithonia Peninsula in Halkidiki). PhD thesis University of Thessaloniki, Aristotle. 300.

Pavlopoulos, K., Triantaphyllou, M., Karymbalis, E., Karkanas, P., Kouli, K., & Tsourou, T. (2007, April 1). Landscape evolution recorded in the embayment of Palamari (Skyros Island, Greece) from the beginning of the Bronze Age until recent times. Géomorphologie : Relief, Processus, Environnement, 13(1), 37–48.

R Development Core Team, (2010). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria ISBN 3-900051-07-0.

Reale, O., Dirmeyer, P. (2000). Modeling the effects of vegetation on Mediterranean climate during the Roman Classical Period Part I: Climate history and model sensitivity. Global and Planetary Change, 25(3–4), 163–184.

Reille, M. (1992). Pollen et spores d'Europe et d'Afrique du Nord. Vol. 543. Laboratoire de Botanique historique et Palynologie, Marseille.

Reille, M. (1995). Pollen et spores d'Europe et d'Afrique du Nord, supplément 1. Laboratoire de Botanique historique et Palynologie, Marseille. 331.

Stuiver, M., & Reimer, P. J. (1993). Extended 14C Data Base and Revised CALIB 3.0 14C Age Calibration Program. Radiocarbon, 35(1), 215–230.

Sugita, S. (1994). Pollen Representation of Vegetation in Quaternary Sediments: Theory and Method in Patchy Vegetation. The Journal of Ecology, 82(4), 881.

Theodoropoulos, K. (199)1. O kathorismos ton fytokoinoniologikon monadon tou panepistimiakou dasous Taxiarchi Halkidikis (Definition and Classification of the Plant Sociological Units of the University Forest of Taxiarchis Halkidiki). PhD thesis University of Thessaloniki, Aristotle. 200.

Tinner, W., & Hu, F. S. (2003). Size parameters, size-class distribution and area-number relationship of microscopic charcoal: relevance for fire reconstruction. The Holocene, 13(4), 499–505.

Tiverios, M. (2008). Greek colonisation of the Northern Aegean. In: Tsetskhladze, G. (Ed.), Greek Colonisation: An Account of Greek Colonies and Other Settlements Overseas 2. 1–154.

Triantaphyllou, M., Kouli, K., Tsourou, T., Koukousioura, O., Pavlopoulos, K., & Dermitzakis, M. (2010). Paleoenvironmental changes since 3000 BC in the coastal marsh of Vravron (Attica, SE Greece). Quaternary International, 216(1–2), 14–22.

Tsigarida, E., Xydopoulos, I. (2015). Halkidiki, landscape, archaeology and ethnicity. In: Gounaris, Basil C. (Ed.), Mines, Olives and Monasteries: Aspects of Halkidiki's Enviromental History. Epikentro Publishers, Pharos Books. 327.

Whitlock, C., Larsen, C. (2002). Charcoal as a fire proxy. In: Smol, John P., Birks, John, Last, William (Eds.), Tracking Environmental Change Using Lake SedimentsTerrestrial, Algal, and Siliceous Indicators vol. 3. Kluwer Academic Publishers, New York. 361.

Zalidis, G.C., Mantzavelas, L.A. (1994). Inventory of Greek Wetlands as Natural Resources (First Approximation). Athens, Greek Biotope/Wetland Centre (EKBY).

# V Vegetation and Climate reconstruction in the Carpathian region during the LGM, from Mohoş

## 5.1 Introduction

The Carpathians, with their rich palaeoecological archives, have long been a focus for scientists investigating the climatic transitions from the Last Glacial (LG) to the Early Holocene (EH). In this context, the Eastern and Southern Carpathians have yielded a plethora of high-resolution pollen records (Farcaș et al.,1999; Feurdean et al., 2001; Feurdean, 2005; Feurdean and Bennike, 2004; Tantau et al., 2003, 2005; Magyari et al., 2006; Magyari et al., 2009), which underscore the region's rapid vegetational shifts in response to post-glacial warming. This body of work has delineated the vegetative dynamics of the LG and EH, with a particular emphasis on the Ciomadul massif—a volcanic structure within the Călimani–Gurghiu–Harghita chain.

The sediment cores from the crater lake St. Ana and the peat sequence from the Mohoş crater have been pivotal in reconstructing the region's vegetation history. These studies, integrating pollen analysis and multi-proxy data, span the period from the LGM to the present (Tantau et al., 2003; Magyari et al., 2006; Magyari et al., 2009). The LGM vegetation at Ciomadul was dominated by grasses, with coniferous forests and minor xerophytic steppes present, while the EH period witnessed a shift towards temperate species in a diverse *Fraxinus* forest environment. These forests underwent sequential changes, with *Corylus*, *Fraxinus*, *Quercus*, *Tilia*, and *Carpinus betulus* all playing roles before the expansion of *Fagus sylvatica* forests which continue to persist (Tantau et al., 2003; Magyari et al., 2006; Magyari et al., 2009).

The St. Ana sediment cores have been crucial in documenting climate and environmental changes throughout the entire period from the LGM onwards. In contrast, the Mohoş peat bog's records, while detailed, only extend back to the Early Holocene, limited by dense tephra and ash layers (Magyari et al., 2014; Wulf et al., 2016). These deposits, which are dated to approximately 12620 – 12750 yrs b.p. (Juvigné et al., 1994), have hindered the retrieval of older sedimentary data.

In an attempt to bridge this temporal gap and potentially extend the environmental reconstructions beyond the Early Holocene, a coring campaign was conducted in the summer of 2014 at the Mohoş peat bog. The operation retrieved 42 core sections (Sediment core MOH-1 and 2) using a hydraulic hammer piston corer. This effort aimed at revealing vegetation dynamics preceding the last known eruptions of the Ciomadul volcano, as well as complementing the existing St Ana lake sediment core data (Magyari et al., 2014; Wulf et al., 2016).

The current study presents these findings, situating them within the broader context of glacial and post-glacial vegetational changes in the Carpathian region, and discusses the implications of this extended record for our understanding of past climate-vegetation interactions.

## 5.2 Study Area

The Mohoş *Sphagnum* peat bog, an ecological treasure, sits within the Ciomadul Massif of the Harghita Mountains near Tuşnad Bai. This 80-hectare preserve is part of the expansive volcanic belt of Călimani-Gurghiu-Harghita, stretching over 200 km in the Eastern Carpathians. Distinctive for its circular volcanic crater, Mohoş, alongside the younger *Santa Ana* crater lake, epitomizes the most recent volcanic events in this chain. Geological evidence points to an ancient origin of regional volcanism, dating back some 9 million years, with the explosion craters of Mohoş and Santa Ana marking the latest significant volcanic activities (Tantau et al., 2003; Szakács et al., 2015). Even today, traces of this turbulent past persist through mineral water springs and gas emissions like carbon dioxide (mofettas) and hydrogen sulfide (solfataras), bearing witness to the mountain's fiery history.

The towering Harghita Mountains reach an altitude of 1301 meters, their foundation comprising sandstone and conglomerate bedrock, overlaid with amphibole biotite dacite magma's intrusive lava domes and pyroclastic deposits (Magyari et al., 2009). The twin craters of Ciomadul were formed in close temporal succession, with the most recent eruption of Santa Ana, dated at around 12,639 years BP, depositing a significant tephra layer onto Mohoş (Juvigné et al., 1994; Magyari et al., 2014).

This tumultuous period was followed by a transitory lake phase in the late Pleistocene, quickly succeeded by a *Sphagnum*-dominated peat bog during the Holocene, the earliest deposits dating back to approximately 11,137 years BP (Tantau et al., 2003). Today, the peat bog's landscape is marked by numerous steep-sided water holes, adding to the area's ecological diversity and complexity.

The detailed environmental history of this region, particularly from the LGM through to the present day, has been pieced together from both the Mohoş peat bog and the St. Ana crater lake. These records are crucial for understanding the climatic and vegetational dynamics of the region, with the latter's sediments deposited above the Late Stone Age (LSA) tephra deposit, forming a comprehensive narrative of the area's past (Magyari et al., 2014; Wulf et al., 2016).

During the LGM, the vegetation was mainly grasslands interspersed with coniferous forests and sparse xerophytic steppes, a landscape frequently reshaped by wildfires. The EH saw a shift to more temperate species within diverse *Fraxinus* forests. Sequentially, these forests underwent transformations: *Corylus* appeared around 8800 cal yr BP, followed by temperate woodlands with *Fraxinus*, *Quercus*, *Tilia*, and the spread of *Carpinus betulus* around 7500 cal yr BP. *Fagus sylvatica* forests later emerged, becoming predominant from 3700 to 3300 cal yr BP, a dominance that continues to the present (Tantau et al., 2003; Magyari et al., 2006; Magyari et al., 2009).The Mohoş cores, retrieved in 2014, aim to extend the existing vegetational and climatic records by probing the periods preceding Ciomadul′*s* last eruptions, potentially offering new insights into the region's distant past beyond the Early Holocene restrictions imposed by dense tephra layers (Tantau et al., 2003; Magyari et al., 2014; Wulf et al., 2016).

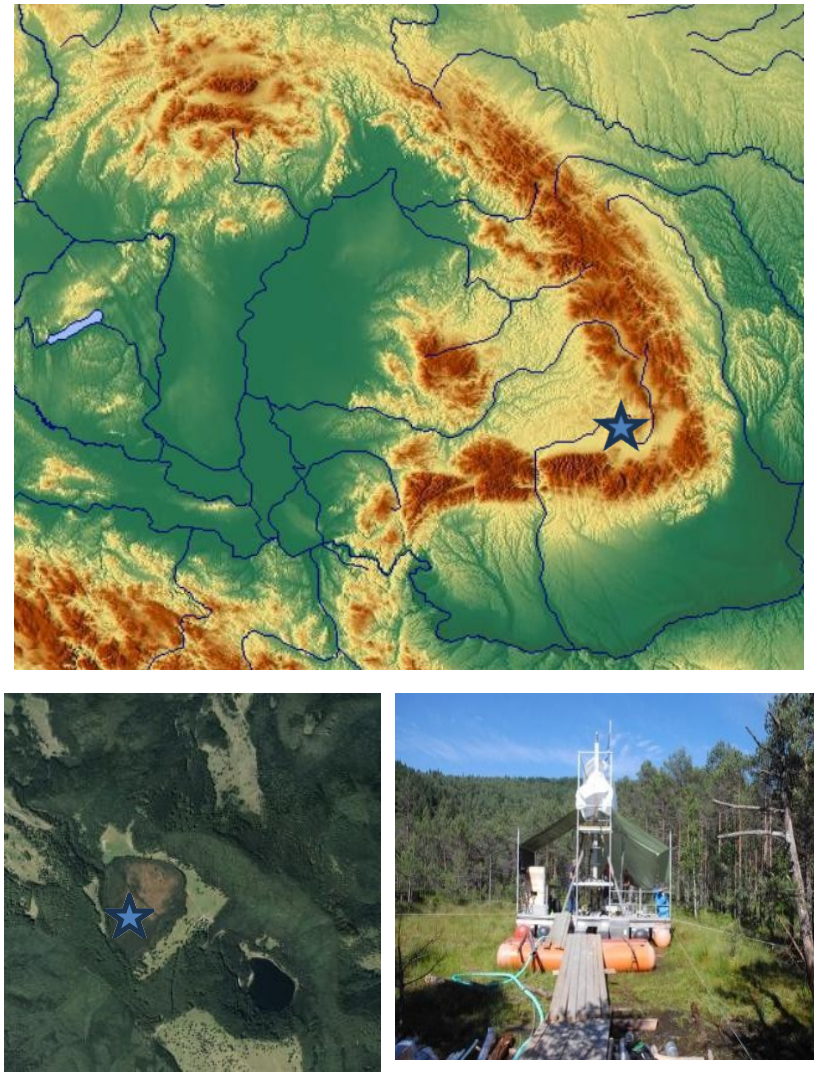

**Fig 5.1:** Location and photos of the drilling campaign (Modified after http://maps-for-free.com) ★indicates the drilling location.

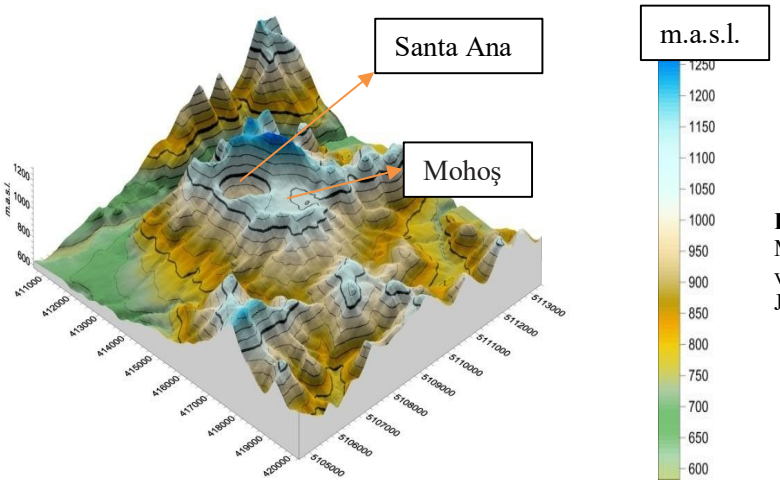


**Fig 5.2:** Digital Elevetion Model of Ciomadul volcano (provided by Dr. Jean Pierre Francois)

### 5.2.1 Current Local Climate and Vegetation

The climate of the Ciomadul Massif is shaped by its elevation and propensity for frost, creating what is known as a "continental mountainous temperate" climate zone (Tantau et al., 2003). The nearby settlement of Baile Tuşnad provides climate records that reflect this, with average temperatures in January dipping to -5˚C and rising to 18˚C in July, the warmest month. Annually, the area receives about 800 to 1000 mm of precipitation, peaking in summer and dwindling in winter (Tantau et al., 2003).

The *Mohoş* peat bog sits at the ecological juncture where the *Fagus sylvatica* and *Picea abies* forests converge, blanketing the higher reaches of the terrain. The bog's own vegetation is notably defined as a *'*Vaccinio uliginosi – Pinetum ilvestri*'* plant association, while the broader regional flora is distinguished as the *'*Symphyto cordati–Fagetum*'* association (Coldea, 1991).

In the periphery of the Mohoş bog, *Picea abies* forests are predominant, with the exception of areas where *Fagus sylvatica* forests ascend due to thermal inversion, an atmospheric anomaly that inverts the typical altitudinal zonation of vegetation. Here, the deciduous *Fagus sylvatica* forests occupy higher altitudes than the coniferous *Picea abies* forests (Magyari et al., 2009). In certain spots, *Abies alba* emerges as a co-dominant species alongside *spruce* or *beech*. The region also sporadically hosts stands of *Pinus sylvestris* and *Quercus petraea*.

Common woody species in these forests include *Corylus avellana*, *Carpinus betulus*, *Betula pubescens*, *Acer platanoides*, *Tilia cordata*, *Fraxinus excelsior*, and *Populus tremula*. These stands display minimal disturbance, as inferred from the limited presence of disturbance indicator species, primarily along forest road edges, based on field observations.

The Mohoş peat bog itself is dominated by *Pinus sylvestris* and *Betula pubescens*, but the edges of the bog boast an increased diversity of woody species, including *Alnus glutinosa*, *Betula pendula*, and various *Salix* species. The bog is also a habitat for several *Ericaceae* species such as *Empetrum nigrum*, *Vaccinium vitis-idaea*, and *Vaccinium oxycoccos*, all of which coexist with *Sphagnum* mosses, adding to the rich tapestry of the bog's ecosystem.

## 5.3 Methodology

### 5.3.1 Coring

During 2014, a methodical coring operation was conducted at the *Mohoş* peat bog. The coring effort employed a hydraulic hammer piston corer with PVC liners, as supplied by UWITEC GmbH, to obtain two full sequences of sediment cores, referred to as MOH-1 and MOH-2. The coring for MOH-1 began at a water depth of 8.30 meters, from which a total length of 29.95 meters of sediment was extracted. Similarly, coring for MOH-2 started at a water depth of 8.81 meters and also reached a length of 29.95 meters.

The coring process faced interruptions due to the presence of very hard lacustrine sediments and compact layers of tephra, which included large volcanic bombs, indicating proximity to past volcanic eruptions.

The findings discussed here are derived from the upper part of the sediment core MOH-2, reaching a depth of 21.13 meters. It is important to note that the lowest sections of the core provided insufficient pollen counts, likely due to poor pollen production or damage after deposition, which limited the pollen analysis. Despite these limitations, the cores obtained from *Mohoş* contribute essential data for understanding the historical vegetation and climate of the area.

### 5.3.2 Lithostratigraphic analysis

The core samples from the MOH-2 section of the Mohoş peat bog were described using a combination of visual and tactile methods. The color of the sediment was categorized using the Munsell color chart, a standardized color system. The texture, determined by the finger test method, helped in assessing the grain size. Sedimentological features, including the presence of layers (laminations) and the size sorting of particles (normal or inverse grading), were also noted. These characteristics are key in interpreting the sediment's depositional environment and history.

### 5.3.3 Chronology

The chronological framework for the Mohoş sedimentary record has been established using both radiocarbon and luminescence dating techniques to ensure precision in the temporal analysis. Radiocarbon dates were meticulously obtained through Accelerator Mass Spectrometry (AMS) at the well-regarded Cologne AMS 14C laboratory, as well as at the Hertelendi Laboratory of Environmental Studies housed within the Institute of Nuclear Research (ATOMKI) in Debrecen, Hungary. A comprehensive set of 28 AMS 14C dates were derived from a diverse array of samples including bulk sediments, plant macrofossils, and pollen concentrates, thereby providing a robust age model for the record.

In addition to radiocarbon dating, the chronology was further refined with five dates acquired via infrared stimulated luminescence (IRSL) dating at the Luminescence

Laboratory of the Institute of Geography, University of Cologne, which specializes in determining the last time sediment grains were exposed to sunlight. This dual-dating approach combines the strengths of both radiometric and luminescence methods, offering a more complete understanding of the timeline.
Ongoing research efforts are also directed towards the detection of cryptotephra within lacustrine sediments from the MOH-2 core, conducted at the Oxford DTP Environmental Research Institute, University of Oxford. This involves the search for microscopic volcanic ash particles that can be linked to specific volcanic events and thus provide additional chronological markers.
Moreover, Ar-Ar dating, an advanced geochronological technique, has been applied to tephra samples from the deepest tephra layers at the Berkeley Geochronology Center in California, USA. This method measures the ratio of argon isotopes, offering a high degree of dating accuracy for volcanic materials. Through these multifaceted dating endeavors, the study aims to construct a detailed and reliable chronology that underpins the environmental reconstructions derived from the Mohoş peat bog record.

### 5.3.4 Pollen and Charcoal Analysis

In the analysis of core MOH-2, samples were systematically collected every 16 cm, with each sub-sample measuring 3 $cm^3$, specifically designated for pollen analysis. These samples underwent a series of preparatory treatments, initially with a KOH solution to soften tissues, followed by acetolysis, as outlined by Faegri and Iversen (1989), to remove extraneous organic material. This was succeeded by treatment with hydrofluoric acid to dissolve silicate minerals, after which individual pollen grains were carefully isolated and mounted in glycerin, a process vital for subsequent microscopic examination. To quantify pollen concentration, standard *Lycopodium* tablets were incorporated into each sample before chemical processing, adhering to the methodology established by Stockmarr (1971).
Microscopic analysis was conducted using a light microscope at 400x magnification, enabling the detailed identification of pollen and spores. Identification relied on established pollen keys and atlases, drawing on the extensive compilations by Reille (1992, 1995), Chester and Raine (2001), and Beug (2004). To ensure statistical significance, at least 500 pollen grains were counted per sample, with a lower threshold of 300 pollen grains acceptable in instances where pollen production was notably sparse. The analysis software Tilia 2.0.2 (Grimm; 2004) facilitated the calculation of pollen percentages, concentrations, and influx rates, while pollen-taxonomic nomenclature followed the conventions detailed by Beug (2004). This meticulous approach ensured the accuracy and reliability of the palynological data extracted from the MOH-2 core.

## 5.4 Results

### 5.4.1 Lithostratigraphy

In the context of the broader geological narrative, our analysis delineated four distinct sediment units within the MOH-2 core, each marked by unique microfabric characteristics and a mix of lithogenic and organic materials, as illustrated in Figure 5.3's core sketch.

**Unit D** (divided in D1, D2, D3) (below 23 m): Comprising the lowest stratigraphic levels, Unit D is primarily composed of reworked materials from the adjacent crater slopes. This includes a variety of sediments ranging from massive sands and silty-sands to a mix of laminated silts and pumice in both fine to coarse textures. Embedded within these are tephra sub-units, reaching thicknesses of up to 0.4 meters, suggesting a dynamic depositional environment influenced by both volcanic activity and gravitational forces.

**Unit C** (divided in C1, C2) (23-15.5 m): Unit C transitions from reworked slope materials below 22.3 meters to lacustrine-derived sediments above. The lower section (Unit C2) is marked by massive silts interspersed with iron oxide laminae and layers of fine to medium pumice, indicative of sedimentary input from both terrestrial and volcanic sources. The upper section (Unit C1) is characterized by heavy sediment lamination, occasionally disrupted, suggesting episodic high-energy events. The uppermost boundary of Unit C is distinguished by a pumice layer, suggesting ongoing volcanic influences during sedimentation or erosive processes on the surrounding slopes.

**Unit B** (divided in B1, B2, B3) (15.5-9.8 m): Initiated by massive silts peppered with coarse pumice (Unit B3), this unit transitions to finely laminated silts enriched with organic content (Unit B2), representing a period of increased biological productivity. The sequence culminates in Unit B1, a layer of massive silts laden with organic remains, capturing a snapshot of the biological and geological processes at play during this interval.

**Unit A** (divided in A1, A2) (9.8 m to core top): The uppermost stratigraphy consists of alternating layers of gyttja and silt/clay laminae, marking a shift from lacustrine sediments to the development of peat, starting at 9.3 meters depth (Units A2 to A1). This transition encapsulates the environmental shift from an aquatic to a terrestrial-dominated ecosystem.

**Organic Chemistry-**

In the analyzed sediment layers, Total Organic Carbon (TOC) and Calcium Carbonate ($CaCO_3$) content presented an intriguing variability. TOC levels were predominantly low, staying under 1% across most measurements. However, a notable peak occurs in

Unit B2, where TOC rises to 0.65% at a depth of 14 meters; the precise value at this peak is unspecified.

$CaCO_3$ content showed a much broader range, oscillating between 0 and 8%. Its highest concentration was around 5% in Unit D1. Within Unit B2, distinct $CaCO_3$ peaks were recorded at depths of 12.5 m, 12.0 m, and 11.5 m, indicative of changes in sedimentary conditions. Yet, from there on, the concentration fluctuates, tapering off to less than 2% throughout Unit B1.

Measurements in Unit D3 revealed consistently low values for both TOC and $CaCO_3$, suggesting stable conditions during the period of deposition. Contrastingly, Unit D2's TOC content shows a significant peak at approximately 27 meters depth in massive silts, with $CaCO_3$ also demonstrating a stepped increase peaking in the same context.

Above the unrecovered sediment in Unit C2, an average TOC content of roughly 0.35% was observed. In this unit, $CaCO_3$ proved to be markedly variable, particularly above a tephra layer situated at 20.5 meters and within laminated silts, before its complete decline to zero at the unit's upper boundary.

In Units C1 and B3, TOC displayed minor fluctuations, ranging between 0.1 and just under 0.4%, while $CaCO_3$ remained consistently absent except for a singular increase at 17 meters. Importantly, no measurements of TOC or $CaCO_3$ were taken in the lowermost tephra, the peat of Units A1 and A2, or the laminated gyttja sediment, leaving a gap in the data for these sections. In sum, these stratified units present a cohesive sequence that chronicles the geological processes and environmental changes impacting the Mohoş peat bog, reflecting a dynamic interplay between the region's volcanic activity and sedimentation patterns.

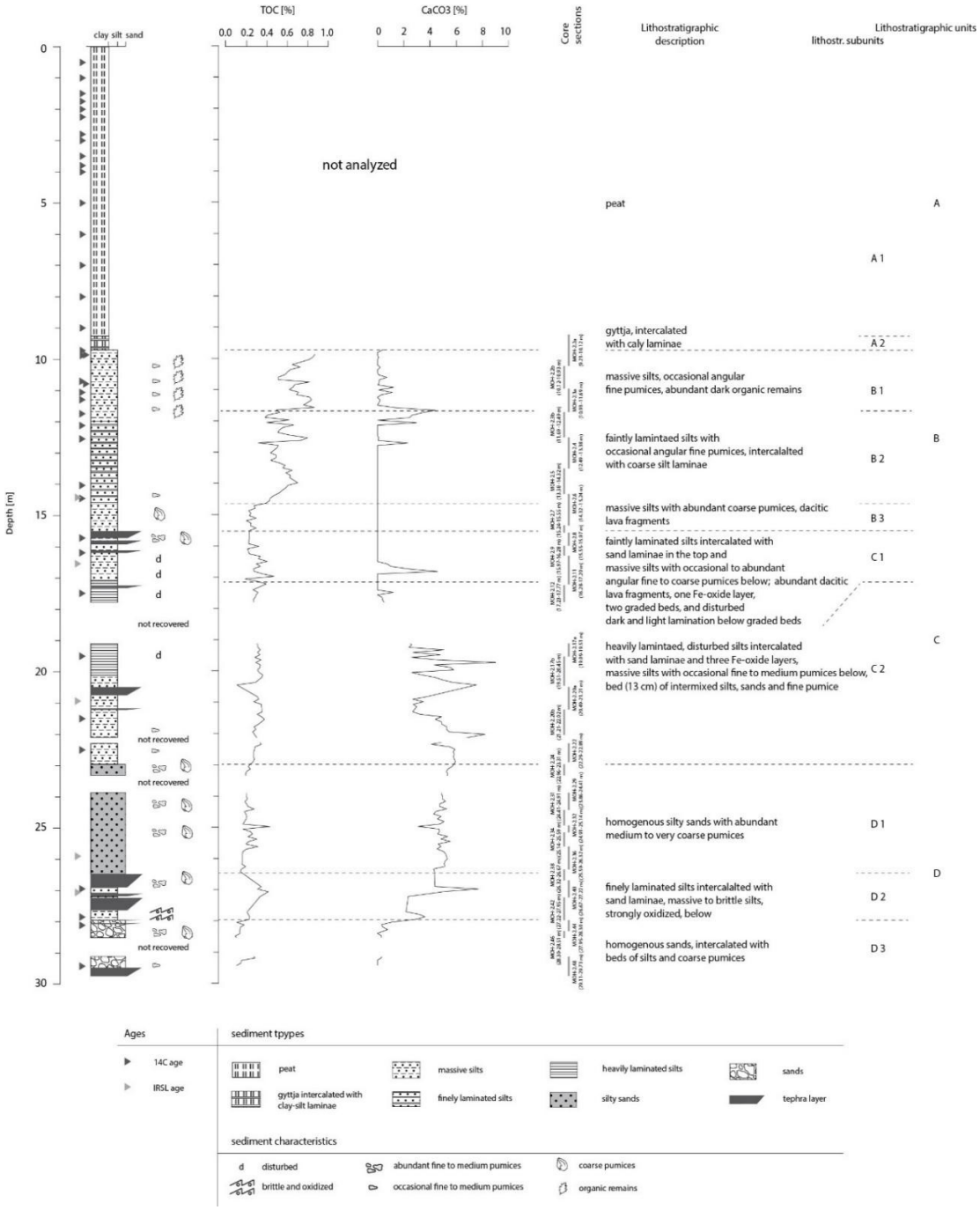


**Fig 5.3:** Lithostratigraphy and Organic Chemistry Results (Data and Graphs provided by Marc Bormann)

### 5.4.2 Chronology

Based on the available ages, the Mohoş record covers the last approximately 40 ka (Fig. 5.4, Bormann et al. Work in progress). However, even with this age data, the limitations in precise calibration, local environmental variability, and complex sedimentary processes can still hinder the effective use of an age-depth model. These factors introduce uncertainties that we must consider when interpreting the core's history.

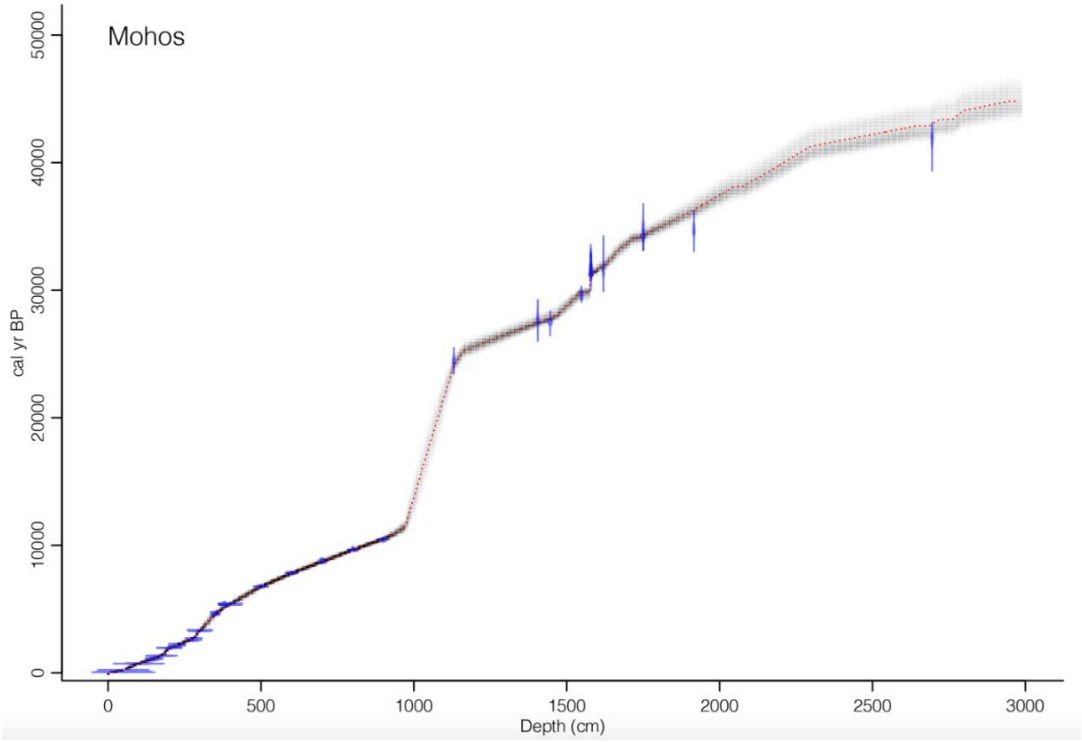


**Fig 5.4:** Age Depth Model (provided by Marc Bormann)

### 5.4.3 Pollen and Charcoal Analysis

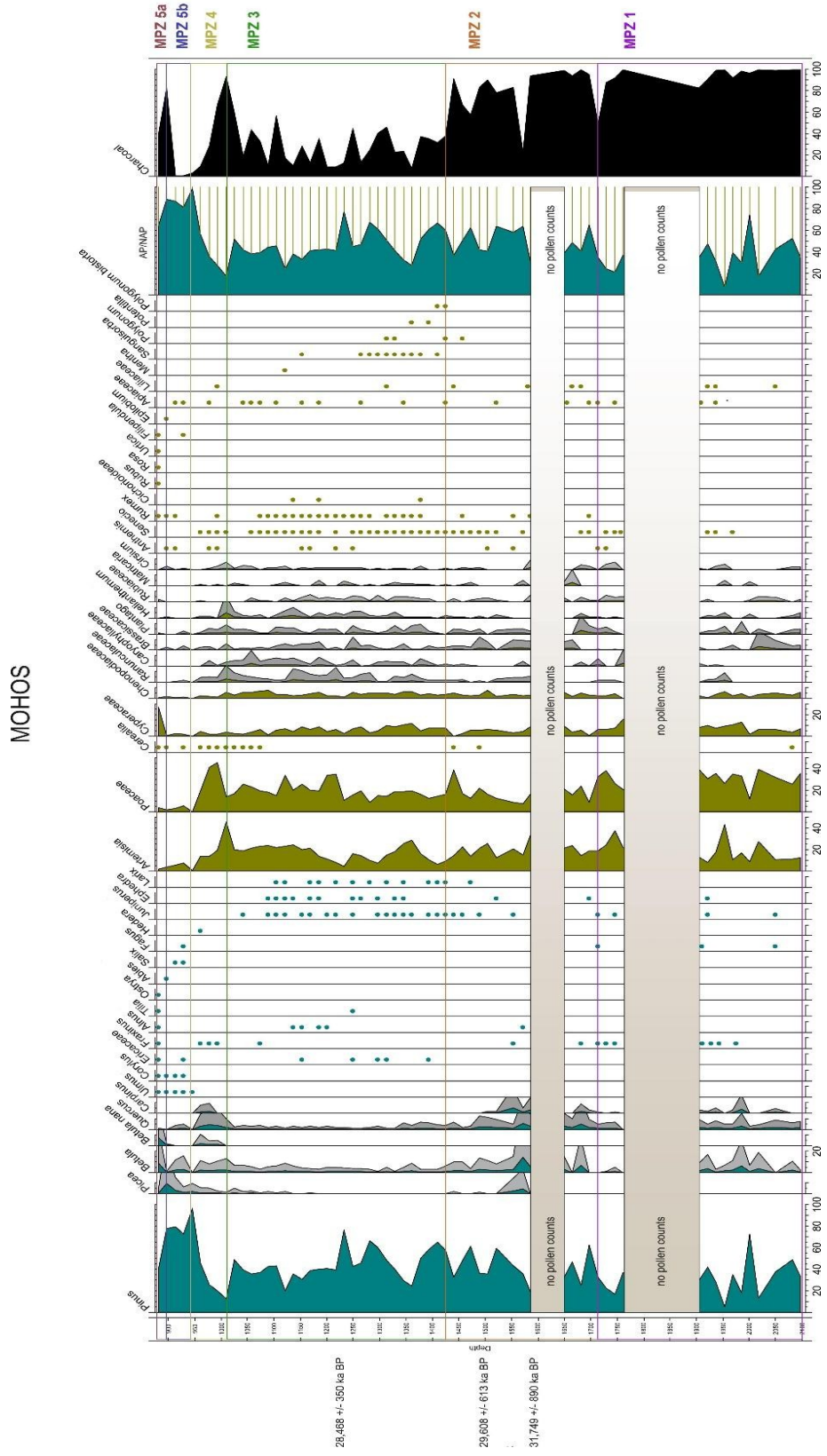


**Fig 5.5:** Pollen Diagram with Pollen Zones Mohoş

The minimum pollen count (300 PGs) was achieved for the majority of the samples between 2.10 and 0.881 m depth, except from a tephra unit at 16.50–15.90 m and where core was not recovered between 19.05 – 17.60 m. According to the pollen counts made in each depth we can detect the following Pollen Zones in the Mohoş core.

| **Mohoş Pollen Zone** | **Depth (cm)** | **Zone characteristics** |
|---|---|---|
| MPZ 1 | 2100 – 1717 | Variable quantities of deciduous trees *Quercus* (5-10%), *Betula* (0-20%), and coniferous species *Pinus* (5 – 85%) and *Carpinus* (0-10%) dominate the arboreal taxa which peaks at 80% ~20 m. Other deciduous trees such as *Fraxinus* and *Fagus* are rarely present. Herbs are dominated by *Artemisia* (10 – 30%) and Poaceae (10 – 40%) and are in antiphase with arboreal species with peaks at 19. 50 m and 20.13 m. Other herbs such as Ranunculaceae (<7.5%) and *Senecio* (<1%) only increase in abundance above 20.00 m, while others such as Brassicacae (0-10%) are abundant below 20.00 m.<br><br>>85% charcoal throughout indicative of high burning.<br><br>Upper boundary is marked by a sudden decrease in charcoal to 50%. |
| MPZ 2 | 1425 – 1717 | Arboreal taxa are dominated by *Pinus* which varies between 30 and 60 %; Deciduous species including *Quercus* (present throughout), *Betula* (0->20%), *Carpinus* (0->10%), and *Picea* (first occurrence) increase to a peak at 1565 cm. *Artemisia* remains while there is a decrease in Poaceae especially where deciduous tree species peak. Increase in Brassicacae.<br><br>Charcoal > 60% with the exception of short lived decline which coincides with a peak in the deciduous species *Betula* and *Quercus*, and the first appearance and large peak in *Picea* and *Alnus*.<br>*Senecio* disappears with the peak in deciduous species at 1565 cm.<br><br>Overall increase in arboreal pollen. |
| MPZ 3 | 1016 – 1425 | AP/NAP varies but remains around average and is heavily represented by *Pinus*. *Larix* occurs within this pollen zone exclusively while *Picea* declines to 0 in |

| | | |
|---|---|---|
| | | the middle of the section before increasing again in the upper part of the section. *Betula, Alnus, Tilia* (first occurrence) and *Quercus* decline significant but do not disappear entirely, while *Carpinus* disappears altogether from the record. *Artemisia* and Poaceae remain between 10 – 40 % with an overall increase in abundance, following a decrease or absence of many species and peak in *Pinus*. Other grassland and meadow species such as Ranunculaceae, Caryophyllaceae, Rubiaceae, *Senecio, Rumex* and Apiaceae among other are all relatively. Low woody shrubs *Ephedra* and *Juniperus* also occur within this interval.<br><br>Overall charcoal is lower remaining between <10 – 55%. |
| MPZ 4 | 945 – 1016 | Decrease in *Pinus* to a low of 15%. Increase in deciduous tree species *Picea, Betula* and *Quercus* and an isolated peak in *Betula nana, Carpinus* and *Fraxinus.* Notable peak in first *Artemisia, Ranunculaceae, Heliathemum* and then Poaceae and large increase in charcoal.<br><br>AP/ANP significantly decreases <20%. |
| MPZ 5b | 945-897 | *Pinus* abruptly increases to highest value in the core at the lower boundary of the zone. *Picea*, together with *Betula* (not *Betula nana* which is absent) and *Quercus*, increases up to a peak at the upper pollen zone boundary, *Ulmus, Corylus, Fagus* and *Salix* appear for the first time. *Artemisia,* Poaceae and most herbs species decrease significantly along with charcoal.<br><br>AP/NAP increases to the highest value. |
| MPZ 5a | 881-897 | *Pinus* decreases significantly while other deciduous tree species except *Quercus* increase or peak. *Ericaceae, Fraxinus, Alnus, Tilia, Ostrya* and *Abies* are either recorded for the first time or following significant absence. *Artemisia* and Poaceae continue to decrease. *Rubus, Rosa,* Urticaceae and *Epilobium* are also recorded for the first time.<br><br>Charcoal increases again to 80%. |

**Table 5.1:** Description of the Mohoş Pollen Zones (MPZ) and Lithological units, and comparison with Regional pollen zone from Lake St. Ana.

## 5.5 Discussion

### 5.5.1 Sedimentary Dynamics and Environmental Transitions

As seen in Fig 5.3 in the deepest section of the core at 28.0 m (Unit D3), we interpret the presence of coarse massive sands as indicative of deposition under high-energy conditions adjacent to ice margins, following the models proposed by Avery et al. (2019) and Zolitschka (1996). Moving slightly up-core to 28.0 – 26.5 m (Unit D2), the finely laminated silt layers interstratified with significant tephra deposits suggest a series of regular, albeit small, meltwater events indicative of a periglacial setting. The observed grain size reduction aligns with an increasing distance from meltwater sources, suggesting a decrease in ice and snow cover near Mohoş, possibly due to a warming climate, as supported by an increase in total organic carbon (TOC), signaling enhanced productivity in the catchment area.

Within this interval, oxidized layers atop finer-grained silts suggest episodes of reduced water column oxygenation due to ice cover, followed by re-oxygenation events leading to iron precipitation, as detailed by Davison (1993). The irregular occurrence of these oxidized layers implies that the surrounding ice cover was not a consistent seasonal event, but rather indicative of intermittent prolonged ice coverage over an otherwise well-oxygenated, ice-free lake.

Transitioning to 26.9 – 23.0 m (Unit D1), a shift to silty-sand sediments with a homogenous structure suggests a return to a more robust sediment delivery system, potentially brought on by an ice advance closer to Mohoş, hinting at cooler climatic conditions. A decrease in TOC further corroborates this hypothesis, while an uptick in calcium carbonate ($CaCO_3$) could signify either a change in biotic activity or a shift in sediment source, likely influenced by the movement of ice and snow.

The segment from 23.0 – 20.1 m (lower Unit C2) continues the trend of reduced grain size, signifying a retreating ice presence. Here, a 13 cm bed of intermixed silt, sand, and pumice is potentially a mass transport deposit (MTD), resulting from sediment reworking due to events such as floods or slope collapses, as characterized by the poorly sorted material suggesting proximity to the sediment source.

From 20.1 – 17.1 m (upper Unit C2), the presence of heavily laminated silts could be indicative of a regular sediment supply, possibly with seasonal variations (varves) and loess input during the dry stages, as described by Zolitschka et al. (2015). However, without microscopic analysis, the origin of these laminations remains speculative, although the inclusion of sand beds suggests variations in sediment delivery.

The transition to 17.1 – 14.5 m (Unit C1 and B3) marks a shift from the laminated structure to fainter laminations and massive silts, possibly pointing to a breakdown in

the regular sedimentation or preservation processes. The presence of graded beds, potentially MTDs, indicates sequential deposition from turbidity flows driven by environmental and climatic shifts. These features, formed by sediment supply from erosion, glacial melting, or slope failures, reflect dynamic changes like sea-level rise or intensified storms, offering insights into past depositional environments.

In the section from 14.5 - 12.0 m (Unit B2), finely laminated silts return, likely reflecting a regular sedimentation regime associated with the Last Glacial Maximum. The increase in TOC during this interval implies enhanced productivity in the catchment, contrary to the cooling climate inferred from the pollen record.

Finally, the segment from 12.0 – 9.8 m (Units B2 and B1) corresponds with post-LGM warming, as evidenced by dark organic remains and elevated TOC levels. The massive silt structure may reflect a transition to shallower lake conditions preceding the onset of peat accumulation in the early Holocene, potentially indicative of a drop in lake levels. Such a drop could lead to increased bioturbation and resuspension of sediments due to wave and wind action, as suggested by Aalderink et al. (1985) and Blazevic et al. (2009). It is also possible that the homogenization of sediments at this stage is a result of bioturbation within a more productive lake environment, as discussed by Eusterhues et al. (2002).

The uppermost section from 9.8 – 9.0 m (Unit A2) marks the transition from lacustrine to peat sediments, with the appearance of gyttja and clay laminae reflecting the warmer and more productive Holocene conditions within the lake. This represents the last phase of lacustrine deposition before the environment transitioned into the current peat bog state.

In summary, the stratigraphic record from the Mohoş peat bog core illustrates a complex interplay of climatic, environmental, and volcanic influences on sediment deposition. The core's lower sections capture the climatic fluctuations of the Last Glacial Maximum, characterized by colder conditions, proximity to ice, and variable lake levels. As the climate warms post-LGM, the record shows an increase in organic productivity and a change in lake dynamics leading up to the development of the peat bog in the Holocene. Further investigation, particularly microscopic analysis of sediment structures and detailed geochemical profiling, would enhance our understanding of the specific processes driving these changes in the Mohoş sedimentary record.

### 5.5.2 Age Model Limitations and Comparative Interpretations

In the absence of a robust age-depth model established through reliable calibrated radiometric dating, the detailed climatic and environmental interpretation of the data from this core must primarily rely on comparing it with regional pollen zones. Notably, the adjacent well-dated lake sediment record of Lake St. Ana, as presented by Magyari et al. in 2014, can serve as a useful reference point for such comparisons. However, it's essential to acknowledge that the lack of precise radiometric dates for this core introduces an element of uncertainty into any age-related interpretations associated with these comparisons.

Despite this limitation, the close proximity of the two records, only 2 kilometers apart, provides a reasonable alternative for cross-referencing and interpreting the data. Given the absence of radiometric dates, comparing the core with the Lake St. Ana pollen zones becomes a necessary and practical approach, considering the spatial proximity of the two sites.

In cases where portions of the Mohoş sediment core cannot be correlated with regional pollen records, their interpretation may need to rely on broader considerations of climate and environmental change.

### 5.5.3 Comparing Mohoş Core Chronology with Lake St. Ana (Magyari 2014) - Taxa-Based Discussion

In this extensive discussion, we undertake a meticulous comparison of the Mohoş core's chronological data with the well-documented chronology of Lake St. Ana, as presented by Magyari et al. in 2014. This detailed examination focuses on specific taxa, their temporal distribution, and their implications for vegetation and environmental changes within the region.

**Temporal Similarities and Consistencies:**

- Fluctuations in Pinus Dominance (9400-8800 BP): Between approximately 9400 and 8800 years Before Present (BP), both the Mohoş core and Lake St. Ana's chronology exhibit substantial fluctuations in the dominance of Pinus pollen. This shared pattern suggests that variations in the presence of coniferous species, specifically Pinus, were regionally consistent during this timeframe. Such consistency may be indicative of common regional climatic shifts or ecological dynamics.
- Deciduous Tree Dynamics (9400-8800 BP): During the same time frame, from 9400 to 8800 BP, the presence of deciduous tree species, including Quercus, Betula, and Carpinus, displays consistent temporal patterns in both records. These trees appear, fluctuate, and sometimes decline in similar ways. This shared pattern implies that these deciduous species responded to environmental changes concurrently. It is plausible that they were influenced by the same climatic shifts or ecological factors in the region during this period.

**Temporal Discrepancies and Variability:**

- Pollen Composition: Despite the observed temporal similarities, the exact composition of pollen varies between the two records during the same time frame (9400-8800 BP). Differences in the timing of appearances and disappearances of specific species highlight regional ecological variations and potential differences in local environmental conditions. Notably, *Betula*, *Quercus*, and *Carpinus* may dominate the deciduous tree dynamics, but variations in the presence of other species need further investigation.
- First Appearances (8800-8600 BP): Between 8800 and 8600 BP, some species appear for the first time in one record but not in the other. This suggests disparities in the timing of ecological changes, which may be influenced by microclimatic conditions, local ecological factors, or specific historical events that affected one site more than the other. For example, the appearance of *Ulmus*, *Corylus*, *Fagus*, and *Salix* at Lake St. Ana during this period indicates distinct ecological shifts.
- Charcoal Peaks Timing (9400-8800 BP): While both records display peaks in charcoal content between 9400 and 8800 BP, the timing and magnitude of these peaks may differ. This indicates variability in fire events or local environmental conditions between the two sites during this specific period. Understanding the causes of these discrepancies in charcoal content will require a more detailed investigation of regional fire history and local environmental conditions.
- Pollen Zone Division: The division into specific pollen zones differs between the Mohoş core and Lake St. Ana's chronology, particularly during the same time frames (9400-8800 BP). This indicates variations in the interpretation of environmental changes and underscores the complexity of drawing precise temporal conclusions. The differences in pollen zone divisions may be influenced by varying criteria for zone boundaries or regional ecological nuances.

In summary, while the temporal comparison between the Mohoş core and Lake St. Ana's chronology reveals both temporal similarities and discrepancies, it highlights the need for a nuanced and context-specific interpretation of palaeoecological records. These records provide invaluable insights into the region's past, but their intricacies underscore the importance of considering local factors, such as microclimate, ecological interactions, and the limitations of age models, in drawing accurate temporal conclusions about past environmental dynamics. Further interdisciplinary research and the refinement of age models will be essential to unravel the complexities of regional environmental history, especially concerning specific taxa and their temporal dynamics.

| Aspect of Comparison | Mohoş Core | Lake St. Ana (Magyari 2014) |
|---|---|---|
| **Temporal Similarities** | | |
| Pinus Fluctuations (9400-8800 BP) | Shared fluctuations in *Pinus* dominance | Shared fluctuations in *Pinus* dominance |
| Deciduous Tree Dynamics (9400-8800 BP) | Consistent temporal patterns in *Quercus*, *Betula*, *Carpinus* | Consistent temporal patterns in *Quercus*, *Betula*, *Carpinus* |
| **Temporal Discrepancies** | | |
| First Appearances (8800-8600 BP) | Disparities in the timing of ecological changes; Differences in species appearance | Appearance of additional species at Lake St. Ana, such as *Ulmus*, *Corylus*, *Fagus*, *Salix*, etc. |
| Charcoal Peaks Timing (9400-8800 BP) | Variability in the timing and magnitude of peaks | Differences in timing and magnitude of charcoal peaks |

**Table 5.2** Comparison betweeen Mohoş Core Chronology with Lake St. Ana (Magyari 2014) - Taxa-Based

### 5.5.4 Climate and Environmental Interpretations

**MPZ 1 (21.06 – 17.13m):**

MPZ 1, located between 21.06 and 17.13 meters in the Mohoş core, presents an interesting mix of pollen types within the heavily laminated section of lithographic unit C2. This interval contains varying proportions of deciduous, coniferous, and tundra-steppe plant species. Notably, the presence of *Artemisia* and, to a lesser extent, Poaceae remains relatively consistent throughout this section, with both types never decreasing below 10%. This suggests the presence of alternating boreal, hemiboreal, and cold temperate forests in areas with lower exposure and higher moisture, as well as open grasslands in drier and more exposed regions.

In this context, the prevalence of *Pinus* pollen, which is a prolific pollen producer, might obscure the actual extent of other species like *Picea* that are characterized by lower pollen productivity and spatial dispersal (Nosova et al., 2015). Nevertheless, the peaks in cold-temperate woodland species within MPZ 1 indicate intermittent relatively warmer periods occurring before approximately 30,000 years before present (ka BP), which may align with events like Greenland Interstadials (GI) 6 or 5.2. Conversely, peaks in open tundra-steppe and xerophytic steppe species (e.g., *Artemisia*, Poaceae, Cyperaceae, and Chenopodiaceae) likely indicate cooler phases (Magyari et al., 2014; Müller et al., 2009; Rasmussen et al., 2014). An example of this cooler phase is suggested by the simultaneous expansion of *Artemisia* and the retreat of *Pinus*, occurring above an unsampled interval between 1905 and 1761 centimeters in the core. MPZ 1 is also characterized by a high charcoal content, which supports the notion of frequent fire episodes in the region. This observation, coupled with the presence of tundra-steppe and boreal biomes, suggests an overall dryer continental climate,

particularly during colder climate phases. This climate likely facilitated the expansion of the more arid steppe-tundra environment. In contrast, slight decreases in charcoal, although still relatively high compared to the entire core, coincide with increases in arboreal pollen. This implies slightly wetter conditions that prevailed during warmer climate phases, allowing for the expansion of moister-loving cold temperate forests.
In summary, MPZ 1 offers insights into the dynamic interplay between vegetation types, climate conditions, and fire events in the region over time. The presence of specific pollen types and the fluctuations in charcoal content provide valuable information about past climatic variations, helping us understand the environmental history of the Mohoş core site. Further research and analysis are necessary to refine our interpretations and gain a more comprehensive understanding of the region's paleoenvironmental evolution during the Last Glacial period.

**MPZ 2 (17.13-14.60m):**

This pollen zone is characterised by greater quantities of arboreal pollen (>40%) especially those associated with cold temperate forests such as *Quercus*, *Betula*, and *Carpinus*, and/or boreal biomes such as *Pinus* and for the first time *Picea* indicating an overall warmer climate than in MPZ 1. As with MPZ 1 *Artemisia* and Poaceae remain high (>10 %) and together with the presence of *Juniperus* show that open tundra-steppe remained prominent, probably at altitude and in other exposed areas.
Overall high charcoal (but reduced compared to the MPZ 1) is indicative of continued high rates of burning but is interjected with a notable decrease in conjunction with the highest peak in arboreal pollen at 15.15 m, further corroborating that wetter conditions accompany warmer more Atlantic climates in the region. Although not well constrained the age of this warmer wetter period is likely to be around 30 ka and so may be contemporary with GI 5(.1 or .2) (Rasmussen et al., 2014).
Faintly laminated sediments with only one rich laminae in the lower section and massive silts in the upper section, suggest that the creating processes i.e. snow melt, ice cover, seasonal differences in water temperature were less extreme than in the MPZ1 (Davison, 1993; Mammarella et al., 2018). Faint lamination is, however, interjected by what are likely to be mass transport deposits (MTDs) which are characterised by sequentially deposited often graded, disturbed sand, silt and clay layers caused by extreme short lived depositional events such as floods and seismic activity (Fielding et al., 2018; Schlolaut et al., 2014). While tephra layers, pumice and lava fragment here could support a seismic origin in association with local volcanism of the MTDs, MTDs may also represent a move to high rates of erosion in the catchment with increasingly wetter conditions (Fielding et al., 2018; Schlolaut et al., 2014).

**MPZ 3 (14.60–10.16):**

The zone is defined by decreasing cold temperate forest cover and the dominance of alternating boreal forest (*Pinus*, *Larix*) with open tundra-steppe, xerophytic steppe, and steppe meadow species (e.g., *Artemisia* and Poaceae and presence of *Ephedra*, *Senecio*, and *Rumex*). Over time, decreasing temperatures led to decreased temperate or hemi-boreal forest cover in favor of boreal forest and more open landscapes. Finely laminated sediments here are probably the result of decreased temperatures leading to more ice and snow cover in the catchment, with seasonal melt driving regular changes in sediment delivery to the lake. Additionally, coarse silt laminae containing angular pumice show occasional higher energy delivery mechanisms such as flooding or prominent melt events, as is observed in modern alpine lakes (Gilli et al., 2003; Simonneau et al., 2013). Although not well constrained radiocarbon dates from below and within (likely reworked older carbon) together with shared characteristics of the nearby Lake St. Ana pollen zones (SZA) mean that MPZ 3 is likely to represent pre- and early Last Glacial Maximum (e.g., GS 3 and 4, 28.6 – 23 ka, Clark et al., 2009; Magyari et al., 2014; Rasmussen et al., 2014).

Although still relatively dry, as indicated by more arid tundra-steppe species (e.g. *Ephedra*, *Sanguisorba*, *Rumex*, *Polygonum ssp.*), the interval is further defined by decreasing charcoal and thus burning. This notable reduction in burning, although still variable, during the Last Glacial Maximum agrees with the overall global trend (Daniau et al., 2010), and to an extent to the nearby Lake St Ana charcoal and micro-charcoal signal during the Last Glacial Maximum (Magyari et al., 2014).

A notable peak in *Pinus* in the middle of MPZ 3, as well as a decrease or absence in steppe-tundra species and lows in charcoal, may indicate a short-lived small increase in temperature and moisture. The presumed timing of this event within the Last Glacial Maximum, together with a comparison with an interval of increased *Pinus* and decreased xerophytic steppe (*Artemisia*) in the Lake St. Ana sediment record between 22,870 – 19,150 cal. yrs. b.p., means it may be associated with GI-2.1/2 (Rasmussen et al., 2014). Notably, however, while charcoal and micro-charcoal increase prominently during this time in the Lake St. Ana sediments, contrasting global trends, here sedimentary charcoal is reduced to the second lowest quantities in the record (Magyari et al., 2014).

Continuous finely laminated sediments, along with the sustained occurrence of *Juniperus*, *Pinus*, *Larix*, and increases in steppe-tundra pollen types (Poaceae and *Artemisia*) in the lower portion of MPZ 3 are further indicative of colder conditions most likely during the middle to latter Last Glacial Maximum (GS 2.1 (b,c), Rasmussen et al., 2014). Throughout MPZ 3, however, a gradual reduction and finally disappearance of some open and wooded-steppe species (e.g., *Larix*, *Ephedra*, *Juniperus*, *Rumex*, and Rubiaceae), together with gradually increasing hemi-boreal or sub-alpine forests (e.g. *Picea*, *Betula*) suggests a move towards warmer, less continental conditions, as is seen locally (Magyari et al., 2014).

The presence of *Quercus*, *Alnus*, *Tilia*, and *Betula* pollen throughout MPZ 3 further corroborates that the Carpathians acted as a refugium for broadleaved tree species (Feurdean et al., 2011; Feurdean et al., 2007; Magyari et al., 2014).
Between 11.21 m and the top of MPZ 3, increased values of *Betula* and *Picea*, together with the continued abundance of *Artemisia*, Poaceae, *Pinus*, and other tundra-steppe species and disappearance of *Juniperus*, *Ephedra*, and *Larix* support the expansion of *Artemisia* steppes over *Juniperus* scrubland, probably coevally with Heinrich-event 1 happening about ~16 ka, as seen at nearby St. Ana. Unlike in the Lake St. Ana sediments, Poaceae remain dominant in the Mohoş record, suggesting that more open steppe-tundra environments persisted outside of the relatively sheltered Lake St. Ana crater (Magyari et al., 2014).

**MPZ 4 (10.16-9.50 m):**

Higher occurrences of temperate deciduous trees (e.g. *Betula*, *Betula nana*, *Quercus*, *Carpinus* and *Fraxinus*) and significant decreases in *Pinus* are very likely to represent relatively warmer temperatures coeval with GIS-1 or the Bølling–Allerød (Lascu et al., 2015). In contrast to some reconstructions however, a notable peak in first *Artemisia*, Ranunculaceae, *Plantago*, *Helianthemum*, and then Poaceae, and a notable peak in charcoal (>90%), indicate a dryer more continental climate through this time. In a palaeo-lake sediment pollen record from Northern Transylvanian similar patterns in pollen are observed and thus here are interpreted as representing a warming wetter climate over all but with dryer hotter summers, perhaps reflecting a more Mediterranean climate (Lascu et al., 2015; Magyari et al., 2014).

**MPZ 5b (9.50 – 8.97 m):**

Represents the largest overall change in vegetation in the record and initiates with the highest arboreal pollen for the whole core dominated by a huge and abrupt increase in *Betula* and *Picea* with *Pinus* being present through the whole pollen zone. This is taken to be indicative of cooler climate Younger Dryas (YD), as seen elsewhere locally (Magyari et al., 2014). Significant decreases in fire activity most likely are indicative of a wetter climate which is further corroborated by the reoccurrence of *Salix*, *Ulmus* and *Corylus* locally.

**MPZ 5a (>8.97 m):**

Rapidly decreasing *Pinus*, and a resurgence in *Picea*, *Betula*, Cyperaceae, and the occurrence of species such as *Ulmus*, *Corylus*, *Alnus*, *Ostrya*, *Rubus*, *Rosa* and *Urtica* are indicative of an increasingly dominant typical temperate European woodland at the beginning of the Holocene following the termination of the Pleistocene. Burning also appears to increase rapidly, possibly reflecting an increase in fuel (expansion in woodland and low woody species) but with sufficient dryness, conducive to burning as

is found locally at St. Ana (Magyari et al., 2014).

## 6.1 Conclusions

The Mohoş peat bog core, extracted from this unique natural archive, offers a wealth of insights into the complex interplay of climatic, environmental, and volcanic influences over time. These insights are primarily gleaned from distinct sedimentary zones or Mohoş Pollen Zones (MPZs) within the core.

The core's stratigraphy documents the dramatic climatic fluctuations of the Last Glacial Maximum, where colder conditions, proximity to ice margins, and variable lake levels are vividly captured. Furthermore, the post-Last Glacial Maximum (LGM) warming is well-evidenced, showcasing increased organic productivity and shifts in lake dynamics, culminating in the development of the peat bog during the Holocene.

One of the key limitations in interpreting this invaluable record is the absence of a robust age-depth model grounded in calibrated radiometric dating. Consequently, age-related interpretations are heavily reliant on comparisons with regional pollen zones. In this respect, the neighboring Lake St. Ana, with its well-dated sediment record, serves as a crucial reference point for understanding the core's data. However, the absence of precise radiometric dates introduces an element of uncertainty into any age-related conclusions associated with these comparisons.

## 6.2 Key Messages

In the midst of the core's intricacies and limitations, several critical messages emerge:

- **The Importance of the Mohoş Core:** The Mohoş peat bog core emerges as an invaluable historical archive, offering insights into the region's paleoenvironmental evolution during the Last Glacial period. Its rich sedimentary record provides a unique window into past climatic and environmental conditions.
- **The Role of Regional Comparisons:** While the core lacks precise radiometric dates, comparing it with well-dated regional records, especially Lake St. Ana, presents a practical approach to interpretation. These comparisons are essential for understanding the data, given the spatial proximity of the two sites.

## 7 References

Aalderink, H. H., Van Der Molen, D. T., & Aalderink, B. J. (1985). On the preservation of laminae in tidal flat sediments. *Marine Geology, 62*(1-4), 305-320.

Avery, M., Brumby, S., & Peyton, S. (2019). High-resolution sedimentary records of tephra deposition from Balloon Lake, south-central Alaska: Implications for the spatial distribution and origins of distal ash on the north Pacific margin. *Geological Society of America Bulletin, 131*(1-2), 295-314.

Beug H-J (2004) Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete. Pfeil, München.

Blazevic, M. J., Knox, R. W., Shaw, P. A., Dewey, J. F., & Burke, K. (2009). Stratigraphy, structure, and tectonic history of the Dinarides: An overview. In *Geology and tectonics of the Dinarides and adjacent regions* (Vol. 298, pp. 1-26). Geological Society of America.

Chester PI, Raine JI (2001) Pollen and spore keys for Quaternary deposits in the northern Pindos Mountains, Greece. Grana 40:299–387.

Clark, P. U., Dyke, A. S., Shakun, J. D., Carlson, A. E., Clark, J., Wohlfarth, B., Mitrovica, J. X., Hostetler, S. W., & McCabe, A. M. (2009). The Last Glacial Maximum. Science, 325(5941), 710–714.

Coldea G (1991) Prodrome des associations végétales des Carpates du sudest (Carpates roumanies). Doc Phytosociol 13:317–539.

Daniau, A. L., Harrison, S., & Bartlein, P. (2010). Fire regimes during the Last Glacial. Quaternary Science Reviews, 29(21–22), 2918–2930.

DAVISON, W. (1993). Iron and manganese in lakes. Earth-Science Reviews, 34(2), 119–163.

Eusterhues, K., Rennert, T., Knicker, H., Kögel-Knabner, I., Totsche, K. U., Schwertmann, U., & Leinweber, P. (2002). Fractionation of organic matter due to reaction with ferrihydrite: Influence of pH and organic carbon content. Soil Science Society of America Journal, 66(5), 141-150.

Faegri, K., Iversen, J. (1989). Textbook of Pollen Analysis. John Wiley & Sons, Chichester. 328.

Farcas S., de Beaulieu L.J., Reille M., Coldea G., Diaconeasa B., Goeury C., Goslar T., Jull T. (1999). First 14C datings of Late Glacial and Holocene pollen sequences from Romanian CarpathesPremières datations 14C de séquences polliniques tardiglaciaires et holocènes des Carpates roumaines. Comptes Rendus de l'Académie des Sciences - Series III - Sciences de la Vie, 322(9): 799-807.

Feurdean, A., Tanţău, I., & Fărcaş, S. (2011). Holocene variability in the range distribution and abundance of Pinus, Picea abies, and Quercus in Romania; implications for their current status. Quaternary Science Reviews, 30(21–22), 3060–3075.

Feurdean, A., Wohlfarth, B., Björkman, L., Tantau, I., Bennike, O., Willis, K. J., Farcas, S., & Robertsson, A. M. (2007). The influence of refugial population on Lateglacial and early Holocene vegetational changes in Romania. Review of Palaeobotany and Palynology, 145(3–4), 305–320.

Feurdean A. & Bennike O. (2004). Late Quaternary palaeoecological and palaeoclimatological reconstruction in the Gutaiului Mountains, northwest Romania, 19(8): 809-827.

Feurdean, Angelica. (2005). Holocene forest dynamics in northwestern Romania. Holocene, 15: 435-446.

Feurdean A., Björkman L. & Wohlfarth B. (2001). A paleoecological reconstruction of the Late Glacial and Holocene based on multidisciplinary studies at Steregoiu site (Gutai Mts., Romania), *Studia UBB Geologia,* 46 (2): 125-140.

Fielding, J.J., Kemp, A.E., Bull, J.M., Cotterill, C.J., Pearce, R.B., Avery, R.S., Langdon, P.G., Croudace, I.W., 2018. Palaeoseismology from microfabric and geochemical analysis of lacustrine sediments, Windermere, UK. Journal of the Geological Society 175, 903-914.

Gilli, A., Anselmetti, F.S., Ariztegui, D., McKenzie, J.A. (2003). A 600-year sedimentary record of flood events from two sub-alpine lakes (Schwendiseen, Northeastern Switzerland), Lake Systems from the Ice Age to Industrial Time. Springer, 49-58.

Grimm EC (1992/2004) TILIA, TILA.GRAPH, and TGView. Illinois State Museum, Research and Collections Center, Springfield, USA

Juvigné, E., Gewelt, M., Gilot, E., Hurtgen, C., Zeghedi, I., Szakács, A., Gábris, G., Hadnagy, A., Horváth, E. (1994). Une eruption vieille d'environ 10700 ans (14C) dans les Carpates orientales (Roumanie). Comptes rendus de l'Académie des sciences. Série 2. Sciences de la terre et des planètes 318, 1233-1238.

Lascu, I., Wohlfarth, B., Onac, B. P., Björck, S., & Kromer, B. (2015). A Late Glacial paleolake record from an up-dammed river valley in northern Transylvania, Romania. Quaternary International, 388, 87–96.

Magyari E., Buczkó K., Jakab G., Braun M., Pál Z., Karátson D. & Pap I. (2009) Palaeolimnology of the last crater lake in the Eastern Carpathian Mountains: a multiproxy study of Holocene hydrological changes. Hydrobiologia, 631: 29–63.

Magyari E., Buczkó K., Jakab G., Braun M., Pál Z., Szántó Z., Molnár M., Pál Z. & Karátson D. (2006). Holocene palaeohydrology and environmental history in the South Harghita Mountains, Romania Holocén hidrológiai és környezeti változások a romániai Dél-Hargita-hegységben Földtani Közlöny, 136(2): 249-284.

Magyari, E., Veres, D., Wennrich, V., Wagner, B., Braun, M., Jakab, G., Karátson, D., Pál, Z., Ferenczy, G., St-Onge, G., Rethemeyer, J., Francois, J. P., von Reumont, F., & Schäbitz, F. (2014). Vegetation and environmental responses to climate forcing during the Last Glacial Maximum and deglaciation in the East Carpathians: attenuated response to maximum cooling and increased biomass burning. Quaternary Science Reviews, 106, 278–298.

Mammarella, I., Gavrylenko, G., Zdorovennova, G., Ojala, A., Erkkilä, K.-M., Zdorovennov, R., Stepanyuk, O., Palshin, N., Terzhevik, A., Vesala, T. (2018). Effects of similar weather patterns on the thermal stratification, mixing regimes and hypolimnetic oxygen depletion in two boreal lakes with different water transparency. Boreal Environment Research, 23, 237-247.

Müller, S., Tarasov, P. E., Andreev, A. A., & Diekmann, B. (2009). Late Glacial to Holocene environments in the present-day coldest region of the Northern Hemisphere inferred from a pollen record of Lake Billyakh, Verkhoyansk Mts, NE Siberia. Climate of the Past, 5(1), 73–84.

Nosova N.B., Elena, S., Volkova, O. & Kosenko, J. (2015). Representation of *Picea* pollen in modern and surface samples from Central European Russia. Vegetation History and Archaeobotany, 24 (2).

Reille M (1992) Pollen et Spores d' Europe et d' Afrique du Nord. Laboratoire de Botanique Historique et Palynologie, Marseille.

Reille M (1995) Pollen et Spores d' Europe et d' Afrique du Nord. Laboratoire de Botanique Historique et Palynologie, Marseille.

Rasmussen, S. O., Bigler, M., Blockley, S. P., Blunier, T., Buchardt, S. L., Clausen, H. B., Cvijanovic, I., Dahl-Jensen, D., Johnsen, S. J., Fischer, H., Gkinis, V., Guillevic, M., Hoek, W. Z., Lowe, J. J., Pedro, J. B., Popp, T., Seierstad, I. K., Steffensen, J. P., Svensson, A. M., . . . Winstrup, M. (2014). A stratigraphic framework for abrupt climatic changes during the Last Glacial period based on three synchronized Greenland ice-core records: refining and extending the INTIMATE event stratigraphy. Quaternary Science Reviews, 106, 14–28.

Schlolaut, G., Brauer, A., Marshall, M. H., Nakagawa, T., Staff, R. A., Bronk Ramsey, C., Lamb, H. F., Bryant, C. L., Naumann, R., Dulski, P., Brock, F., Yokoyama, Y., Tada, R., & Haraguchi, T. (2014). Event layers in the Japanese Lake Suigetsu 'SG06' sediment core: description, interpretation and climatic implications. Quaternary Science Reviews, 83, 157–170.

Simonneau, A., Chapron, E., Vannière, B., Wirth, S. B., Gilli, A., Di Giovanni, C., Anselmetti, F. S., Desmet, M., & Magny, M. (2013). Mass-movement and flood-induced deposits in Lake Ledro, southern Alps, Italy: implications for Holocene palaeohydrology and natural hazards. Climate of the Past, 9(2), 825–840.

Stockmarr J. (1971). Tablets with Spores used in Absolute Pollen Analysis. Pollen et Spores, 13: 615-621.

Szakács, A., Seghedi, I., Pécskay, Z., & Mirea, V. (2015). Eruptive history of a low-frequency and low-output rate Pleistocene volcano, Ciomadul, South Harghita Mts., Romania. Bulletin of Volcanology, 77(2).

Tantau, I., Reille, M., de Beaulieu, J. L., Farcas, S., Goslar, T., & Paterne, M. (2003). Vegetation history in the Eastern Romanian Carpathians: pollen analysis of two sequences from the Moho? crater. Vegetation History and Archaeobotany, 12(2), 113–125.

Tantau I., Reille M., de Beaulieu J.-L. & Farcas, S. (2005). Late Glacial and Holocene vegetation history in the southern part of Transylvania (Romania): pollen analysis of two sequences from Avrig. Journal of Quaternary Science, 21: 49–61.

Wulf S., Dräger N., Ott F., Serb J., Appelt O., Guðmundsdóttir E., van den Bogaard C., Słowiński M., Błaszkiewicz M., & Brauer A. (2016). Holocene tephrostratigraphy of varved sediment records from Lakes Tiefer See (NE Germany) and Czechowskie (N Poland). Quaternary Science Reviews, 132: 1-14.

Zolitschka, B. (1996). Recent sedimentation in a high arctic lake, northern Ellesmere Island, Canada. Journal of Paleolimnology, 16(2).

Zolitschka, B., Negendank, J. F., & Wagner, B. (2015). Annually laminated lake sediments and varves. Developments in Paleoenvironmental Research, 16, 153-178.

# VI Summary and Perspectives


## Abstract

This study provides a comprehensive overview of pollen-vegetation relationships and their significance in reconstructing past environmental dynamics and vegetation changes. By integrating multiple perspectives from various research areas and approaches, the study advances our understanding of vegetation responses to climate change, ecosystem dynamics, and the reliability of pollen records as indicators of past vegetation.

A comparative approach is employed, analyzing pollen assemblages alongside surrounding vegetation to evaluate the accuracy of pollen records in inferring past vegetation dynamics. Through the examination of composition and diversity at different spatial scales, are identified biases and limitations in reconstructing past vegetation. Additionally, the relationship between pollen type diversity and species diversity in vegetation is explored, determining the strongest correlation by analyzing richness and evenness components.

Understanding the correspondence between pollen assemblages and vegetation gradients is essential, and multivariate techniques like co-correspondence analysis offer valuable insights into the reliability of using pollen assemblages to infer vegetation patterns and dynamics. The study addresses knowledge gaps in southeast Europe, particularly in the Pieria mountains and the Ciomadul lava-dome complex, contributing to our understanding of vegetation dynamics and pollen-vegetation relationships in this region.

Research conducted in coastal Mediterranean sites, such as Halkidiki, sheds light on the complex interactions between human activities, climate change, and vegetation dynamics in coastal regions across the Mediterranean basin. Case studies in Halkidiki employ a multidisciplinary approach, integrating palynological analysis, archaeological excavations, historical sources, and sediment core studies to investigate past vegetation changes, generate an environmental history, and assess the dynamics of the coastal ecosystem.

Furthermore, studies in the Eastern and Southern Carpathians extend temporal coverage and explore vegetation responses to climate change during the Last Glacial and Early Holocene periods. By analyzing pollen records from the Mohoş peat bog core sections, researchers gain insights into past climatic conditions and their influence on vegetation changes. The integration of palynological data with archaeological excavations, historical archives, and marine cores enables a comprehensive understanding of past environmental and human dynamics. Additionally, the investigation of the Mohoş peat bog provides valuable insights into the impact of volcanic events on vegetation and ecosystem resilience.

## 6.1 Perspectives

Overall, this study significantly contributes to the field of paleoecology by bridging multiple research areas and providing a holistic perspective on pollen-vegetation relationships, expanding our knowledge of past vegetation dynamics, and advancing our understanding of the intricate interactions between climate, human activities, and ecosystems. It ambitiously sets out to dissect the intricate patterns of vegetation distribution and biodiversity across the Balkans, with an eye on the ecological narrative that transitions from the Last Glacial period into the Holocene. By employing a suite of analytical techniques—including modern pollen analysis, the study of fossil pollen data, assessing climatic variations, and examining the impacts of human activities—it aims to paint a detailed picture of the ecological and climatic history of the region. This comprehensive investigation serves as a platform to understand the underlying dynamics of plant migration, speciation, and the broader spectrum of environmental change, as reflected in the following scientific questions.

## 6.2 Main Scientific Questions

### 6.2.1 Pollen Representation and Biodiversity:

The comprehensive study conducted in the Pieria mountains and Ciomadul regions has provided a nuanced understanding of the correspondence between pollen assemblages and actual vegetation. Despite the existence of both similarities and differences, the overall correspondence is relatively weak, with values indicating a generally poor relationship. The study underscores that while pollen analysis offers valuable insights, it does not exhaustively represent vegetation due to variabilities in pollen productivity and dispersal.

In the Pieria mountains, for example, the dominant Fagus species in the vegetation is underrepresented in pollen assemblages. This discrepancy could be attributed to factors like altitude and forest maturity, which affect Fagus pollen dispersal, as well as human practices like coppicing. Conversely, Pinus, known for its prolific pollen production, is overly represented in pollen assemblages. This contrast sharply with Ciomadul, where the representation bias leans more towards herbaceous plants, and woody taxa are more accurately captured, especially within smaller radii of vegetation sampling.

The research demonstrates that pollen assemblages can serve as a reliable proxy for understanding aspects of biodiversity and ecological gradients within a specific radius of sampling. This finding is particularly evident in the strong relationship between herb and total floristic and palynological richness in Pieria. However, when focusing solely on herbaceous vegetation, the relationship becomes less clear, emphasizing the challenges in accurately capturing the complete biodiversity through pollen data alone.

Combining the findings from both regions, it's clear that factors like pollen productivity, dispersion mechanisms, representation bias, and the influence of wind-pollinated taxa contribute significantly to the mismatch between pollen data and vegetation. Although pollen assemblages provide a valuable tool for reconstructing past vegetation, the study highlights the importance of considering these discrepancies for a more accurate interpretation of palynological data.

In sum, while the representational accuracy of pollen assemblages is limited, they nonetheless contribute significantly to our understanding of past vegetative biodiversity and ecological gradients. To overcome this limitation, studying and understanding pollen-vegetation relationships, using modern pollen analogues in each site, is essential. The insights from the Pieria mountains and Ciomadul provide a clearer picture of how vegetation has responded over time to both natural and anthropogenic influences, offering a crucial perspective for interpreting ecological and environmental changes throughout the Balkans.

### 6.2.2 Human Landscape Interactions in Halkidiki, Greece:

The integrated study of palynological, archaeological, and historical data offers a comprehensive narrative of human influence on the landscape of Halkidiki and the broader Balkan region. Pollen analyses have uncovered periods of significant human impact, marked by agricultural expansion, deforestation, and changes in land management practices. The decrease in arboreal pollen, particularly from olive trees, alongside archaeological evidence, points to a transition from woodland to agricultural land use.

In examining specific historical periods, such as the Mycenean/Roman and Byzantine/modern eras, the study reveals how human activities like controlled burning, overgrazing, and metallurgical processes shaped the vegetation structure and composition. Controlled fires promoted the growth of certain plant species, while overgrazing led to landscape degradation. The pollen diagram from Tristinika Marsh, indicative of vegetation management practices, aligns with historical records detailing extensive olive cultivation and other agricultural activities.

The decline in human activities during events such as the "plague of Justinian" led to significant ecological shifts, evidenced by changes in pollen data, such as the reduction of Mediterranean pine woodlands and the expansion of natural woody vegetation. Subsequent recovery periods saw a shift back to traditional land use practices, including olive cultivation and viticulture, which were reflected in the pollen record.

Both sets of data also highlight the resiliency and adaptability of vegetation amidst human disturbances. The comparison with marine core SL 152 underscores the consistency of certain pollen types, like Erica, Quercus, and Ostrya/Carpinus orientalis,

across different studies, suggesting a persistent presence in the region's vegetation despite varying human influences.

In summary, the findings indicate a complex, dynamic relationship between humans and their environment, with societal practices both shaping and responding to the ecological conditions of the time. The landscape of Halkidiki, as captured through the multi-disciplinary approach of this study, is both a reflection of human history and a contributor to the cultural narrative of its inhabitants, showcasing the intertwined nature of ecological and human histories.

### 6.2.3 Mohoş Peat Bog Investigation:

The detailed pollen zones (MPZ) described in the study indicate the presence of specific arboreal and herbaceous taxa during different periods, along with associated levels of micro charcoal, suggesting varying degrees of burning activities. These changes in vegetation composition and fire events provide a window into the ecological gradients present at different times. For instance, the dominance of Pinus in the pollen record points to its prevalence during glacial conditions, while the continuous presence of Quercus and Betula suggests a consistent arboreal backdrop amidst changing climates.

Pollen assemblages from the Mohoş peat bog reveal not only the vegetational shifts in response to climatic changes but also the fire history, which plays a crucial role in shaping ecological gradients. The correlation between the AP/NAP curve and the charcoal curve with the well-dated St Ana core supports the reliability of the pollen data in reflecting the vegetational history accurately. The results also highlight the dominance of herbaceous taxa such as Poaceae and Artemisia during the MIS 2, which, combined with the high frequency of wildfires, indicates a very continental climate with warm and dry summers.

In conclusion, the comprehensive pollen and charcoal analyses from the Mohoş peat bog cores, along with comparisons to regional pollen records from Lake St. Ana, demonstrate that pollen data can effectively capture the ecological gradients and environmental characteristics of the vegetation. These findings underscore the utility of pollen assemblages as proxies for understanding past vegetational and climatic dynamics, albeit with the need for cautious interpretation due to potential limitations in dating precision and the influence of tephra deposits on pollen preservation.

## 6.3 Conclusion

The overarching message taken from this thesis is that pollen assemblages serve as a valuable proxy for reconstructing past vegetation and understanding ecological transitions over time, despite some inherent limitations. Through meticulous analysis, the study demonstrates that:

1. Pollen data can effectively reflect the composition and biodiversity of ancient vegetation, even though it may not capture the full complexity due to factors like pollen dispersal and preservation biases.
2. Human activities have played a substantial role in shaping landscapes, as evidenced by the integration of palynological data with archaeological and historical records. The interplay between human interventions and natural vegetational responses over millennia has been dynamic, leading to significant ecological shifts.
3. Detailed investigations like the Mohoş Peat Bog study illuminate the ecological gradients within a region, providing insights into past climatic conditions and vegetational responses to these changes, including fire history and species prevalence during different climatic phases.

In essence, the thesis communicates that the integration of palynological analysis with other historical data provides a nuanced understanding of past human-ecosystem interactions and the resilience and adaptability of vegetation to changing climates. It underscores the importance of such interdisciplinary approaches in informing current and future conservation strategies and understanding the ecological legacies that shape today's natural landscapes.

## 6.4 Future Research

Future research in the field of pollen-vegetation relationships encompasses several directions. These include refining reconstruction techniques, conducting multi-site comparative studies, establishing long-term monitoring programs, integrating multi-proxy approaches, exploring untapped paleoenvironmental archives, and advancing quantitative reconstruction models. Refining techniques will improve the accuracy of

pollen-based reconstructions, while comparative studies will identify common patterns and drivers across regions and ecosystems. Long-term monitoring programs will validate pollen-vegetation relationships and track changes over time. Integrating multiple proxies and socio-economic data will provide a comprehensive understanding of past environmental dynamics. Exploring untapped archives and developing quantitative models will expand the coverage of pollen-vegetation studies. Pursuing these research directions will enhance our understanding of past vegetation changes and improve our ability to predict and manage future vegetation changes in the face of global environmental transformations.

# Zusammenfassung

Diese Studie bietet einen umfassenden Überblick über die Beziehungen zwischen Pollen und Vegetation sowie deren Bedeutung für die Rekonstruktion vergangener Umweltveränderungen und Vegetationsentwicklungen. Durch die Integration verschiedener Perspektiven aus verschiedenen Forschungsbereichen und Ansätzen trägt die Studie zu unserem Verständnis der Reaktion der Vegetation auf Klimaveränderungen, der Dynamik von Ökosystemen und der Zuverlässigkeit von Pollenanalysen als Indikatoren vergangener Vegetation bei. Ein vergleichender Ansatz wird angewendet, indem Pollenassemblagen neben der umgebenden Vegetation analysiert werden, um die Genauigkeit von Pollenanalysen zur Ableitung vergangener Vegetationsdynamiken zu bewerten. Durch die Untersuchung von Zusammensetzung und Vielfalt auf verschiedenen räumlichen Skalen werden Verzerrungen und Limitationen bei der Rekonstruktion vergangener Vegetation identifiziert. Zusätzlich wird das Verhältnis zwischen der Diversität von Pollenarten und der Artenvielfalt in der Vegetation erforscht, wobei die stärkste Korrelation durch die Analyse von Artenreichtum und Gleichmäßigkeitselementen bestimmt wird.

Das Verständnis der Übereinstimmung zwischen der Pollenzusammensetzung und den Vegetationsgradienten ist entscheidend, und multivariate Techniken wie die Co-Korrespondenzanalyse bieten wertvolle Einblicke in die Zuverlässigkeit der Verwendung von Pollenanalysen zur Ableitung von Vegetationsmustern und -dynamiken. Die Studie schließt Wissenslücken in Südosteuropa, insbesondere in den Pieria-Bergen und dem Ciomadul-Lavadom-Komplex, und trägt so zu unserem Verständnis der Vegetationsdynamik und der Beziehung zwischen Pollen und Vegetation in dieser Region bei.

Forschung in küstennahen mediterranen Gebieten wie Halkidiki beleuchtet die komplexen Wechselwirkungen zwischen menschlichen Aktivitäten, Klimaveränderungen und Vegetationsdynamiken in Küstenregionen des gesamten Mittelmeerraums. Fallstudien in Halkidiki nutzen einen interdisziplinären Ansatz, der palynologische Analysen, archäologische Ausgrabungen, historische Quellen und Sedimentkernstudien integriert, um vergangene Vegetationsveränderungen zu untersuchen, eine Umweltgeschichte zu erstellen und die Dynamik des Küstensystems zu bewerten.

Des Weiteren erweitern Studien in den östlichen und südlichen Karpaten die zeitliche Abdeckung und erforschen die Reaktion der Vegetation auf Klimaveränderungen während der letzten Eiszeit und des frühen Holozäns. Durch die Pollenanalysen aus Kernabschnitten im Mohoş-Moor erhalten Forscher Einblicke in vergangene klimatische Bedingungen und deren Einfluss auf die Vegetationsveränderungen. Die Integration von palynologischen Daten mit archäologischen Ausgrabungen, historischen Archiven und marinen Bohrkernen ermöglicht ein umfassendes Verständnis vergangener Umweltveränderungen unter anthropogenem Einfluss. Die Untersuchung im Mohoş-Moor liefert zudem wertvolle Erkenntnisse über die Auswirkungen von vulkanischen Ereignissen auf

die Vegetation und die Resilienz des Ökosystems.
Insgesamt leistet diese Studie einen signifikanten Beitrag zum Bereich der Paläoökologie, indem sie mehrere Forschungsbereiche miteinander verbindet und eine ganzheitliche Perspektive auf die Beziehung zwischen Pollen und Vegetation bietet. Sie erweitert unser Wissen über vergangene Vegetationsdynamiken und vertieft unser Verständnis der komplexen Interaktionen zwischen Klima, menschlichen Aktivitäten und Ökosystemen.

# Appendix

**Table A.1:** Taxa identified in Vegetation of Ciomadul.

| Taxon | Pollination Type |
|---|---|
| *Abies alba* | wind pollinating |
| *Acer campestre* | insect pollinating |
| *Acer platanoides* | insect pollinating |
| *Acer pseudoplatanus* | insect pollinating |
| *Achillea* species | insect pollinating |
| *Actaea spicata* | insect pollinating |
| *Ajuga reptans* | insect pollinating |
| *Alnus Glutinosa* | insect pollinating |
| *Anemone ranunculoides* | insect pollinating |
| *Arctium lappa* | insect pollinating |
| *Arrhenatherum elatius* | wind pollinating |
| *Asarum europaeum* | insect pollinating |
| *Astragalus glycyphyllos* | insect pollinating |
| *Athyrium filix-femina* | spores |
| *Betula pubescens* | wind pollinating |
| *Brachypodium sylvaticum* | wind pollinating |
| *Bromopsis benekenii* | wind pollinating |
| *Campanula persicifolia* | insect pollinating |
| *Campanula rapunculoides* | insect pollinating |
| *Campanula sparsa* | insect pollinating |
| *Cardamine bulbifera* | insect pollinating |
| *Cardamine enneaphyllos* | insect pollinating |
| *Cardamine impatiens* | insect pollinating |
| *Carex digitata* | wind pollinating |
| *Carex Pilosa* | wind pollinating |
| *Carex sporesicata* | wind pollinating |
| *Carex sylvatica* | wind pollinating |
| *Carpinus betulus* | wind pollinating |
| *Chaerophyllum aureum* | insect pollinating |
| *Chelidonium majus* | insect pollinating |
| *Circaea lutetiana* | insect pollinating |
| *Clinopodium* species | insect pollinating |
| *Cornus mas* | insect pollinating |
| *Corylus avellana* | wind pollinating |
| *Dactylis glomerata* | wind pollinating |
| *Daphne mezereum* | insect pollinating |
| *Digitalis* species | insect pollinating |
| *Drymochloa drymeja* | wind pollinating |
| *Dryopteris filix-mas* | spores |

| Taxon | Pollination Type |
|---|---|
| *Dryopteris remota* | spores |
| *Epilobium montanum* | spores |
| *Euphorbia amygdaloides* | insect pollinating |
| *Evonymus europaeus* | insect pollinating |
| *Evonymus verrucosus* | insect pollinating |
| *Fagus sylvatica* | wind pollinating |
| *Festuca heterophylla* | wind pollinating |
| *Fragaria vesca* | insect pollinating |
| *Fraxinus excelsior* | insect pollinating |
| *Galeopsis bifida* | insect pollinating |
| *Galeopsis speciosa* | insect pollinating |
| *Galium aparine* | spores |
| *Galium mollugo agg.* | insect pollinating |
| *Galium odoratum* | insect pollinating |
| *Geranium robertianum* | spores |
| *Geum urbanum* | spores |
| *Glechoma hirsuta* | insect pollinating |
| *Gymnocarpium dryopteris* | spores |
| *Hieracium murorum* | insect pollinating-spores |
| *Hieracium* species | insect pollinating-spores |
| *Hylotelephium telephium* | spores |
| *Hypericum maculatum* | insect pollinating |
| *Impatiens noli-tangere* | insect pollinating |
| *Lactuca muralis* | spores |
| *Lamium galeobdolon subs. galeobdolon* | insect pollinating |
| *Lamium maculatum* | insect pollinating |
| *Lapsana communis* | spores |
| *Lathyrus vernus* | insect pollinating |
| *Lonicera xylosteum* | insect pollinating |
| *Luzula luzuloides* | wind pollinating |
| *Luzula Pilosa* | wind pollinating |
| *Maianthemum bifolium* | insect pollinating |
| *Malus pumila* | insect pollinating |
| *Melittis melisophyllum subs. albida* | insect pollinating |
| *Mercurialis perennis* | wind pollinating |
| *Milium effusum* | wind pollinating |
| *Moehringia trinervia* | spores |
| *Myosotis sylvatica* | insect pollinating-spores |
| *Neottia cordata* | insect pollinating |
| *Neottia nidus-avis* | insect pollinating |

| Taxon | Pollination Type |
|---|---|
| *Neottia ovata* | insect pollinating |
| *Orthilia secunda* | insect pollinating |
| *Oxalis acetosella* | insect pollinating |
| *Paris quadrifolia* | wind pollinating-spores |
| *Picea abies* | wind pollinating |
| *Pinus sylvestris* | wind pollinating |
| *Plantago major* | wind pollinating |
| *Platanthera* | insect pollinating |
| *Poa nemoralis* | wind pollinating |
| *Polygonatum odoratum* | insect pollinating |
| *Polystichum braunii* | spores |
| *Populus tremula* | wind pollinating |
| *Prunella vulgaris* | insect pollinating |
| *Prunus avium* | insect pollinating |
| *Prunus cerasifera* | insect pollinating |
| *Pulmonaria rubra* | insect pollinating |
| *Quercus petraea* | wind pollinating |
| *Ranunculus* species | insect pollinating |
| *Ribes uva-crispa* | insect pollinating |
| *Rosa canina* | insect pollinating |
| *Rosa pendulina* | insect pollinating |
| *Rubus hirtus* | insect pollinating |
| *Rubus idaeus* | spores |
| *Rumex* species | wind pollinating |
| *Salix caprea* | insect pollinating |
| *Salvia* species | insect pollinating |
| *Sambucus nigra* | insect pollinating |
| *Sanicula europaea* | insect pollinating |
| *Satureja vulgaris* | insect pollinating |
| *Saxifraga* species | insect pollinating |
| *Schedonorus giganteus* | wind pollinating |
| *Scrophularia nodosa* | insect pollinating |
| *Securigera varia* | insect pollinating |
| *Senecio nemorensis agg.* | insect pollinating |
| *Silene atropurpurea* | insect pollinating |
| *Silene viridiflora* | insect pollinating |
| *Solidago virgaurea* | insect pollinating |
| *Sorbus aucuparia* | insect pollinating |
| *Stellaria holostea* | insect pollinating |
| *Stellaria nemorum* | insect pollinating |

| Taxon | Pollination Type |
|---|---|
| *Symphytum tuberosum subs. angustifolium* | insect pollinating |
| *Taraxacum* species | insect pollinating |
| *Tilia cordata* | insect pollinating |
| *Torilis* species | insect pollinating |
| *Ulmus glabra* | wind pollinating |
| *Urtica dioica* | wind pollinating |
| *Vaccinium myrtillus* | spores |
| *Vaccinium vitis-idaea* | insect pollinating |
| *Verbascum* species | insect pollinating |
| *Veronica chamaedrys* | insect pollinating |
| *Veronica officinalis* | insect pollinating |
| *Veronica urticifolia* | insect pollinating |
| *Viburnum opulus* | insect pollinating |
| *Vicia dumetorum* | insect pollinating |
| *Vicia* species | insect pollinating |
| *Viola reichenbachiana* | insect pollinating |
| *Vitis vinifera* | wind pollinating |

**Table A.2:** Taxa identified in Vegetation of Pieria.

| **Taxon** | **Pollination Type** |
|---|---|
| *Abies borisii-regis* | wind pollinating |
| *Acer campestre* | insect pollinating |
| *Acer monsporesessulanum* | insect pollinating |
| *Acer obtusatum* | insect pollinating |
| *Acer pseudoplatanus* | insect pollinating |
| *Achillea millefolium* | insect pollinating |
| *Aegilops triuncialis* | wind pollinating |
| *Agrostis* species | wind pollinating |
| *Aira elegantissima* | wind pollinating |
| *Ajuga genevensis* | insect pollinating |
| *Alyssum murale* | insect pollinating |
| *Anisantha sterilis* | spores |
| *Anisantha tectorum* | wind pollinating |
| *Anthoxanthum odoratum* | wind pollinating |
| *Arabis sagittata* | insect pollinating |
| *Aremonia agrimonoides* | insect pollinating |
| *Aristolochia* species | insect pollinating |
| *Armeria canescens* | insect pollinating |
| *Arrhenatherum* species | wind pollinating |
| *Asporeshodeline liburnica* | insect pollinating |
| *Asporeslenium ceterach* | spores |
| *Asporeslenium trichomanes* | spores |
| *Avenella flexuosa* | wind pollinating |
| *Bellis perennis* | insect pollinating-spores |
| *Brachypodium pinnatum* | wind pollinating |
| *Brachypodium sylvaticum* | wind pollinating |
| *Bromopsis ramosa* | wind pollinating |
| *Bromus hordeaceus* | wind pollinating |
| *Buglossoides arvensis* | spores |
| *Campanula sporesatulata* | insect pollinating |
| *Cardamine hirsuta* | spores |
| *Carduus* species | insect pollinating |
| *Carex divulsa* | wind pollinating |
| *Carex flacca* | wind pollinating |
| *Carpinus orientalis* | wind pollinating |
| *Carthamus lanatus* | spores |
| *Castanea sativa* | wind pollinating |
| *Centaurea phrygia subs. stenolepis* | insect pollinating |
| *Centaurea* species | insect pollinating |

| Taxon | Pollination Type |
|---|---|
| *Centaurium erythraea* | spores |
| *Cerastium brachypetalum subs. roeseri* | spores |
| *Cerastium* species | spores |
| *Cichorium intybus* | insect pollinating |
| *Cistus creticus* | insect pollinating |
| *Clinopodium alpinum* | insect pollinating |
| *Clinopodium vulgare* | insect pollinating |
| *Convolvulus arvensis* | insect pollinating |
| *Cornus mas* | insect pollinating |
| *Cota tinctoria* | insect pollinating |
| *Crataegus monogyna* | insect pollinating |
| *Crucianella angustifolia* | insect pollinating |
| *Cruciata glabra* | insect pollinating |
| *Cruciata pedemontana* | insect pollinating |
| *Cyclamen hederifolium* | insect pollinating |
| *Cynosurus echinatus* | wind pollinating |
| *Cytisus triflorus* | insect pollinating |
| *Dactylis glomerata* | wind pollinating |
| *Daphne laureola* | insect pollinating |
| *Dasypyrum villosum* | wind pollinating |
| *Dianthus formanekii* | insect pollinating |
| *Digitalis viridiflora* | insect pollinating |
| *Doronicum orientale* | insect pollinating |
| *Dorycnium hirsutum* | insect pollinating |
| *Dorycnium pentaphyllum subs. herbaceum* | insect pollinating |
| *Draba muralis* | spores |
| *Echium* species | insect pollinating |
| *Epilobium angustifolium* | insect pollinating |
| *Erica arborea* | insect pollinating |
| *Eryngium amethystinum* | insect pollinating |
| *Eryngium campestre* | insect pollinating |
| *Erysimum pusillum subs. microstylum* | insect pollinating |
| *Euphorbia amygdaloides* | insect pollinating |
| *Euphorbia cyparissias* | insect pollinating |
| *Euphrasia* species | spores |
| *Fagus sylvatica* | wind pollinating |
| *Festuca heterophylla* | wind pollinating |
| *Festuca ovina agg.* | wind pollinating |
| *Filago* species | spores |
| *Filinsect pollinatingendula vulgaris* | insect pollinating |

| Taxon | Pollination Type |
|---|---|
| *Fragaria vesca* | insect pollinating |
| *Fraxinus ornus* | insect pollinating |
| *Galium aparine* | insect pollinating |
| *Galium divaricatum* | insect pollinating |
| *Galium mollugo agg.* | insect pollinating |
| *Galium odoratum* | insect pollinating |
| *Galium rotundifolium* | insect pollinating |
| *Galium verum* | insect pollinating |
| *Genista carinalis* | insect pollinating |
| *Geranium columbinum* | insect pollinating |
| *Geranium lucidum* | insect pollinating |
| *Geranium macrorhizum* | insect pollinating |
| *Geranium molle* | insect pollinating |
| *Geranium robertianum* | insect pollinating |
| *Geranium sanguineum* | insect pollinating |
| *Geranium* species | insect pollinating |
| *Geranium versicolor* | insect pollinating |
| *Geum urbanum* | insect pollinating |
| *Hedera helix* | insect pollinating |
| *Helianthemum nummularium* | insect pollinating |
| *Hieracium bracteolatum* | insect pollinating-spores |
| *Hieracium murorum agg.* | insect pollinating-spores |
| *Hieracium olympicum* | insect pollinating-spores |
| *Hinsect pollinatingpocrepis emerus* | insect pollinating |
| *Hypericum montanum* | insect pollinating |
| *Hypericum olympicum* | insect pollinating |
| *Hypericum perforatum* | insect pollinating |
| *Inula* species | insect pollinating |
| *Juniperus communis* | wind pollinating |
| *Juniperus communis subs. nana* | wind pollinating |
| *Juniperus oxycedrus* | wind pollinating |
| *Knautia arvensis* | insect pollinating |
| *Knautia drymeia* | insect pollinating |
| *Knautia* species | insect pollinating |
| *Lamium maculatum* | spores |
| *Lapsana communis* | spores |
| *Lathyrus alpestris* | insect pollinating |
| *Lathyrus laxiflorus* | insect pollinating |
| *Lathyrus nissolia* | insect pollinating |
| *Leontodon* species | insect pollinating |

| Taxon | Pollination Type |
|---|---|
| *Linaria peliseriana* | insect pollinating |
| *Linum* species | insect pollinating |
| *Lotus corniculatus* | insect pollinating |
| *Luzula forsteri* | wind pollinating |
| *Luzula luzuloides* | wind pollinating |
| *Luzula multiflora* | wind pollinating |
| *Luzula sylvatica* | wind pollinating |
| *Lysimachia punctata* | insect pollinating |
| *Malus* species | insect pollinating |
| *Medicago lupulina* | insect pollinating |
| *Medicago* species | insect pollinating |
| *Melilotus* species | insect pollinating |
| *Mentha* species | insect pollinating |
| *Mercurialis* species | wind pollinating |
| *Minuartia attica* | insect pollinating |
| *Minuartia hybrida* | insect pollinating |
| *Muscari neglectum* | insect pollinating |
| *Myosotis ramosissima* | spores |
| *Myosotis sylvatica* | spores |
| *Neottia ovata* | insect pollinating |
| *Ochlopoa annua* | wind pollinating |
| *Orchidaceae* species | insect pollinating |
| *Origanum vulgare* | insect pollinating |
| *Orlaya daucoides* | insect pollinating |
| *Ostrya carpinifolia* | wind pollinating |
| *Ostrya carpinifolia* | |
| *Phleum* species | wind pollinating |
| *Physospermum cornubiense* | insect pollinating |
| *Pilosella bauhini* | insect pollinating-spores |
| *Pilosella hoppeana* | insect pollinating-spores |
| *Pinus nigra* | wind pollinating |
| *Pinus sylvestris* | wind pollinating |
| *Plantago lanceolata* | wind pollinating |
| *Plantago major* | wind pollinating |
| *Platanus orientalis* | |
| *Poa bulbosa* | wind pollinating |
| *Poa nemoralis* | wind pollinating |
| *Poa* species | wind pollinating |
| *Poaceae* species | wind pollinating |
| *Polygala nicaeensis* | insect pollinating |

| Taxon | Pollination Type |
|---|---|
| *Populus tremula* | insect pollinating |
| *Potentilla argentea* | insect pollinating |
| *Potentilla micrantha* | insect pollinating |
| *Potentilla recta* | insect pollinating |
| *Primula acaulis* | insect pollinating |
| *Primula veris* | insect pollinating |
| *Prunella laciniata* | insect pollinating |
| *Prunella vulgaris* | insect pollinating |
| *Prunus cocomilia* | insect pollinating |
| *Pteridium aquilinum* | spores |
| *Ptilostemon strictus* | insect pollinating |
| *Pyrus communis* | insect pollinating |
| *Pyrus sporesinosa* | insect pollinating |
| *Quercus frainetto* | wind pollinating |
| *Quercus petraea* | wind pollinating |
| *Quercus pubescens* | wind pollinating |
| *Ranunculus bulbosus subs. aleae* | insect pollinating |
| *Roripa thracica* | insect pollinating |
| *Rosa arvensis* | insect pollinating |
| *Rosa canina* | insect pollinating |
| *Rubus caesius* | insect pollinating |
| *Rubus canescens* | insect pollinating |
| *Rubus hirtus* | insect pollinating |
| *Rubus idaeus* | insect pollinating |
| *Rubus sanctus* | insect pollinating |
| *Rumex acetosella* | wind pollinating |
| *Rumex* species | wind pollinating |
| *Ruta* species | insect pollinating |
| *Salix caprea* | insect pollinating |
| *Sanguisorba minor* | wind pollinating |
| *Sanicula eurapaea* | insect pollinating |
| *Saxifraga tridactylites* | spores |
| *Schedonorus arundinaceus* | wind pollinating |
| *Scorzoneroides cichoriacea* | insect pollinating |
| *Securigera varia* | insect pollinating |
| *Sedum amplexicaule* | insect pollinating |
| *Sedum annuum* | insect pollinating |
| *Sedum caesporesitosum* | insect pollinating |
| *Sedum* species | insect pollinating |
| *Senecio nemorensis* | insect pollinating |

| Taxon | Pollination Type |
|---|---|
| *Sherardia arvensis* | wind pollinating |
| *Silene coronaria* | insect pollinating |
| *Silene italica* | insect pollinating |
| *Silene viridiflora* | insect pollinating |
| *Silene vulgaris* | insect pollinating |
| *Sonchus arvensis* | insect pollinating |
| *Sorbus aria* | insect pollinating |
| *Sorbus torminalis* | insect pollinating |
| *Stachys* species | insect pollinating |
| *Symphytum bulbosum* | insect pollinating |
| *Symphytum ottomanum* | insect pollinating |
| *Taraxacum* species | insect pollinating |
| *Tephroseris integrifolia* | insect pollinating |
| *Teucrium chamaedrys* | insect pollinating |
| *Thlasporesi* species | spores |
| *Thymus longicaulis* | insect pollinating |
| *Thymus sibthorpii* | insect pollinating |
| *Thymus* species | insect pollinating |
| *Tordylium officinale* | insect pollinating |
| *Torilis arvensis* | spores |
| *Tragopogon* species | insect pollinating |
| *Trifolium alpestre* | insect pollinating |
| *Trifolium angustifolium* | insect pollinating |
| *Trifolium arvense* | spores |
| *Trifolium campestre* | insect pollinating |
| *Trifolium fragiferum* | insect pollinating-spores |
| *Trifolium medium* | insect pollinating |
| *Trifolium nigrescens* | insect pollinating |
| *Trifolium ochroleucon* | insect pollinating |
| *Trifolium pignantii* | insect pollinating |
| *Trifolium pratense* | insect pollinating |
| *Trifolium repens* | insect pollinating |
| *Trifolium scabrum* | spores |
| *Trifolium* species | insect pollinating |
| *Trifolium tenuifolium* | insect pollinating |
| *Vaccinium myrtillus* | insect pollinating |
| *Valerianella* species | spores |
| *Verbascum nigrum* | insect pollinating |
| *Verbascum* species | insect pollinating |
| *Veronica arvensis* | spores |

| **Taxon** | **Pollination Type** |
|---|---|
| *Veronica chamaedrys* | insect pollinating |
| *Veronica species* | insect pollinating |
| *Veronica verna* | insect pollinating |
| *Vicia cassubica* | insect pollinating |
| *Vicia cracca* | insect pollinating |
| *Vicia grandiflora* | insect pollinating |
| *Vicia hirsute* | spores |
| *Vicia lathyroides* | insect pollinating |
| *Vicia sativa* | spores |
| *Vicia tenuifolia subs. dalmatica* | insect pollinating |
| *Vicia tetrasporeserma* | insect pollinating |
| *Vicia villosa* | insect pollinating |
| *Viola alba* | insect pollinating |
| *Viola species* | insect pollinating |
| *Viola tricolor* | insect pollinating |
| *Vulpia myurus* | spores |

**Table A.3:** Pollen and Spores identified in Moss samples in Pieria and Ciomadul.

**Pollen**

*Abies*
*Allium ursinum* - Type
*Alnus*
Apiaceae
*Artemisia*
*Asphodelus* - Group
Asteraceae
*Astragalus* - Type
*Betula*
Brassicaceae
*Campanula trachelium* - Type
Cannabinaceae
*Carduus* – Type
*Carpinus*
*Carpinus betulus*
Caryophyllaceae
*Castanea*
*Centaurea jacea*
*Centaurea montana*
*Cerastium* - Type
Cerealia
cf *Oenanthe*
cf *Onobrychis*
Chenopodiaceae
Cichorioideae
*Cistus albidus* - Type
*Conium* – Type
*Cornus*
*Cornus sanguinea*
*Corylus*
*Crepis* – Type
Cyperaceae
*Daphne*
*Dianthus*
*Eryngium*
*Euphorbia*
*Fagus*
*Filipendula*
*Fraxinus*

**Pollen**

*Fraxinus excelsior* - Type
*Galeopsis* - Type
*Galium*
*Genista* – Type
*Granineae*
*Helianthemum nummularium* – Group
*Hypericum perforatum* - Type
*Ilex aquifolium*
*Juglans*
Juncaceae
*Juniperus* - Type
*Knautia*
*Lotus*
*Matricaria* - Type
*Medicago lupulina* - Type
*Melampyrum*
*Mentha* – Type
*Muscari neglectum* - Type
*Olea europaea*
*Ostrya* - Type
*Osyris alba*
*Phillyrea*
*Phyteuma* – Type
*Picea*
*Pinus*
*Pistacia*
*Plantago*
*Platango lanceolata* - Type
*Platanus orientalis*
Poaceae
*Populus*
*Potentilla* - Type
*Primula veris* - Type
*Quercus*
*Quercus cerris* - Type
*Quercus ilex* - Type
*Quercus robur - pubescens* - Type
*Ranunculus acris* - Type
*Rhinanthus* - Group
*Robinia pseudoacacia*

**Pollen**

*Rosa*
Rubiaceae
*Rubus*
*Rumex acetosa* – Type
*Salix*
*Sanguisorba minor* - Type
*Saussurea* – Type
*Saxifraga stellaris* - Type
*Senecio* – Type
*Silene* – Type
*Soldanella* – Type
*Sorbus* – Group
*Spergularia* - Type
*Stachys (Galeopsis* - *Ballota* - Group*)*
*Stellaria graminea* - Group
*Teucrium chamaedrys* - Type
*Thalictrum*
*Tilia cordata* - Type
*Trifolium repens* - Type
*Ulmus*
Urticaceae
*Vaccinium* – Type
*Verbascum*
*Veronica* – Type
*Vicia* – Type
*Viola odorata* - Type
*Viscum album*
*Vitis*
*Xanthium spinosum* - Type
*Zea*

**Spores**

*Asplenium trichomanes*
*Botrychium*
*Cystopteris*
*Dryopteris*
*Preridium*
*Pteridophyta*
*Polystichum*

**Table A.4:** Pollen and Spores identified in Tristinika core.

**Pollen**

*Abies*
*Alnus*
Amaranthaceae
Apiaceae
*Arbutus*
*Artemisia*
*Asphodelus – Group*
*Astragalus – Type*
*Betula*
Boraginaceae
Brassicaceae
*Campanula trachelium* – Type
*Carduus* – Type
*Carpinus*
Caryophyllaceae
*Castanea*
*Centaurea jacea*
Cichorioideae
*Cistus albidus* – Type
*Convolvulus*
*Corylus*
Cyperaceae
*Equisetum*
*Erica*
*Fagus*
*Fraxinus*
*Geranium*
*Hedera*
*Juglans*
Juncaceae
*Juniperus* – Type
Liliaceae
*Matricaria* - Type
*Mentha* – Type
*Myriophyllum*
*Olea europaea*
*Ostrya* - Type
*Paliurus*
*Phillyrea*

**Pollen**

*Picea*
*Pinus*
*Pistacia*
*Plantago lanceolata* - Type
*Platanus orientalis*
Poaceae
Polygonaceae
*Portulacca*
*Potentilla* - Type
*Quercus ilex - Type*
*Quercus robur - pubescens* - Type
*Ranunculus acris* - Type
Rubiaceae
*Salix*
*Sarcopoterium*
*Secale*
*Senecio* - Type
*Silene* - Type
*Teucrium chamaedrys* - Type
*Tilia* -Type
*Trifolium repens* - Type
*Triticum*
*Typha*
*Ulmus*
*Veronica* - Type
*Vitis*
*Xanthium*

**Spores**

*Asplenium*
*Botrychium*
*Cystopteris*
*Dryopteris*
*Thelypteris*
*Polypodium*
*Pteridium*
*Selaginella*

**Table A.5:** Pollen and Spores identified in Mohoş core.

**Pollen**

*Abies*
*Alnus*
*Anthemis* -Type
Apiaceae
*Artemisia*
*Betula*
*Betula nana*
Brassicaceae
*Carpinus betulus*
Caryophyllaceae
Cerealia
Chenopodiaceae
Cichorioideae
*Cirsium* -Type
*Corylus*
Cyperaceae
*Ephedra*
*Epilobium*
Ericaceae
*Fagus*
*Filipendula*
*Fraxinus*
*Hedera*
*Helianthemum nummularium* - Group
*Juniperus* - Type
*Larix*
Liliaceae
*Matricaria* - Type
*Mentha* – Type
*Ostrya* - Type
*Picea*
*Pinus*
*Plantago*
Poaceae
*Polygonum* - Type
*Polygonum bistorta*
*Potentilla* - Type
*Quercus robur - pubescens* - Type
Ranunculaceae

**Pollen**

*Rosa*

Rubiaceae

*Rubus*

*Rumex acetosa* - Type

*Salix*

*Sanguisorba minor* - Type

*Senecio* - Type

*Tilia cordata* - Type

*Ulmus*

Urticaceae

**Spores**

*Ascospores*

Polypodiaceae

# Chapter Contributions

**Paper I (Chapter III)**: Testing the potential of pollen assemblages to capture composition, diversity and ecological gradients of surrounding vegetation in two biogeographical regions of southeastern Europe.

In this chapter, Papadopoulou was involved in fieldwork, where she collected moss samples and vegetation data. Later, in the laboratory, she analyzed the moss samples and extracted pollen. She also participated in statistical analysis, interpretation of results, and contributed to the writing process as the head writer.

**Paper II (Chapter IV)**: Human-landscape interactions in Halkidiki (NC Greece) over the last 3.5 millennia, revealed through palynological, and archaeological-historical archives.

In this chapter, Papadopoulou participated in the drilling campaign. She described the sediment cores in the laboratory and extracted pollen and microcharcoal. She provided a pollen diagram and an age-depth model. Additionally, she participated in interpreting the results and contributed to the writing process.

**Paper III (Chapter V)**: Vegetation and Climate reconstruction in the Carpathian region during the LGM, from Mohoș (first results)

In this chapter, Papadopoulou participated in the drilling campaign. She described the sediment cores on field and extracted pollen and microcharcoal in the laboratory. She provided a pollen diagram and interpreted the results. She is the main author of this chapter.

# Erklärung

Ich versichere, dass ich die von mir vorgelegte Dissertation selbständig angefertigt, die benutztenQuellen und Hilfsmittel vollständig angegeben und die Stellen der Arbeit −einschließlich Tabellen, Karten und Abbildungen−, die anderen Werken im Wortlaut oder dem Sinn nachentnommen sind, in jedem Einzelfall als Entlehnung kenntlich gemacht habe; dass diese Dissertation noch keiner anderen Fakultät oder Universität zur Prüfung vorgelegen hat; dasssie −abgesehen von unten angegebenen Teilpublikationen− noch nicht veröffentlicht worden ist, sowie, dass ich eine solche Veröffentlichung vor Abschluss des Promotionsverfahrens nicht vornehmen werde.

Die Bestimmungen der Promotionsordnung sind mir bekannt. Die von mir vorgelegte Dissertation ist von Prof. Dr. Frank Schäbitz betreut worden.

Nachfolgend genannte Teilpublikationen liegen vor:

1. Papadopoulou M, Tsiripidis I, Panajiotidis S, Fotiadis G, Veres D, Magyari E, et al. Testing the potential of pollen assemblages to capture composition, diversity and ecological gradients of surrounding vegetation in two biogeographical regions of southeastern Europe. Vegetation History and Archaeobotany 2021;31:1–15. https://doi.org/10.1007/s00334-021-00831-4.
2. Panajiotidis S, Papadopoulou ML. Human-landscape interactions in Halkidiki (NC Greece) over the last 3.5 millennia, revealed through palynological, and archaeological-historical archives. Journal of Archaeological Science: Reports 2016;7:138–45. https://doi.org/10.1016/j.jasrep.2016.03.050.

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