Holocene vegetation history and environmental change in the forest-grassland mosaic of the Central Highlands of Madagascar

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Thesis presented for the Degree of
DOCTOR OF PHILOSOPHY
Department of Biological Sciences
UNIVERSITY OF CAPE TOWN
October 2021

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For my mum, Gisèle Ravoahanginirina

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ABSTRACT

The origin and classification of open and mosaic ecosystems, particularly in the tropics and subtropics, have led to controversy worldwide. This has affected biodiversity conservation and, in some cases, promoted the establishment of afforestation projects based on the assumption that open and mosaic ecosystems are degraded forests. Although this initiative can have benefits in terms of carbon storage and climate mitigation if carefully planned and managed, it can also cause biodiversity loss and degradation when afforestation takes place in areas that were previously open ecosystems, or where unsuitable species are used. Madagascar, a world biodiversity hotspot, is one of the countries targeted for the implementation of afforestation projects. The Central Highlands of Madagascar, dominated by grassland matrix with forest patches, is the main region targeted. The nature and origin of the landscape are hotly debated, however, and it is not clear whether these open ecosystems are ancient or anthropogenically derived. Understanding of landscape history is therefore required to identify and conserve ancient open ecosystems, and to distinguish them from areas that have been deforested by people. This research aims to reconstruct the vegetation history and environmental change in the Central Highlands of Madagascar during the Holocene using palaeoecological methods, in order to inform appropriate conservation and management plans. We provide new records of vegetation, hydrological change, fire and herbivory activities by using a multiproxy approach, which includes fossil pollen, stable carbon isotopes, diatoms, charcoal and coprophilous spores, that allows for a comprehensive investigation into the history and drivers of vegetation change. Sediment cores were collected from two sites, Tampoketsa-Ankazobe wetland and Lake Dangovavy, located in the eastern and western slopes of the highlands, respectively.

Results indicated that the surrounding area of both sites was composed of mosaic ecosystems, comprising of forest patches of variable extent in a matrix of open grassland and ericoid shrubland vegetation, at least from the Early and Mid-Holocene to ca. 1000 cal years BP, driven mainly by climate variability and fire occurrence.

In Tampoketsa-Ankazobe wetland (eastern slopes), the vegetation was characterised by a mosaic of ericoid shrubland and mid-elevation forest taxa, between ca. 11 200 and 8300 cal years BP, under warm/wet period and low fire occurrence. The vegetation in the area changed to a mosaic of ericoid shrubland with more dominance of high-elevation forest from ca. 8300

to 1000 cal years BP under a drier climate and consistent low fire occurrence. The abundance of shrubs and trees during those two periods were confirmed by the dominance of C_3 plants as reflected by the stable carbon isotopes results, and coincided with low herbivory activities in the Tampoketsa-Ankazobe site from ca. 11 200 to 1000 cal years BP.

In parallel, the pollen record from Lake Dangovavy (western slopes), between ca. 6200 and 5400 cal years BP, suggests a mosaic ecosystem, dominated by more C_3 montane grass, ericoid shrubland and high elevation forest patches promoted by cool/dry climate with low fire occurrence and herbivory activities. Between ca. 5400 and 4200 cal years BP, vegetation in the area was dominated by a mosaic of ericoid shrubland and mid-elevation forest under a wetter period, moderate fire occurrence, and herbivory activities. This mosaic was controlled by climate, fire refugia and herbivory feedbacks. The vegetation changed into a forest-savanna mosaic with an abundance of grassland and pioneer/fire-resistant trees between ca. 4200 and 3000 cal years BP. The period was characterised by an initial increase of local fire followed by a regional drought event. This suggests that a threshold might have been reached, with a resulting shift in vegetation composition. Between ca. 3000 and 1000 cal years BP, reoccurrence of ericoid shrubland with woodland savanna taxa was recorded in the area. The vegetation was conditioned by variation of climate from wet (until ca. 2000 cal years BP) to dry period (ca. 2000–1000 cal years BP) with moderate fire occurrence and herbivory activities. In addition, stable carbon isotope results show that between ca. 6200 to 1000 cal years BP, the site was characterised by C_3 plants.

During the last ca.1000 cal years BP, pollen records from both sites in the Central Highlands of Madagascar showed a shift to a more open landscape dominated by grassland. Trees and shrubland in the highlands experienced a massive decrease and this correlated with an abundance of C_4 plants associated with reduced diversity. The shift of vegetation during this period was likely a result of a centennial severe drought period at ca. 950 cal years BP, as recorded in the literature and confirmed by the peak in aerophilous taxa in our diatom record. The drought was followed by a dramatic increase of fire occurrence and herbivory activities in the region, as recorded in the charcoal and spore records from both sites, indicating human activities at ca. 700 and 500 cal years BP for Lake Dangovavy and Tampoketsa-Ankazobe wetland, respectively.

Though the vegetation at both sites in Central Highlands of Madagascar was very dynamic until ca. 1000 cal years BP, complex interactions between climate and fire allowed the forest

and ericoid elements to persist, consistent with a heterogeneous mosaic landscape. This changed from 1000 years ago with the occurrence of a regional severe drought event followed by an increase in human activities leading to an increase of grass, a decline in forest and ericoid elements.

Our findings suggest that although, the eastern and western slopes in Madagascar might have different vegetation histories over time as a response to the complex climatic-fire drivers at least until ca. 1000 cal years BP, they both:

a) Contained ancient open ecosystems such as grasslands and/or ericoid shrubland, and a mosaic landscape which should be considered typical of the highland region.
b) Experienced a loss of forest, woodland and mosaic elements, a trend that is consistent with the anthropogenic conversion of some forests to grasslands since ca. 1000 cal years BP.

Such findings have implications in terms of conservation, fire management and afforestation projects in the Central Highlands, and provide additional knowledge that contributes to the understanding of its ecological processes and history prior to human arrival on the island. Indeed:

1) Ancient grasslands and ericoid shrubland need to be identified and conserved because of their antiquity and unique biodiversity. To date, there has been some focus on ancient grasslands, but the presence of ancient heathlands has not been discussed.
2) It is important to distinguish ancient from derived grasslands and to target the latter for reforestation, using species that are typical of the remaining forest patches.
3) Fire management should be conducted at a local scale and should incorporate the landscape fire history, considering, for example, the differences between two slopes in the Central Highlands.

Keywords: Holocene, grassland, forest-grassland mosaic, ericoid shrubland, fire history, herbivory, hydrological change, conservation, reforestation, Central Highlands Madagascar

ACKNOWLEDGEMENTS

Who thought that the little guy passionate about pollen from Madagascar would bring and apply its passion (pollen) for the conservation of Madagascar biodiversity one day? I will never thank enough the Almighty God for that. I believe that despite my efforts and perseverance I could not go through and finished this PhD journey without His guidance and protection particularly under the current pandemic. Glory be to Him.

I would not thank enough also my supervisors, Professor Lindsey Gillson and Professor (Emeritus) William John Bond for giving me the opportunity to accomplish one of my dreams. I am very grateful for their patience, guidance, support and belief in me. They both are such an inspiration to me and really helped bring out the best of me. To Prof. Gillson, thank you for building me to become one of the African palaeoecologists and guiding me to be able to participate in producing research that is applied and would help in understanding and solving the current and future challenges of conservation. To Pr. Bond, thank you for increasing my knowledge of ecology and opening my mind to the importance of open ecosystems. Not only as excellent and inspirational supervisors, but they truly have also had been close to being parents and friends for me and my little family. The relationships build over time had facilitated our interaction and discussion smoothly.

In addition to my supervisors, I would like also to thank personally Dr. Kelly Kirsten who agreed to help me with my diatom analysis. She taught me what I currently know about diatom analysis from the lab to the data interpretation. I have learned a lot and know enough to teach the younger generation, thanks for that. It was not only limited to that, but she gave support and guidance on my PhD journey and was like my personal mentor.

To the Plant Conservation Unit (PCU) at the department of Biological Sciences, University of Cape Town, South Africa, which was my second home during my PhD journey, thank you. I would like to thank particularly the director of the unit, Professor Timm Hoffman, which is acting as a father for the unit and who is bringing good vibes with his jokes. I also thank Ms Samantha Venter and Dr. Gina Arena for their advice and feedback given on my writing. Not to forget, all people in the Palaeoecology Laboratory and repeat photos that I have interacted with and got to know during my PhD journey. My particular thanks go also to the department of Forest and Environment at Ecole Supérieure des Sciences Agronomiques (ESSA), Université d'Antananarivo Madagascar. I would like to highlight Professor Joelisoa

Ratsirarson and Dr. Jeannin Ranaivonasy who facilitated the permit for field work in Madagascar. My gratitude goes as well to the field assistants during the core collection of the samples in Madagascar along with iThemba Laboratory at the University of Johannesburg and Stable Light Isotope Laboratory at the University of Cape Town who ran freely and partially free my samples for carbon content analysis.

This research would not have been possible also without the generosity and support from the three following organisations and funders: African Centre for Climate and Earth Systems Science (ACCESS), Palaeontological Scientific Trust (PAST) and National Research Foundation / African Origins Platform (NRF / AOP)

Last but not least, I would like to give a special thank you to my family. For my wife, Dr. Estelle Razanatsoa and my son Happy Razafinaharintsoa, thank you for being so supportive, patient and very comprehensive with me during these years and particularly my stressful moments. Estelle, thank you as well for the tips, feedback and advice that you gave me. Love you guys. For our family in Madagascar, thank you for all your prayers and moral supports.

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Chapter 1 INTRODUCTION

1.1 General introduction

The world is facing convergence of threats linked to climate change and biodiversity loss. There is an urgent need for improved conservation and sustainability with various global initiatives underway to address these threats (IUCN, 2021). Underpinning this, is an understanding of the distribution and abundance of biodiversity. Tracking changes in biome distribution and composition are keys to planning effective conservation interventions. Biome, a key community ecological and biogeographical concept, defines the distribution and classification of vegetation worldwide (Mucina, 2019). Terrestrial biomes are subdivided into forested and non-forested biomes, which cover 41.5% and 58.5% of the Earth's land area, respectively (Dinerstein et al., 2017). The latter includes open ecosystems represented by grasslands, shrublands, savannas and open woodlands (Willis, Gillson & Virah-Sawmy, 2008; Bond, 2019) often forming mosaics with closed forest patches. These open ecosystems exist and even dominate some areas where the climate is warm and wet enough for forests (Bond, 2019), leading to confusion and massive controversies in terms of their origin and distribution across the globe. Specifically, tropical and subtropical open and mosaic ecosystems are often classified as secondary or degraded forests, an assumption based on the current high deforestation rate and other anthropogenic activities recorded in these regions (Repetto, 1990; Houghton, 2012). Such perceptions have led to the establishment of reforestation projects in these regions for carbon sequestration, habitat restoration and biodiversity conservation (Dave et al., 2018). Although some of these projects have demonstrated success in maintaining habitat for forest biodiversity and landscape connectivity (Geldenhuys, 1997; Feyera, Beck & Lüttge, 2002; Sheldon, Styring & Hosner, 2010), others have failed by using non-native species leading to further ecological issues, such as species invasion and destruction of open and mosaic ecosystems (Gaertner, Richardson & Privett, 2011; Calviño-Cancela & Rubido-Bará, 2013; Wills et al., 2017). In these cases, afforestation has actually changed the nature of the ecosystems further away from, rather than closer to, pre-human disturbance states, highlighting the need for further investigations on the ecology of open landscapes, particularly on the nature and the origin of these ecosystems (Bond & Zaloumis, 2016).

Multiple lines of evidence from various continents, e.g. from Africa (Bond, 2019), Asia (Ratnam et al., 2016), and South America (Veldman & Putz, 2011) have emerged demonstrating that open ecosystems have existed long before any human interventions, contrary to the assumption that open ecosystems are a product of human deforestation. These open ecosystems, particularly ancient grasslands, were characterised as “old growth” and differed from deforested anthropogenic land by their high herbaceous species richness maintained by fire, herbivory and soil characteristics not suitable for tree growth (Veldman et al., 2015). Moreover, open and mosaic ecosystems provide various ecosystem services including, but not limited to, carbon storage, (e.g. Grace et al., 2006), wood for non-timber products and grass for pastoralism (e.g. Kull, 2002a), and maintaining the biodiversity of surrounding environments (e.g. Magagula & Samways, 2001; Bond & Parr, 2010; Soto-Shoender et al., 2018).

The confusion between ancient open and anthropogenic-induced open landscapes might mislead conservation and reforestation efforts. It is important to identify these ancient ecosystems to avoid the potential negative impacts of afforestation efforts on biodiversity conservation (Kemppinen et al., 2020). In addition, the planted species in reforestation projects should reflect the composition of areas that were formerly forested. This is particularly important for the African continent, also known as “the grassiest continent” (Bond et al., 2019) for its vast areas of grassland and open savannas dominated by C_4 plants, originating around 10 million years ago (Ma) (Polissar et al., 2019). Although emerging evidence suggests the urgent need to conserve and restore these open ecosystems (Veldman et al., 2015), debates are still ongoing, particularly in countries such as Madagascar, where the idea of a whole-island forest still persists.

1.2 Madagascar

Madagascar, the fourth biggest island in the world, is separated from the African mainland sometime around 160 Ma (Briggs, 2003; De Wit, 2003). The island is a biodiversity hotspot, home to unique species, which evolved due to the island’s geographic isolation, climatic and geological diversity. The vegetation on the island of Madagascar is estimated to be dominated by at least 70% of grasslands and shrublands (Bond et al., 2008; Vorontsova et al., 2016; Zhang et al., 2020) compared to forest and cultivated land, which covers ca. 22% and 7%, respectively (Vieilledent et al., 2018; Zhang et al., 2020). The island contains evergreen humid forest in the east; an open ecosystem dominated by forest-grassland mosaic vegetation, ericoid shrubland and grassland in the central region; and tropical dry forest; succulent forest and spiny thickets in the west. Madagascar has high species richness and endemicity in terms of vascular plants and is considered to be one of the richest worldwide (Mutke & Barthlott, 2005). However, the continental island is experiencing a high rate of degradation and is threatened by climate change and human activities (Vieilledent et al., 2018; Jones et al., 2019; Wan et al., 2021).

Madagascar's government recently committed to reforesting 4 million ha of "degraded" forest on the island by the end of 2030, particularly targeting open ecosystems in the Central Highlands of Madagascar (Lacroix et al., 2016; Ranjatson et al., 2019). These areas have been prioritised on the basis of the high abundance of grass in the region and the associated assumption of deforestation that occurred within the region since human arrival (Lacroix et al., 2016). In fact, grassland covers more than 80% of the vegetation in the Central Highlands (Bond et al., 2008). However, vegetation cover in the region has long been the subject of a scientific debate on the state of the landscape, whether or not forested, the origin and the expansion of the grassland, as either anthropogenic or natural vegetation. The view that existing grasslands in the region are the result of anthropogenic activities has been based on the deforestation narrative and the assumption that the island was entirely forested prior to human arrival (Humbert, 1927; Perrier de la Bathie, 1928; Gade, 1996). Forests in the Central Highlands region currently occur in patches and are suggested to be the remnants of once-extensive forest cover that has been cleared through deforestation, not only during the last 50 years (Gade, 1996; Harper et al., 2007; Grinand et al., 2013; Vieilledent et al., 2018), but extending back to human settlement ca. 2000 years ago (Burney et al., 2004). This narrative has been widely accepted throughout the 20th and even the 21st century (e.g. Lowry, Schatz & Phillipson, 1997; Harper et al., 2007). However, recent investigations on the Malagasy grasslands suggest that due to their similarity to the African grasslands, their high endemicity rate, molecular dating of Malagasy clades and ecological traits, these grasslands should be considered ancient vegetation (Bond et al., 2008; Vorontsova et al., 2016; Hackel et al., 2018; Solofondranohatra et al., 2018, 2020). Despite the evolutionary and ecological evidence, there are as yet, few long-term palaeoecological records that investigate the origin and antiquity of these grasslands and the existence of forest-grassland mosaics.

Palaeoecological investigations have proven to be effective in shifting narrative around vegetation cover particularly in open ecosystems across the world. For instance, it allowed to understand the history of the landscape and its relationship between people's culture and its environment over time, e.g. in Colombia (Mayle & Iriarte, 2014), identify the history savanna over the Pleistocene (Behling, 2002) and evaluate the drivers of change within these open ecosystems, e.g in Kenya (Wooller, Street-Perrott & Agnew, 2000); and in South Africa (Bond & Archibald, 2003). Similar studies in open ecosystems are still lacking in Madagascar to investigate the extent and history of the vegetation which are still debated, and the drivers of change in such ecosystem prior to and after human settlement. To date, only two palaeoecological studies, conducted in two sites in the Central Highlands where open ecosystems are dominant, attempted to cover such topics (see, Figure 1.1). One in Lake Itasy (from ca. 11 500 cal years BP) and the other in Lake Tritrivakely (from ca. 11 000 cal years BP), both of which cover the Holocene epoch (Burney, 1987a; Straka, 1996) (Figure 1.1). Their results showed that the vegetation at both sites was dominated by an open ecosystem but with a dominance of ericoid bush at Lake Itasy and ericoid grassland mosaic associated with high fire frequency in Lake Tritrivakely. Records are limited in the region primarily due to the access to sites that are preserved for environmental analyses. In addition, the use of palaeoecology in exploring current environmental challenges has mostly started to emerge in the last decades allowing expansion and exploration of new sites and recent questions. Environmental questions focus on areas with forest-dominated ecosystems to evaluate the drivers of change rather than on the landscape history and challenging the debate and assumption around the vegetation cover in Central Highlands Madagascar.

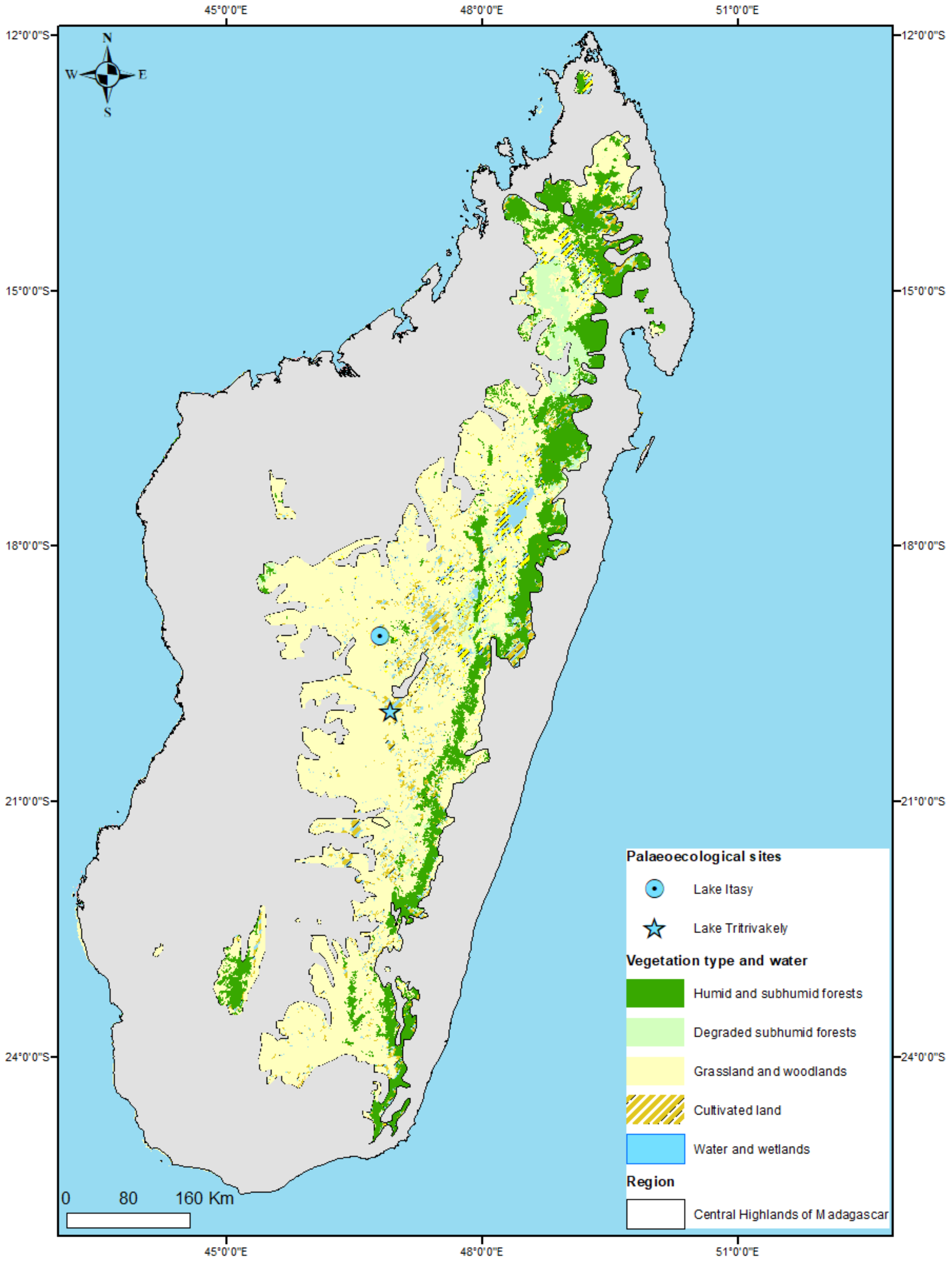


Figure 1.1: Current distribution of forest, open and mosaic vegetation in the Central Highlands of Madagascar with the only two palaeoecological sites, Lake Itasy (blue circle) and Lake Tritrivakely (blue star), which cover environmental change during the Holocene Grey indicates the lowlands in the eastern and western part of Madagascar.

It is difficult, however, to conclude the origin of the vegetation and the role of fire in the entire highlands with the insufficiency of palaeoecological records, and to deduce whether the results are only locally applicable or reflect wider patterns of landscape change across the entire highlands. In addition, records of herbivore activities and fire, which are thought to have maintained grassland vegetation (Solofondranohatra et al., 2020), are scarce prior to humans with only one record in Tritrivakely site showing a low rate of herbivory and high fire frequency (Burney, 1987a; Burney, Robinson & Burney, 2003). Furthermore, climatic fluctuation between major cold/warm cycles was recorded during the Late Quaternary and are suggested to have led to vegetation change over time at these sites (Gasse & Van Campo, 1998, 2001).

Yet, up-to-date high-resolution palaeoclimate records are lacking to aid in understanding the role of climate in terms of vegetation change in the Central Highlands of Madagascar compared to the other regions on the island such as the northwest, southwest and southeast (Virah-Sawmy, Willis & Gillson, 2010; Voarintsoa et al., 2017; Razanatsoa, 2019; Wang et al., 2019). This lack is particularly noted from the period of human settlement (from ca. 2000 cal years BP as per Burney et al., 2004 & Douglass et al., 2019) that coincided with megafauna extinction and proposed island-wide aridification (Virah-Sawmy, Willis & Gillson, 2010; Godfrey et al., 2019a). Critically, the interaction between aridification and increased anthropogenic activities, especially fire, has implications for the resilience of the vegetation, as characterised by mosaic ecosystems in the region, with the possibility of meeting ecological thresholds for more water-dependent and fire-sensitive elements in the future. Moreover, the Central Highlands are home to a diverse range of ethnicities that depend on these open ecosystems (Klein, Réau & Edwards, 2008; Razafimanantsoa et al., 2013). Local people rely on these open ecosystems, for example, for pastoral activities, using fire to maintain pastures and prepare crop fields (Kull, 2002b). Yet, due to the misunderstanding of the drivers of change, the role of fire in the landscape, and the narrative around the degradation of these ecosystems, government legislation bans fire and focusses on intensifying afforestation, often using non-native species (Lacroix et al., 2016). This has already promoted peasant protests, where the landscape has often been intentionally burned (Kull, 2002b). Together with the lack of long-term knowledge, ban of fire, afforestation and the urgent need for livelihoods tend to exacerbate the situation, and consequently complicate the management and conservation of biodiversity in the region. Therefore, there is an urgent need for better documentation of the impacts and roles of these drivers (*viz.* herbivory, fire, climate and human impacts) as well as the influence of humans on the vegetation dynamics in the Central Highlands of Madagascar over the Holocene.

Understanding the temporal and spatial changes in the landscape are central to informing the debates over former forest extent and the role of anthropogenic fires in creating open ecosystems. Such studies are fundamental to demonstrating which areas are more influenced by anthropogenic factors and which are areas proven to be naturally dominated by open ecosystems. This knowledge would help to focus on reforestation of areas that were formerly forested and would also help to identify which are most appropriate to accommodating human livelihoods and ecosystem services for the local community. Establishing appropriate reforestation projects, conservation of biodiversity and fire management in the Central Highlands of Madagascar requires further research that would consider the knowledge of vegetation history and its dynamics through time with the main drivers of change. These could also help to inform appropriate land-use in the region, thereby helping to mitigate socio-ecological conflicts between the local community and the government.

1.3 Aims and Objectives

The thesis aims to understand the landscape history and environmental change in the forest-grassland mosaic ecosystems of the Central Highlands of Madagascar, through temporal and spatial palaeoecological investigation, and use these results to propose appropriate conservation and management strategies of the landscape.

The main objectives of the research are:

a) To reconstruct vegetation history of the Central Highlands of Madagascar from the Early to Late Holocene using fossil pollen and stable carbon isotopes.
b) To assess the literature on environmental change of the Holocene in the Central Highlands.
c) To reconstruct hydrological changes in the region and infer climate variation through diatom analysis of the last 2000 years.
d) To reconstruct fire history and herbivory activities in the region from the Early to Late Holocene using charcoal and coprophilous spores.
e) To assess the timing and impact of climate and human activities through herbivory and fire on the forest-grassland mosaic in the Central Highlands of Madagascar during the Holocene.

f) To interpret the results in terms of the origin and antiquity of open ecosystems in the surroundings of the investigated sites of the highlands and to infer changes in the wider landscape.

g) To propose conservation strategies that could be applied to open and mosaic ecosystems in the region based upon the palaeoecological evidence mentioned above.

1.4 Hypotheses and research questions

- Hypothesis 1: The Central Highlands of Madagascar was a mosaic ecosystem, at least since the Early Holocene, comprising a high abundance of grassland before human settlement in the region (ca. 2000 –750 cal years BP).
  - What were the vegetation dynamics of the forest-grassland mosaic of the Central Highlands during the Early and Mid-Holocene?
  - What vegetation types are these ecosystems composed of and how did they vary in composition and abundance over time?
  - Were there major shifts in vegetation in the area and, if so, when and where did they occur, and how can these shifts be described?
- Hypothesis 2: Climate was variable in the region over time, but dry periods have increased during the last 2000 years and have exacerbated the effects of human activities on the vegetation.
  - How did climate vary in the Central Highlands during the Holocene?
  - What was the impact of climate variability on the vegetation during the Holocene?
  - Particularly during the last ca. 2000 years (after human settlement)
    - When were the wettest and driest periods in the region in the last 2000 years?
    - How did the climate vary in the Central Highlands post-human settlement?
    - How was fire activity related to the climate variability during the last 2000 years?
- Hypothesis 3: Fire and herbivory activities in the Central Highlands of Madagascar have shaped the forest-grassland mosaic and have accelerated during the last two millennia due to increased human settlement and activities.
  - How have fire history and herbivory activities in the Central Highlands varied during the Early and Mid-Holocene?
  - How did early human presence and settlement in the region affect the changes in fire regime and herbivory activities?

1.5 Structure of the thesis

The thesis is divided into seven chapters that respond to the objectives and research questions described above. The content of each chapter is outlined below.

Chapter 1: Introduction

The first chapter places the research project in a wider context particularly emphasising global reforestation projects that are targeting open and mosaic ecosystems. It provides background information about the state of the open and mosaic landscape in the Central Highlands of Madagascar. It highlights the complexity of the Highland's region including the debates around the origins of the vegetation, the drivers of change in the landscape over time, and the current conservation challenges facing these ecosystems. The chapter also outlines the research aims, objectives, hypotheses and research questions that form the basis of the thesis.

Chapter 2: Literature review

This chapter reviews theories around Madagascar's vegetation cover and drivers of change over time, including climate, fire, and herbivory activities by focusing on the mosaic landscape of the Central Highlands. It also summarises the evidence of human arrival/settlement and looks at the management challenges that biodiversity conservation in the central region faces. It combines contemporary and palaeorecord reviews to underline some of the gaps that will be addressed by the present research.

Chapter 3: Study area and methods

This chapter provides a detailed description of the modern environmental setting of the Central Highlands of Madagascar including phytogeographical divisions of the highlands (eastern and western slopes) along with the contemporary geology, soil, climate, and vegetation. It also locates and describes the two study sites, i.e., one in the eastern slopes and the other one in the western slopes of the Central Highlands. In addition, this chapter describes the palaeoecological approaches, methods and statistical analyses applied in this research.

Chapter 4 and 5: Results

Chapters four and five present the palaeoecological results from both sites. These chapters provide descriptions of the stratigraphy, sedimentology, and chronology of the sediment cores, fossil pollen and stable carbon isotope results for investigating vegetation dynamics, micro- and macro-charcoal results to examine regional and local fire histories, coprophilous spore results to determine herbivory activities and diatom data to describe hydrological changes. These chapters also describe the statistical results to evaluate the complex interaction between these proxies.

Chapter 6: Discussion

This chapter interprets and discusses the palaeoecological results from both sites in the Central Highlands of Madagascar. Landscape history and environmental changes at local and regional scales are interpreted from the palaeoecological proxies to examine the drivers of change and the relative importance of, and interactions between, climatic and anthropogenic factors. Particular attention is paid to the last vegetation shift in the region that occurred ca. 1000 cal years BP which coincided with human expansion. The discussion also considers how the data contribute to the debates of the antiquity and management of the Central Highlands of Madagascar.

Chapter 7: Synthesis and conclusion

The final chapter provides a synthesis of the main findings of landscape history and environmental changes in the eastern and western slopes of the highlands and contextualises them for the entire region during the Holocene. It also provides contributions to biodiversity conservation and management strategies in the Central Highlands of Madagascar based on the local palaeoecological data.

Chapter 2 VEGETATION COVER, DRIVERS OF CHANGE AND CONSERVATION CHALLENGES IN MADAGASCAR

2.1 Introduction

Madagascar's current vegetation is characterised by an abundance of open ecosystems compared to forests. The island's landscapes are the subject of debate, particularly over the origin and antiquity of mosaic and open ecosystems. This chapter will review current patterns of vegetation distribution and summarise the main debates about changes around vegetation cover on the island by highlighting the mosaic and open landscapes of the Central Highlands of Madagascar, which is the focus of this study. This will be followed by a review of the published palaeoecological research on the drivers of vegetation (climate, fire, and herbivory activities) and their impact on the vegetation dynamics over time. This chapter will review also the *Malagasy* human history (i.e. human presence and settlement) in the context of current conservation and management questions.

2.2 Madagascar vegetation cover

2.2.1 Current vegetation distribution in relation to climate and geology

Madagascar is divided into two main phytogeographical regions (eastern and western regions) which differ in vegetation, rainfall quantity and soils (Donque, 1972; Koechlin, 1972; Moat & Smith, 2007). The eastern Malagasy regions are dominated by roughly homogenous, metamorphic and igneous Precambrian basement rock (Du Puy & Moat, 1996) and include humid forests, subhumid forests and ericoid thickets ecoregions (Burgess et al., 2004; see Figure 2.1). The western Malagasy regions has a complex geology characterised by an abundance of unconsolidated sands, Tertiary and Mesozoic limestone (Du Puy & Moat, 1996) and hosts the dry forests, succulent forests and spiny thickets ecoregions (Burgess et al., 2004).

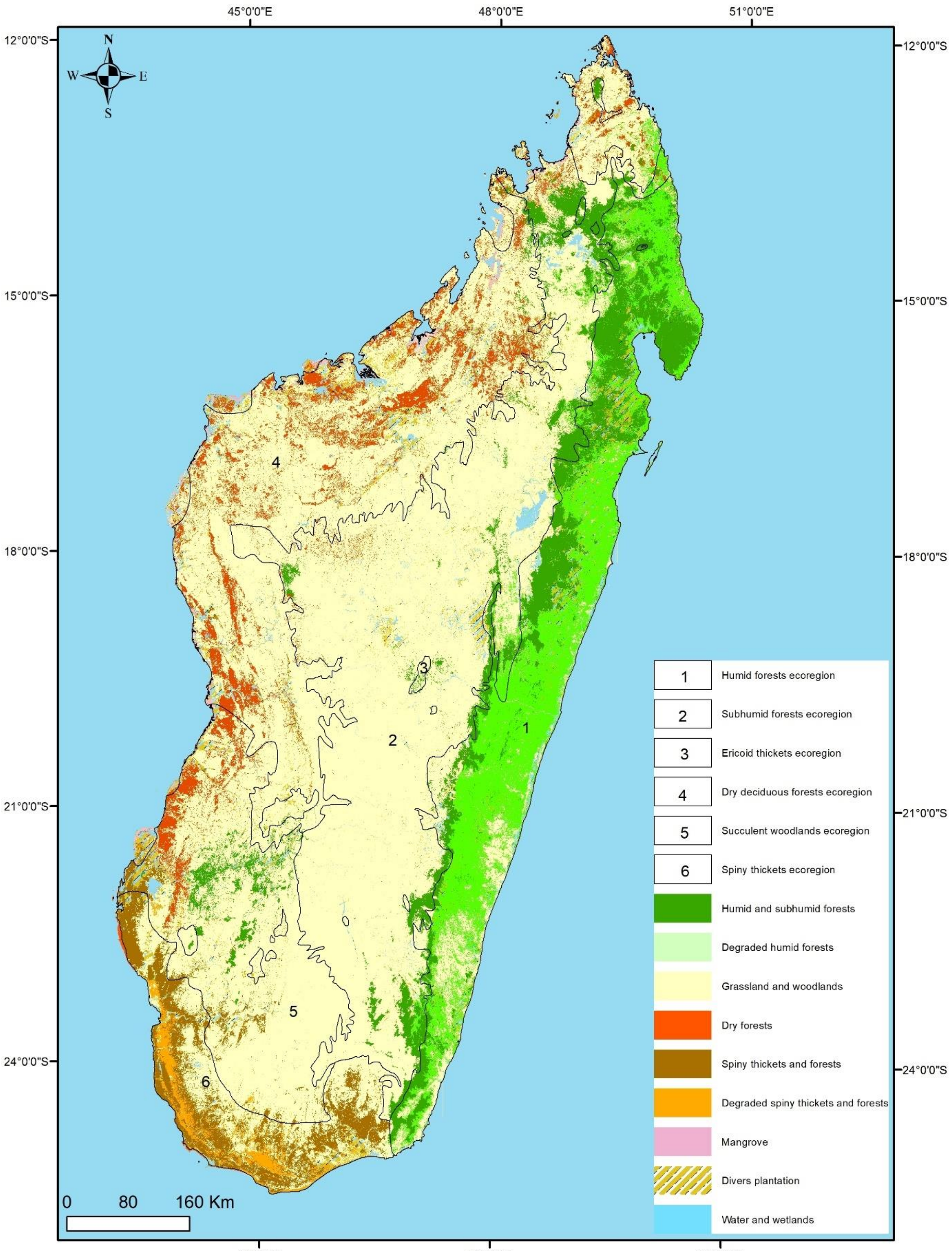


Figure 2.1: Distribution of different vegetation type within Madagascar ecoregions. Vegetation type based on Moat and Smith (2007) and ecoregions based on Burgess et al. (2004)

The humid forests ecoregion located in the coastal east of Madagascar expand from 0 to 800 m of elevation and receive more than 2000 mm rainfall per year with barely two months of dry season (Koechlin, 1972; Burgess et al., 2004). The humid forests are characterised by a high diversity of species making the region the most diverse habitat on the island (Burgess et al., 2004). The ecoregion is characterised by a tropical evergreen rain forest with a closed canopy, *Savoka* or secondary forest, and a littoral forest (Moat & Smith, 2007). In general, the vegetation is marked by the dominance of high canopy species 30-35 m at a low and mid-elevation, which decrease in height at higher elevation. Vegetation is dominated by Myristicaceae and *Anthostema* (Euphorbiaceae) with widely represented families such as Anacardiaceae, Araliaceae, Rubiaceae and Sapindaceae (Koechlin, 1972; Burgess et al., 2004). Some *Pandanus* species (Pandanaceae), bamboos (Poaceae), and epiphytic plants are also abundant in the region (Lowry, Schatz & Phillipson, 1997).

The subhumid forests ecoregion is found in the Central Highlands of Madagascar, where this research study is focused. The subhumid forests are today present between 800 to 2000 m above sea level, they receive ca. 1500 mm per year precipitation and there is pronounced dry season between May to September (Koechlin, 1972; Burgess et al., 2004). The Central Highlands of Madagascar are currently characterised by the dominance (ca. 65%) of grasslands with some fragmented patches of sub-humid forests/woodlands mainly in ravines and riverine areas (Burgess et al., 2004; Rabarivola et al., 2019) forming a wooded grassland-bushland mosaic (Moat & Smith, 2007). Grassland taxa are mainly composed of the Poaceae family represented by, for example, *Loudetia simplex*, *Trachypogon spicatus*, and *Schizachyrium sanguineum* (Solofondranohatra et al., 2018). Ericaceae and Asteraceae are found coupled with the grassland in areas where the fire is less frequent i.e. 5-10 years (Rakotondrainibe, Jeannoda & Radimbison, 1988; Radimbison, 1990). Ericoid shrublands are intrinsically flammable. They burn less frequently than grassy vegetation and are most likely to burn after hot dry periods following prolonged droughts. Through resprouting, these ecosystems are known to establish a positive fire feedback at low fire regimes, as found in African mainland (Gil-Romera et al., 2019). This might promote the contemporary abundance of such ecosystem in some areas of the highlands as the Ankazobe region (Radimbison, 1990; Ratsirarson & Goodman, 2000) with a moderate rainfall (not too dry and not too wet). An ericoid system with high species richness is currently abundant in the high montane (Burney, 1996; Wang et al., 2018) but was probably abundant at lower elevation in cooler climate than today (Straka, 1996; Gasse & Van Campo, 1998). The forest/woody taxa are represented by *Alberta minor* (Rubiaceae), *Cussonia bojeri* (Araliaceae), *Dodonaea madagascariensis* (Sapindaceae), *Ilex mitis* (Aquifoliaceae), *Podocarpus madagascariensis* (Droseraceae), *Psychotria* sp. (Rubiaceae), *Schefflera* sp. (Araliaceae), *Vitex humbertii* (Lamiaceae) and *Tambourissa gracilis* (Monimiaceae) and many more (Humbert, 1955a; Moat & Smith, 2007). Some remaining riparian forest taxa are also found in the valleys (called *Baiboho*) mostly transformed into rice fields (Gade, 1996; Kull, 2012). There has been a substantial increase of introduced plant species, such as *Eucalyptus*, *Pinus* and *Acacia* in the landscape, particularly within the grassland area (Tassin et al., 2009).

The ericoid thickets ecoregion is situated above ca. 2000 m on the major massifs montane on the island and receive more than 2500 mm of rainfall per year with seasonal and daily variation in temperature (Koechlin, 1972; Burgess et al., 2004). The length of the dry season in the ecoregion is similar to the subhumid forests ecoregion (e.g., Raxworthy & Nussbaum, 2010). The ecoregion is heterogenous and characterised by the dominance of sclerophyllous forest and ericoid thicket (Burgess et al., 2004). The sclerophyllous forest is in general dominated by Cunnoniaceae, Ericaceae, Pandanaceae and Podocarpaceae families. This type of vegetation is replaced by ericoid thickets mainly dominated by Asteraceae and Ericaceae families at a higher elevation within low temperature, less fire frequency but high humidity (Burgess et al., 2004; Raxworthy et al., 2008).

A decreasing quantity of rain (less than 1500 mm per year) with extended dry season occurs moving southwards (Donque, 1972; Koechlin, 1972). The dry forests ecoregion in the northwest part of the island with an elevation range from sea level to 600 m presents a mean annual rainfall range between 1000 to 1500 mm with a dry season from May to October (Donque, 1972; Burgess et al., 2004). The ecoregion is characterised by diverse geology (Moat & Smith, 2007). The calcareous soils contain an abundance of *Adansonia* spp. (Malvaceae), and *Pachypodium* (Apocynaceae). The *Tsingy* massifs contain an abundance of *Dalbergia*, *Cassia* (Fabaceae), *Ficus* (Moraceae), with some *Adansonia* and Asclepiadaceae and Rubiaceae (Burgess et al., 2004).

The succulent forests and spiny thickets ecoregions are located in the driest part of the island. The succulent forests ecoregion in the southwestern and central western of the island with an elevation between 600 to 800 m presents a mean rainfall of 600 to 1300 mm per year (Burgess et al., 2004). The length of the dry season is six months from May to October as the dry ecoregions (Burgess et al., 2004; Moat & Smith, 2007). The succulent woodland is recognised as a transition forest between the dry deciduous and spiny thickets and the vegetation is dominated by a mosaic of succulent xeric adapted plants and deciduous forests (Burgess et al., 2004). It is characterised by trees and shrubs of Burseraceae, Euphorbiaceae, Fabaceae, and Sapindaceae, as well as two baobab species*: Adansonia grandidieri* and *A. za* (Burgess et al., 2004; Moat & Smith, 2007). The spiny thickets ecoregion located in the southern and southwestern parts of the island with an elevation range from sea level to 200 m presents the lowest rainfall range between 350 to 500 mm per year (Burgess et al., 2004). The dry season expands from nine to eleven months (Donque, 1972; Burgess et al., 2004) and the vegetation is characterised by species adapted to low and unpredictable rainfall. The latter is dominated by dry spiny forest-thicket represented by Didiereaceae and the arborescent *Euphorbia* spp. which vary in composition depending on their location and substrate (Moat & Smith, 2007).

The vegetation on the island is, however, experiencing changes, particularly over the last 50 years, with an estimated loss of 44% of forest (Vieilledent et al., 2018), mainly associated with human activities through swidden agriculture and pastoralism (e.g., Kull, 2002b; Harper et al., 2007; Scales, 2011). These activities contributed to the opening of the vegetation causing decline in forest cover in many areas of the island (Grinand et al., 2013). Such recent changes have been used to support the theoretical narrative that Madagascar was fully forested before human arrival and the expansion of open ecosystems such as grasslands, ericoid shrubland and woodlands have been supposedly caused by anthropogenic activities (e.g., Humbert, 1927; Perrier de la Bathie, 1928; Lowry, Schatz & Phillipson, 1997). However, the narrative does not support the possibility that many forests in Madagascar are naturally limited to small areas where local conditions of fire, topography and hydrology are favourable. This whole-island forest narrative is not supported by the few palaeoclimate data records on the island (Virah-Sawmy, Gillson & Willis, 2009; Virah-Sawmy, Willis & Gillson, 2010; Razanatsoa et al., 2022) and the antiquity of Malagasy grasslands (Bond et al., 2008; Vorontsova et al., 2016; Hackel et al., 2018; Solofondranohatra et al., 2018; Hagl et al., 2021).

2.2.2 Debates around vegetation cover: environmental narrative vs ecological and palaeoecological evidence

2.2.2.1 Madagascar environmental narratives

The island of Madagascar is popularly seen as the “green island” (e.g., Humbert, 1927; Perrier de la Bathie, 1928; Lowry, Schatz & Phillipson, 1997), where forests supposedly covered the entire island before human settlement at ca. 2000 cal years BP (Burney et al., 2004; Douglass et al., 2019). The high and rapid deforestation rate which extends back to human arrival supposedly transformed the green island to its current state termed the “red island”(Velo & Zafitsara, 2020). In addition, this narrative assumed that vegetation other than closed forest, including open and mosaic ecosystems such as grasslands, heathland and open woodlands, is the result of anthropogenic degradation (Humbert, 1927; Perrier de la Bathie, 1928) due to deforestation. The theory of “green island” emerged from naturalists in the 1920s, and spread in contemporary writing between the 1950s and 1980s, and became dominant in the 1990s where it was used in many scientific publications and by environmental organisations (e.g., Gade, 1996; Lowry, Schatz & Phillipson, 1997). Such a narrative has dominated major policies around the conservation of the island’s biodiversity and was vulgarised in the media blaming the local people as the main source of degradation of the environment (e.g. Gade, 1996; Kull, 2000, 2002c). The growth and poverty of the Malagasy population were suggested to have pushed them to extend and intensify deforestation, clearing the primary forest by *Tavy* agriculture (swidden agriculture), and leading to the formation of forest patches and grasslands (Erdmann, 2003).

The frequency of fire, narratively suggested to have been the tool used by humans to destroy the island’s forest, has been proved to increase during the last 50 years (Gade, 1996; Harper et al., 2007; Grinand et al., 2013; Vieilledent et al., 2018). In fact, 95% of the current fire incidence is classified as human-induced (Bloesch, 1999; Waeber et al., 2016). In addition, fire is a major component of land-use for the livelihood of the local population, not only for swidden agriculture and grazing for pastoralism, but also used for socio-cultural reasons (Kull, 2000, 2002b). Mismanaged and non-controlled use of fire was often one source of loss of forest habitat and land area (Kull, 2012). Meanwhile, the introduction of pastoralism, especially with the zebu cattle to the island at ca. 950 years BP (Stachurski et al., 2013) motivated the local people to expand grassland land area for grazing by burning forest (Gade, 1996).

One case study often used by naturalists to prove the environmental degradation narrative is the Central Highlands of Madagascar. Currently, the region is almost totally devoid of trees but mostly dominated by grasslands, except in a few protected areas in ravines, as well as scattered plantations of exotic trees (Gade, 1996; Klein, 2002; Kull, 2002b, 2012). In addition, the Central Highlands of Madagascar present the highest fire incidence on the island which is considered as a source of biological impoverishment that was supposed to cause soil erosion in the landscape (Kull, 2000). The presence of a large number of gullies, called *lavaka*, was widespread in the region which was supposedly caused by the growing human presence through canal irrigation and tree burning for rice paddies on the hills (Klein, 2002; Brosens et al., 2021, but see Cox et al 2010). All these conjectures were used to support the theory that closed forest pre-dominated before human arrival, and proposed anthropogenic fire as the main source of degradation of the environment on the island, particularly in the central region. However, the nature and role of fire in the environmental history of Madagascar remains unclear and there is evidence of ancient fire-adapted landscapes (Virah-Sawmy, Willis & Gillson, 2009). The narrative of the "green island" has been a subject of debate, especially in the last 50 years (Kull, 2000; Bond et al., 2008). Further studies are required to confirm the origin of vegetation, and the role of fire, prior to and after human presence.

2.2.2.2 Antiquity of open and mosaic ecosystems

Recent scientific investigations on the open ecosystem, particularly the Malagasy grasslands suggested that they are ancient vegetation (Bond et al., 2008; Vorontsova et al., 2016; Hackel et al., 2018; Solofondranohatra et al., 2018, 2020). This conclusion was based on the molecular dating of Madagascan grass clades, the abundance of endemic Malagasy grass species, its similarity to the African grasslands, and the different ecological traits between grass in forest and grassland ecosystems. In addition, the abundant Malagasy grass species, *Loudetia simplex*, was recently proven to be genetically differentiated from South African's grass (Hagl et al., 2021) reinforcing the natural presence of grassland on the island. This antiquity of grasslands is in accordance with findings in a Malagasy Oleaceae shrub within the open woodlands on the island, dated back to the Late Miocene (ca. 6.5 million years), suggesting the open landscape as a natural formation (Salmona et al., 2020), as well as the few palaeoecological investigations conducted on the island, particularly in the Central Highlands of Madagascar (Burney, 1987a; Straka, 1996).

The dynamic nature of landscapes is well-recognised in the literature and the shift from equilibrium to non-equilibrium paradigms in ecology has changed the nature of conservation philosophy and practice. Whereas under an equilibrium paradigm early conservation attempted to prevent change and maintain balance, modern conservation now works with ecosystems in flux (Pickett et al.2012; Gillson, 2015). This requires a thorough understanding of the processes that drive change, the ranges of variability and the resilience of ecosystems. Palaeoecology has an emerging role in these debates, as will be illustrated in the current study. Indeed, palaeoecological records from the Central Highlands shows that these landscape and ecosystems were dynamics over time with pre-dominance of open ecosystems prior to human arrival (Burney, 1987a; Straka, 1996; Gasse & Van Campo, 2001). It was not continuously forested as narratively thought but was heterogenous with an abundance of ericoid shrubland and grasslands. From the pollen records in the region, open vegetation existed back to the full glacial period between ca. 150 000 and 20 000 cal years BP, where the vegetation was dominated by ericoid shrubland (Straka, 1996; Gasse & Van Campo, 2001). This was followed by a decrease of ericoid shrubland and an appearance of grass and woody taxa during the last deglaciation period (ca. 17 000-10 000 cal years BP). The woodland vegetation was dominated by *Celtis*, Combretaceae, *Macaranga*-type *Trema,* and *Uapaca* (Straka, 1996; Gasse & Van Campo, 2001). After which, the Early Holocene, from ca 11 200-8000 cal years BP, was characterised by an alternate abundance of grassland and ericoid shrubland (Burney, 1987a; Straka, 1996). A shift of the vegetation started to occur during the Mid-Holocene (8000-4000 cal years BP) with decreasing ericoid and increasing abundance of grass and woodland taxa (Burney, 1987a). Since the last ca. 2000 cal years BP, when humans are thought to have settled in the Central Highlands of Madagascar (Burney et al., 2004), the vegetation was dominated by an increasing abundance of grassland toward the present period (Burney, 1987a,b).

The spatial and temporal resolution of existing records are low, notably defining the timing of change is challenging for the open and mosaic ecosystems of the island. More studies are needed to investigate the timing, rate and drivers of change in the extent of forest and open ecosystems in the Highlands. Little can be discerned about the period before, and during, human arrival and settlement in the island for vast areas of the Central Highlands of Madagascar. Thus the natural variability of the landscape, particularly the history and ecological dynamics of the grasslands still needs to be ascertained. Here, palaeoecological studies prioritising high resolution reconstructions based on a host of proxies would assist in establishing a clear timeline of the main changes in vegetation in relation to human presence and other drivers of change. Spatial resolution through an increasing number of sites, provide the distinction of areas with more abundance of ancient or anthropogenic grassland, as well as the timing and impact of human activities in local areas. Having such data for the island of Madagascar, could provide insights more widely applicable to mosaic and open landscapes whose origins are contested or unknown.

In addition, research that will address the gaps in our understanding of the relationships between historical climate, fire and herbivory activities with the historical vegetation of the island may be useful in informing the development of appropriate strategies for biodiversity conservation in Madagascar.

2.3 Drivers of vegetation change in Madagascar

The abundance and distribution of vegetation in Madagascar are related to soil and topography but also variability in climate, fire, and herbivory activities over time (e.g., Burney, 1987a; Du Puy & Moat, 1996; Gasse & Van Campo, 1998; Ratsirarson & Goodman, 2000; Moat & Smith, 2007; Solofondranohatra et al., 2020). Particularly during the last millennia, human land-use and aridification affected fire activity, megafauna abundance and woody vegetation cover (e.g., Virah-Sawmy, Willis & Gillson, 2010; Crowley et al., 2017; Railsback et al., 2020). Landscape change is therefore a result of several interacting drivers where the relative importance of which has varied over time.

2.3.1 Climate variability

Findings across Madagascar using different approaches such as palaeoecology, modelling and instrumental records suggest that climate has played an important role in shaping variation of vegetation on the island over time (Gasse & Van Campo, 1998, 2001; Virah-Sawmy, Willis & Gillson, 2010; Ohba et al., 2016; Voarintsoa et al., 2017; Wang et al., 2019; Razanatsoa et al., 2021). Palaeoclimate records mostly based on diatoms, speleothems and tree rings published to date in Madagascar are temporally sparse but cover the Late Pleistocene to the present period (Gasse & Van Campo, 2001; Razanatsoa, 2019; Wang et al., 2019). These records attest to the magnitude of variations in temperature and rainfall which were used to investigate the vegetation response across the island over time (Virah-Sawmy, Willis & Gillson, 2010; Voarintsoa et al., 2017; Razanatsoa, 2019; Razanatsoa et al., 2022)). The Late Pleistocene to the Holocene are of low temporal resolution and appear to be characterised by a succession of cold/warm phases periods (Gasse & Van Campo, 2001; Ohba et al., 2016). The cold periods were supposed to present a temperature significantly lower than today (Gasse & Van Campo, 2001). These periods were associated with high local summer insolation and represented by the abundance of Ericaceae shrubland in the pollen records (Gasse & Van Campo, 1998, 2001; Williamson et al., 1998). The main cold periods on the island were recorded at ca. 115 000–110 000, 94 000–88 000, 75 000–69 000 and 22 000–17 000 cal years BP (Gasse & Van Campo, 1998, 2001). The warm periods were associated with low summer insolation and were dominated by wooded grassland or forest tree under dry or wet conditions, respectively (Gasse & Van Campo, 1998, 2001; Williamson et al., 1998). These periods were recorded around 125 000, 100 000, 83 000 and 60 000 cal years BP (Gasse & Van Campo, 2001). In addition to the cold/warm phases, past climate recorded on the island was characterised by driest periods at ca. 27 000 and 24 000 and 17 000 cal years BP (Reyes, 1993; Gasse & Van Campo, 2001), and wettest periods were around 116 000 and between 84 000–75 000 cal yr BP (Burney, 1996; Gasse & Van Campo, 2001).

The Holocene period represents an increasing temporal resolution for climate reconstructions on the island compared to the previous periods, despite poor chronological constraint. From ca. 11 000 cal years BP to the present period, climate on the island was slightly warmer than before with dry and wet oscillations relative to the escarpment contrasting the west and east Malagasy regions (Burney, 1996; Gasse & Van Campo, 2001; Wang et al., 2019). The reason for these changes is linked to the gradients from topography, trade wind patterns, and tropical cyclone frequency that influence the regional climate in the island (Donque, 1972; Razanatsoa, 2019).

Focusing in the Central Highlands of Madagascar included as part of the eastern escarpment, (see section 2.2.1), the climate was warmer and wetter in the Early Holocene until ca. 10 000 cal years BP. This condition promoted the establishment of forest elements in the region (Gasse & Van Campo, 1998, 2001). This period coincided with the beginning of the African humid period (AHP) characterised by the influence of African monsoon climate on the continent (DeMenocal & Tierney, 2012; Tierney & DeMenocal, 2013). During the Early-Middle Holocene (10 000–8000 cal years BP), the warming period stops and the vegetation was characterised by slight abundance of ericoid shrubland in the pollen record (Gasse & Van Campo, 1998) and this is in correspondence with the northern hemisphere 8.2ka cooling event (Alley et al., 1997). The Mid-Holocene was more variable but the most notable climate events recorded in the region were the wettest period at ca. 5000 cal years BP (Burney, 1996) and the driest period probably indicating drought at ca. 4000 cal years BP as interpreted from a peak of grass pollen in the record (Gasse & Van Campo, 1998). The latter corresponds to the widespread climate anomaly recorded between 4200 and 3900 referred to as 4.2ka event (Carolin et al., 2019) characterised by regional drought event on the island (Scroxton et al., 2020). It also coincided by the end of the humid period in tropical Africa (Gasse, 2000; Mayewski et al., 2004). Between ca. 3000 and 2000 cal years BP, the climate in the region became cooler and wetter, characterised by increases of Ericaceae pollen and a peak of mineral magnetic susceptibility and increases of Ericaceae pollen in the sediment suggesting a runoff event (Williamson et al., 1998). The latter is in contrast to east Africa which experienced widespread aridity during the period (Haug et al., 2001), reinforcing the climate contrast between the Malagasy eastern regions and eastern Africa (Mayewski et al., 2004). From the last ca. 2000 cal years BP, the Central Highlands of Madagascar and the entire island was suggested to be characterised by a dry period with an aridification event recorded at ca. 1000 cal years BP (Burney, 1996; Gasse & Van Campo, 1998, 2001; Virah-Sawmy, Willis & Gillson, 2010; Wang et al., 2019). The change to drier conditions in the region during the last millennium corresponded with the Medieval Warm Period (MWP) in Africa and Arabia due to solar forcing and ocean cycles (Lüning, Gałka & Vahrenholt, 2017). Yet, knowledge on climate variability in the Central Highlands region during the past millennium is very limited due to the lack of high temporal resolution records available in the region. Such data would allow for a comparison, not only for inter-regional variability, but also a wider climatic events, such as the Little Ice Age (LIA) recorded from ca. AD1300 to 1800 (650-150 cal years BP) in southern Africa (Tyson et al., 2000).

2.3.2 Fire history

Pre-human fire could have played an important role on vegetation dynamics in Madagascar, particularly in maintaining open and mosaic ecosystems in areas where there is enough rainfall to support forest. Wildfire was recorded on the island postulated human settlement (ca. 2000 cal years BP; Burney et al., 2004) and this was reflected by the presence of charcoal deposition recorded since the Miocene in the North (Burney, 1987c) and elsewhere on the island during the Early and Mid-Holocene (Burney, 1987a; Virah-Sawmy, Gillson & Willis, 2009). Natural fire was ignited mainly by lightning events on the island (Kull & Laris, 2009) with an intensification of volcanic eruptions in some areas of the Central Highlands and high montane massifs (Andrianaivo & Ramasiarinoro, 2015; Raharimahefa & Rasoazanamparany, 2018). The Late Holocene period was characterised by increasing evidence of charcoal concentration inferring an increase of fire activity across the island (e.g., Burney, 1987c,a,b; Matsumoto & Burney, 1994; Virah-Sawmy, Gillson & Willis, 2009; Virah-Sawmy, Willis & Gillson, 2009; Razanatsoa et al., 2021). Fire activity varied from one region to another on the island during the Holocene.

For the case of the Central Highlands of Madagascar, the charcoal record at Lake Tritrivakely suggests that fire was more frequent during the Early to Mid-Holocene compared to the Late Holocene (Burney, 1987c, 1996). The presence of fire in the area prior to human arrival coincided with the abundance of non-forest taxa in pollen records represented by ericoid shrubland and grasslands forming open ecosystems in the area (Burney, 1987a). In addition, multivariate abundance models and cluster of grass functional traits analysis suggested that fire maintained the abundance of grass in the region over time (Solofondranohatra et al., 2020). During the Late Holocene, declining fire activity was noted in the Central Highlands from the charcoal record in Lake Tritrivakely. This was particularly noteworthy between ca. 4000 and 1500 cal years BP (Burney, 1987c). Charcoal started to increase again in the region at ca. 1300 cal years BP to the present period, but not to the same levels as previously recorded prior to human arrival according to Burney (1987c). The increase of charcoal during the last millennium coincided with a decrease of woody taxa and an increase in the grass component, according to the pollen records in the region (Burney, 1987b,c,a). In some areas of the Central Highland’s region, like the Vakinankaratra region for example, fire abundance started to decrease in the last two centuries (Burney, 1987b) while in others like the Itasy region it continued to increase with maintained grass and tree abundance (Burney, 1987a; Straka, 1996).

Therefore, high-resolution evidence of fire activity on the island is needed to understand the fire impact on environmental change over time, particularly in the region dominated by open and mosaic ecosystems like the Central Highlands. Additional spatial analysis, through careful site selection, is also needed to bring additional fire evidence, particularly during the Early/Mid-Holocene, to confirm or refute the natural source of fire and vegetation response in the region.

2.3.3 Megafauna and herbivory activities

The continental island was home to abundant megafauna like giant lemurs, pygmy hippopotamus, giant fossa, elephant birds and giant tortoise during the Holocene (e.g., Simons et al., 1995; Crowley et al., 2017; Hansford et al., 2018; Samonds et al., 2019) until at least ca. 1000 cal years BP (Godfrey et al., 2008; Crowley, 2010). Megafaunas went extinct during the last millennium with more evidence from the western region (Crowley, 2010) and there is debate over the causes and drivers of this extinction, with various authors proposing climate change, humans or synergy between the two (Crowley et al., 2017; Godfrey et al., 2019b; Hixon et al., 2021; Razanatsoa et al., 2022). The loss of megafauna may have changed ecosystem structure and function on the island particularly in the grassland ecosystem. A related debate is currently on going on how megafauna would have contributed to the maintenance of the Malagasy grassland particularly found dominant in the Central Highlands (Solofondranohatra et al., 2020).

The Central Highlands presents limited subfossil megafauna sites with remaining bones compared to other regions on the island (Crowley, 2010; Crowley et al., 2021). Above 1300 m a.s.l, extinct megafauna were represented by hippos and elephant birds which relied on C_3 and mixed C_3-C_4 diets, respectively (Crowley et al., 2021). The hippos could have maintained grazing lawns in the area over time which could be dominated by C_3 grass according to the worldwide grass traits (Archibald, Hempson & Lehmann, 2019). Below 1300 m a.s.l. in the Central Highlands, the extinct megafauna were represented by giant lemurs and hippos with C_4, and mixed C_3-C_4 diets, while fossa, a carnivore, had C_3 diets, suggesting mosaic landscapes in the region prior to humans (Crowley et al., 2021). Yet, the relationship between extinct/extant herbivory activities and vegetation dynamics over time, particularly during the Holocene, are lacking. Coprophilous fungal spores have been widely used to reconstruct pastoral activity, as they are an indicator of high densities of large herbivores, like cattle, near lakes in southwest (Razanatsoa et al. 2021, 2022). In addition, these have been used to reconstruct abundance of giant tortoise (e,g. Galápagos Islands; Froyd 2014).

The only up to date published herbivory activities record in the region come from the analysis of fossil coprophilous spores from Lake Tritrivakely and Lake Kavitaha dated at ca. 10 000 cal years BP and ca. 1500 cal years BP, respectively to inform the dynamic of herbivores biomass around these sites (Burney, Robinson & Burney, 2003). These findings suggested low herbivory activities during the Early and Mid-Holocene in the region but an increase from the Late Holocene particularly at ca. 1000 cal years BP. Herbivory activities were coupled with fire increase particularly during the Late Holocene on the island (Burney, 1987b; Burney et al., 2004). Coprophilous spores analysis allowed us to understand the presence of megafauna and herbivores such as giant tortoise and pastoralism in the highlands. These trends of increasing herbivory and fire activities are often associated with the human presence and activities linked to pastoralism on the island particularly in the Central Highlands (Kull, 2000). Additional reconstruction of herbivory activities through coprophilous spore analyses is indispensable in the region to understand past herbivory activities and their potential effects on the vegetation over time.

2.4 Malagasy human history: presence, and settlement on the island

Human impact is usually seen as the main factor leading to the opening of ecosystems, as prescribed by the environmental degradation narrative (section 2.2). Understanding the history, the timing of human presence and its settlement would be beneficial for the interpretation of the vegetation dynamics over time and in informing restoration and management plans.

Over the last two decades, palaeoenvironmental (palaeoecological and paleontological) and archaeological approaches investigated the timing of human presence and settlement on the island. Palaeoenvironmental approaches used the abundance of introduced (i.e. non-indigenous) pollen in a sediment core (Burney et al., 2004), and radiocarbon dating (^{14}C dating) of cut-marked megafaunal bones (e.g., Gommery et al., 2011; Hansford et al., 2018), while archaeological investigations use material culture and radiocarbon dates (e.g., Dewar et al., 2013; Radimilahy & Crossland, 2015; Douglass et al., 2019). A comparison of archaeological criteria used worldwide was also conducted (Mitchell, 2019). Many sites were explored across the island, but they are not equally distributed especially for palaeontology and archaeology sites due to the differences in preservation potential across ecoregions (Crowley, 2010).

Despite these difficulties, during the last decades, the early settlement of humans on the island was suggested at least ca. 2000 cal years BP based on chronometric hygiene radiocarbon dating (Douglass et al., 2019). This method consisted in gathering all dated materials available for Madagascar and selecting them based on their reliability, precision and their association to past human activities. This was reinforced by archaeological results which even proposed human activity no earlier than ca. 1400 cal years BP (Radimilahy &

Crossland, 2015). However, new findings have shaken this previous theory and supposed a presence of humans earlier at ca. 10 000 cal years BP on the island (Hansford et al., 2018). This was based on findings of marked bones of extinct elephant birds *Aepyornis* and *Mullerornis* in Christmas River and Lamboharana (Southwest region) dated at ca. 10 500 and 6200 cal years BP, respectively. This early presence of humans by Hansford et al. (2018) complicated the theory of early human settlement on the island but the time lag between first human arrival and human settlement still highly debated due to the lack of cultural activity, and contextual information on the environmental change recorded during these periods on the island compared to the Late Holocene (Douglass et al., 2019; Mitchell, 2019).

Despite the debates, evidence suggested that the arrival and settlement of the human in Madagascar differ from one region to another with the southwest between ca. 10 500 and 6000 cal years BP (see above, Hansford et al., 2018). The presence of humans in the northwest is recorded around 3810±35 years BP as inferred from cut marks on bones of subfossil dwarf hippopotami in Anjohibe cave (Gommery et al., 2011). Further investigations in the northeast with the excavation of Lakaton'i Anja suggested human presence during the Mid-Holocene around 4380±400 years BP (Dewar et al., 2013) which has been highly disputed due to the poor dating techniques used (Ekblom et al., 2016). In the eastern part of the island, excluding the extreme southeast and northeast, the presence of humans was noticed at ca. 2050 cal years BP inferred by an increase of grass pollen from the palaeoecological site of Torotorofotsy (Straka, 1996). This region requires further investigations with the fewest archaeological and palaeoenvironmental published sites on the island (Burney et al., 2004; Crowley, 2010). A table listing the evidence for people, type of materials dated, the dating method, the dates (including uncertainty) and the location can be found in Douglass et al. (2019).

The arrival of humans in the Central Highlands of Madagascar, where this study focuses, was set at ca. 2000 cal years BP as inferred by the appearance of introduced plants *Humulus-Cannabis* and ruderal plants in the sediment cores (Burney, 1987a; Burney et al., 2004). The Austronesians and East Africans, known as the ancestors of Malagasy people due to their genetic, linguistic and cultural affiliations (Beaujard, 2011; Pierron et al., 2017) have been recognised, settled in Central Highlands from ca. 1400 cal years BP. The evidence of this human settlement in the region was reflected by the sudden increasing macrocharcoal record reflecting an increase in local fire frequency at ca. 1300 cal years BP (Burney, 1987c, b,a, 1997). The Austronesians practice agriculture with rice and yam and increase their fields by land clearing (Beaujard, 2011). A second settlement was recorded in the Central Highlands during the second millennium AD (around 950 cal years BP) increasing cultivation practices and complexity of cultures in the region (Beaujard, 2011). This period is also associated with the introduction of livestock practises in the region (Stachurski et al., 2013). The latter was reflected by the increasing abundance of coprophilous spores and charcoal interpreted as an increase of herbivory activities and fire activity, respectively, in the sediment cores from the region at ca. 950-750 cal years BP (Burney, 1987c,a,b; Burney, Robinson & Burney, 2003). Swidden agriculture was intensified and pastoralism was introduced shortly after 750 cal years BP (Klein, Réau & Edwards, 2008).

The timing of human presence and settlement on the island is still debated and disputed (Hansford et al., 2020; Mitchell, 2020) due to the insufficiency of conclusive evidence of human impacts on environmental change. Human presence is suggested to be recorded for at least ca. 2000 cal years BP with a possible Early Holocene arrival (Douglass et al., 2019). For the case of Central Highlands of Madagascar with scarce archaeological sites, further evidence by multiple proxies during the Early/Mid-Holocene are needed to confirm existing dates along with environmental change.

2.5 Conservation challenges

Biodiversity conservation in Madagascar has received a lot of attention considering the island high species richness but also the recorded degradation rate of its ecosystems. Indeed, a rapid decline of forest cover has been recorded in the last few decades through satellite data (Vieilledent et al., 2018). This forest loss is associated with land-use using fire, for example for swidden agriculture, but the response of biodiversity to climate change and its effect on the fire activity is not clear (Burney, 1993). Efforts have been made for the protection of the Malagasy biodiversity in terms of implementing protected area networks, advancing research techniques and elaborating new legislative environment frameworks (Rakotomanana, Jenkins & Ratsimbazafy, 2013). In addition, there were also attempts to integrate local knowledge on biodiversity conservation allowing the inclusion of sacred forests into protected areas schemes (Kull, 2002c; Marie et al., 2009; Fritz-Vietta et al., 2011; Virah-Sawmy, Gardner & Ratsifandrihamanana, 2014) along with the establishment of a community managed protected area like *Ankodida* (Gardner et al., 2008).

The island has currently established about 9.4 million hectares of protected land and sea (CORSON, 2014). Most conservation so far has been based on the forested island narrative, where there is a need to conserve the remaining forest but also to conduct massive reforestation across areas that are assumed to be the results of anthropogenic degradation (Lacroix et al., 2016). Indeed, most of these protected areas have been established around forested patches particularly in the Central Highlands (e.g., Ambohitantely reserve) with not much representation of open grassland and heathlands. Understanding the extent of such open and mosaic vegetation types and their abundance over time could provide a basis for including them within the conservation framework. Also, multiple reforestation projects were conducted across the region to restore the so-called “green island” (Velo & Zafitsara, 2020), yet most of these have failed due to the non-adaptability of the used species to local fire regimes, topography and also hydrology (e.g., Pareliussen, 2004; Pareliussen, Olsson & Armbruster, 2006). Only invasive taxa such as *Pinus* and *Eucalyptus* have survived and can currently be observed across the landscape as a result of these initiatives (Bertrand, 1999).

Moreover, over the last 100 years (in the 1900s) French and Malagasy governments establishment of fire suppression on the island often results in conflict with local people (Kull, 2002b). This is due to the narrative of the capacity of fire to destroy the tree component of the vegetation resulting in management oriented to fire suppression. Yet, fire could be considered as a tool for maintaining biodiversity and participating in human livelihoods, as well as an ancient feature of many of Madagascar’s landscapes. In addition, conservation projects often underestimate the perception of the local community (Klein et al., 2007) where some depend on pastoralism for their livelihoods (Klein, Réau & Edwards, 2008) and continue to use fire particularly during dry season. At the same time, the majority (64%) of the population on the island depends on subsistence farming of rice and cattle and are dispersed in rural areas under poverty (Bouley et al., 2018). These factors with the increasing population growth on the island are suggested to be one of the main drivers of deforestation (Clark, 2012).

Many of these assumptions on land degradation has been based on the lack of historical knowledge in terms of ancient ecosystems and species that occupied these areas. In addition, there is also a lack of understanding of the drivers of vegetation change including climate, fire and human land-use which could greatly contribute to the conservation of the biodiversity in Central Highlands Madagascar. Though palaeoecology, historical ecology and related disciplines have much to contribute to such debates they are currently underutilised in conservation practice.

2.6 Summary

This literature review highlighted narratives, theories of change and drivers of vegetation in Madagascar particularly in the Central Highlands of Madagascar during the Holocene. The arrival of humans and their settlement during the Late Holocene accompanied by a parallel decline of trees and an increase of open ecosystem taxa triggered the theories of change on the island, particularly in the Central Highlands region. Narrative theory pointed out humans as the main cause of environmental degradation, responsible for the disappearance of forests and the promotion of grassland. The emerging theory states that open ecosystems have been always present and maintained by extinct megafauna and ecological fire. Yet, both theories rely on quantitative and qualitative past ecological data which remain scarce, both temporally and spatially, particularly in the central region. These includes high temporal resolution reconstructions of vegetation history, fire and herbivory activities as well as past climate. The narratives of environmental degradation in the highlands are influential in shaping policies of fire suppression and afforestation. Despite some successes, there are also challenges faced in biodiversity conservation in Madagascar which could be improved through the understanding of the nature of the landscape and the drivers of vegetation change.

Chapter 3 STUDY AREA AND METHODOLOGY

3.1 Introduction

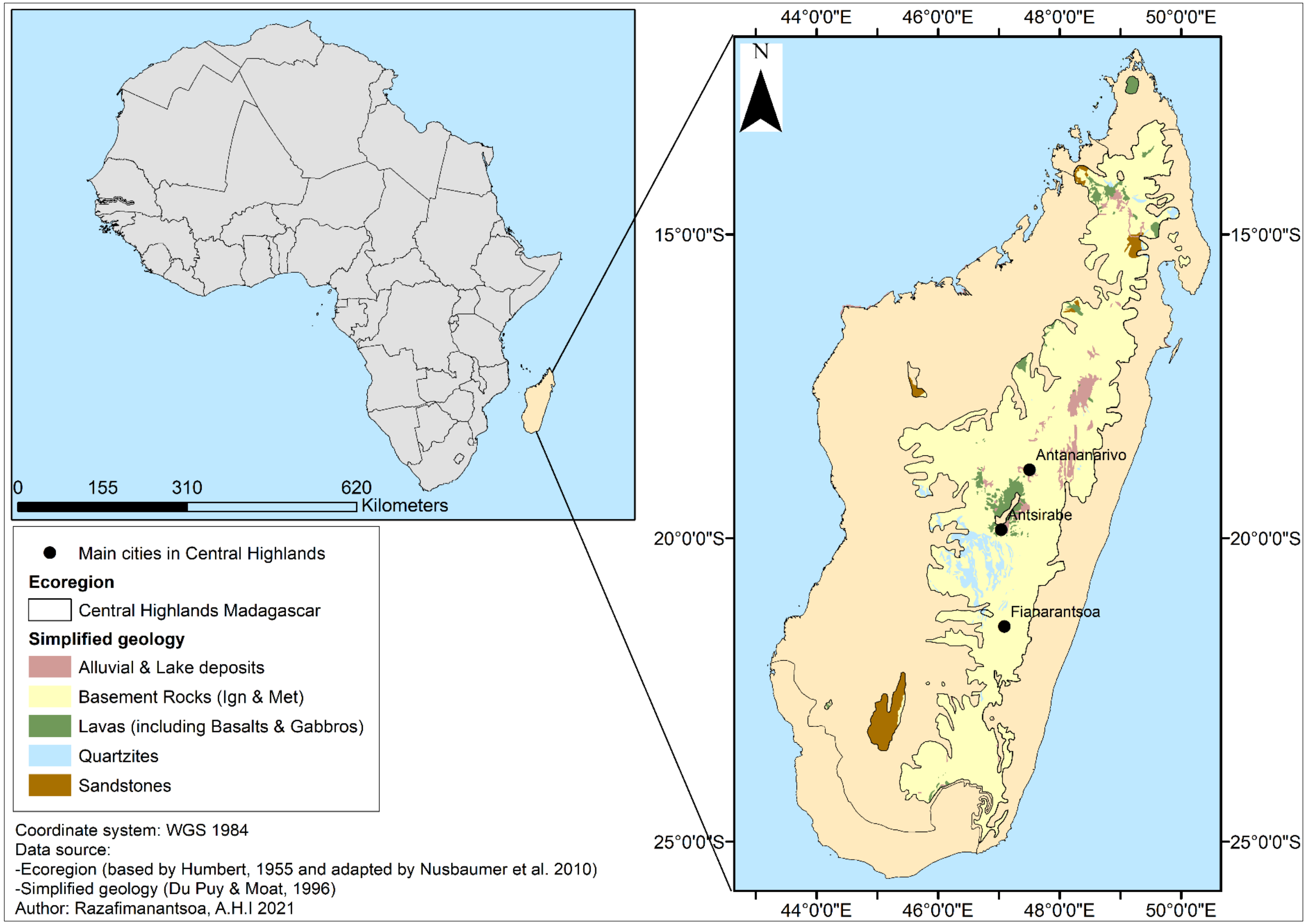
This chapter provides a description of a modern environmental setting, including the geology, soil, climate, and vegetation of the Central Highlands of Madagascar, the focal area of the present study. Human subsistence and livelihoods in the landscape will be also described. In addition, this chapter provides the location and nature of the investigated sites and the methodological approaches used to reconstruct vegetation history and environmental changes over time.

3.2 Study area: The Central Highlands of Madagascar

The Central Highlands of Madagascar, also called the central domain is situated in the centre of Madagascar, and has an elevation ranging from 800 to 2000 m above sea level (a.s.l) (Humbert, 1955a). The region covers an area of ca. 192 141 km^2 (Humbert, 1955b), equivalent to almost one-third of the island's total land area and contains three of the largest cities, namely Antananarivo, Antsirabe and Fianarantsoa (Figure 3.1).

3.2.1 Geology and soils

The Central Highlands of Madagascar are dominated by Precambrian basement rocks dated between 3000 and 550 million years ago (Ma) with some sandstones, lavas, and quartzites (see Figure 3.1; Du Puy & Moat, 1996; Moat & Smith, 2007). The Precambrian basement is composed of a complex of metamorphic and igneous rocks, covered by lateritic clay soils (Du Puy & Moat, 1996; Cox et al., 2010). Sandstones, which are sedimentary rocks composed of eroded sand from the Precambrian basement, are mainly dominant in some high massifs of the landscape, such as Isalo and Itremo (Du Puy & Moat, 1996). However, lavas and quartzites, which are volcanic and metamorphic rocks, respectively, are dominant around the main cities in the Central Highlands (Figure 3.1). The soils in the landscape depend on the geology but in general are lateritic and tend to be thin and colluvial in some areas (Moat & Smith, 2007). These variations of geology and soils are one of the many factors that contribute to the diversity of the landscape in the Central Highlands of Madagascar.



Coordinate system: WGS 1984
Data source:
-Ecoregion (based by Humbert, 1955 and adapted by Nusbaumer et al. 2010)
-Simplified geology (Du Puy & Moat, 1996)
Author: Razafimanantsoa, A.H.I 2021

Figure 3.1: Geology and soils of the Central Highlands of Madagascar. Light brown is unspecified as not part of the study region.

3.2.2 Climate and vegetation

The Central Highlands of Madagascar are characterised by a subhumid climate (Rajeriarison & Faramalala, 1999; Burgess et al., 2004). The climate is mostly controlled by the southeast trade winds from the southern subtropical Indian Ocean (Donque, 1972; Gasse & Van Campo, 2001). This wind belt brings warm and humid air throughout the year and influences the temperature and rainfall, with mean annual temperature and rainfall between 15-20 °C and 1000-1500 mm yr^{-1}, respectively (Donque, 1972). The Central Highlands of Madagascar are classified within the central ecoregion (Solofondranohatra et al., 2018) and present two different phytogeographical divisions called the western and eastern slopes (Humbert, 1955a) (see Figure 3.2) with a characteristic vegetation unit according to the geology and rainfall quantity receive, see table 3.1 (Koechlin, 1972; Moat & Smith, 2007).

Table 3.1: Description of environmental variables between the eastern and western slopes of the Central Highlands

Description	Eastern slopes	Western slopes	References
Classification type	• Séries of *Tambourissa-Weinmannia* -Forêt dense ombrophile et sylve à lichens. • Savane arborée and arbustive	• Series of *Uapaca bojeri* and Chlaenaceae • Savane and Savane arborée.	Humbert (1955;a); Humbert & Cours Darne (1965)
Vegetation type	Wooded grassland-bushland mosaic	Plateau grassland-wooded grassland mosaic, the *Tapia* forest and some woodland grassland-bushland mosaic	Moat & Smith (2007)
Climate	Trade winds are cooler	Trade winds are more hot and dry	Humbert (1955a); Koechlin (1972)
Mean annual rainfall	1300 mm	1260 mm	Moat & Smith (2007)
Dry season	1-4 months	5-6 months	Humbert (1955a)

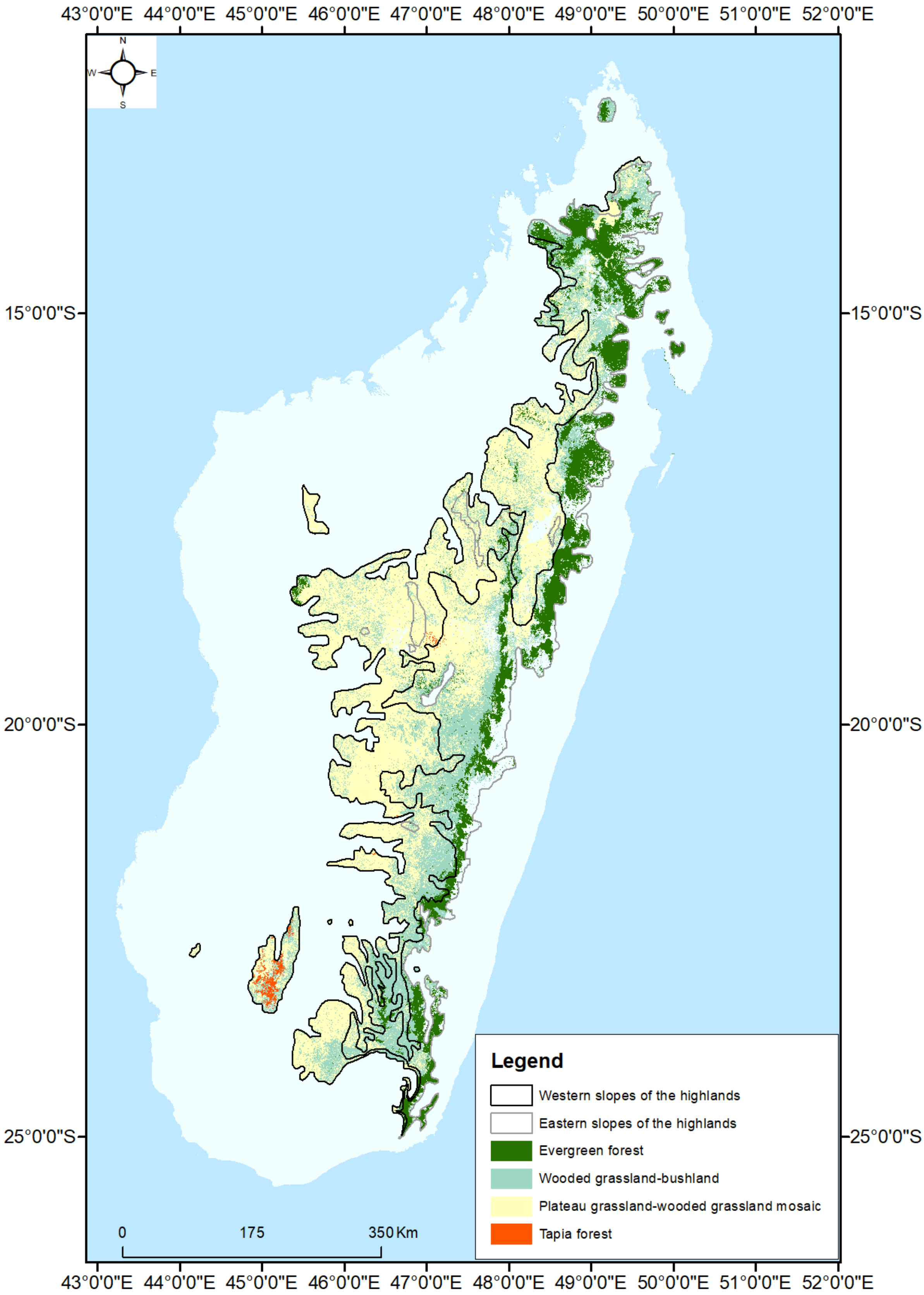


Figure 3.2: Central Highlands of Madagascar showing the western and eastern slopes, with the main vegetation units based on Moat & Smith (2007). Grey is unspecified as not part of the study region

The eastern slopes of the Central Highlands of Madagascar, referred to as a series of *Tambourissa* (Monimiaceae) and *Weinmannia* (Cunoniaceae) (Humbert & Cours Darne, 1965), are represented by plateau grassland-wooded grassland mosaic and wooded grassland-bushland (Moat & Smith, 2007). Forest trees and shrubs are dominated by species of Asteraceae, Rubiaceae, Lauraceae, Verbenaceae, Ericaceae families with some *Faurea* (Proteaceae), *Podocarpus* (Podocarpaceae) and *Ilex mitis* (Aquifoliaceae) in the high-elevation (1300 – 2000 m) (Humbert, 1955a; Koechlin, 1972). In the middle elevation (800 - 1300 m), forest trees are characterised by dominance of *Tambourissa* (Monimiaceae), *Weinmannia* (Cunoniaceae), *Symphonia* (Clusiaceae), *Diospyros* (Ebenaceae), *Eugenia* (Myrtaceae) and *Dalbergia* (Fabaceae) but also some other species of Fabaceae, Euphorbiaceae and Myrtaceae families (Humbert, 1955a; Koechlin, 1972; Faramalala, 1995). Woodlands are characterised particularly by Combretaceae and Arecaceae families (Madagascar Catalogue, 2021). Herbaceous species are mostly represented by the Poaceae families (Koechlin, 1972) with genres such *Oplismenus* spp. and also *Arundinella* present in the undergrowth of forest vegetation while some species such as *Loudetia simplex*, *Schizachyrium sanguineum*, and *Trachypogon spicatus* abundant in the grassland vegetation (Solofondranohatra et al., 2018).

The western slopes, on the other hand, are classified as a series of *Uapaca bojeri* and Chlaenaceae (Humbert & Cours Darne, 1965); and includes the plateau grassland-wooded grassland mosaic, the *Tapia* forest and some woodland grassland-bushland mosaic (Moat & Smith, 2007). Forest trees and shrubs are dominated by *Faurea forficuliflora* (Proteaceae), *Dodonaea madagascariensis* (Sapindaceae), *Rhus taratana* (Anacardiaceae), *Weinmannia bojeriana* (Cunoniaceae) with some Ericaceae and Asteraceae in the high elevation (1300 m to 2000 m) (Humbert, 1955a; Kull, 2002a). Between 800 m and 1300 m (mid-elevation), woodland taxa are most commonly represented by *Uapaca bojeri* with an average density of 653±2 stems per ha (Razafimanantsoa et al., 2013). Sarcolaenaceae family represented by *Sarcolaena eriphora*, *Leptolaena* sp. and *Xerochlamys bojeriana* with some Asteraceae species (*Brachylaena microphylla*, *Dicoma madagascariensis*) are also common in the middle elevation (Humbert, 1955a). Herbaceous species are dominated by Poaceae family with the abundance of the same taxa with similar ecological affiliation to the eastern region.

Whether in the eastern or western slopes, the lowlands called *Baiboho* are characterised by wetlands and some riparian forest but have mostly been transformed into a rice field in the region (Gade, 1996; Kull, 2012). Besides, a large increase in plantations of introduced plants, like the *Eucalyptus* spp., *Pinus* spp. and *Acacia* spp., has replaced the woody components in much of the landscape (Tassin et al., 2009).

3.2.3 Human: livelihoods and subsistence

There is currently a mixture of people from different ethnicities in the Central Highlands of Madagascar due to increasing migration (Rakotonarivo et al., 2010). These ethnic groups are mainly represented by the Merina, Betsileo, Bara and Tsimihety groups. The Merina and Betsileo mostly occupy the centre of the landscape and are known to be farmers on the island, transforming land into crops (Toillier et al., 2011). Tsimihety and Bara, mainly herders and pastoralists, are found in the northern and southern parts of the region, respectively (Saint Sauveur, 2007).

Generally, farmers in the region mostly cultivate irrigated rice for their livelihoods in terraced fields on the slopes of steep hills or in marshlands at the valley bottom (Toillier et al., 2011; Kull, 2012). The traditional agricultural system is based on a swidden agriculture, which relies on fire to clear the land for the rice field and/or for other food crops like cassava, sweet potato and taro. Farmers also use fire to fertilise soils and clean the irrigation canals and field edges in their land (Kull, 2002b). On the other hand, herders manage pastures for cattle grazing by annual burning of the landscape. It allows renewal of pastures, removes lignified grass, and promotes new grazing (Kull, 2000, 2002b).

In times of economic and/or climatic hardship (late rainy season), people in the highlands, including farmers and herders, exploit forest patches for their subsistence. Local people often switch to woody charcoal production, which is not only limited to the cutting of trees in the forest (Gade, 1996), but also exposes the forest to a high risk of fire spreading from one patch of forest to another (Bloesch, 1999). This practice has become more and more intensified and is supposed to be one of the main drivers contributing to the deforestation of the ecoregion (Vieilledent et al., 2018).

3.3 Study sites

3.3.1 Choice of study sites

The current state of vegetation cover in the Central Highlands of Madagascar is a subject of debate as to its origin and the factors that may have contributed to its current distribution, particularly the former extent of forest and woodland cover (see Chapter 1 & 2). The study sites were carefully chosen to take into account the current contrast in the distribution of forest and grassland across the landscape as well as differences in human practices. Exploration of potential sites was conducted on Google Earth prior to fieldwork. Sites were primarily selected within the two different slopes in the highlands, and then, as a function of abundance in the presence or absence of forest patches. The contrast between human livelihoods and subsistence was also considered when selecting the sites.

Accordingly, eight sites were visited with three located on the eastern and five sites on the western slopes of the highlands. In total, 11 sediment cores were collected in the Central Highlands of Madagascar during the fieldwork conducted between 11th and 22nd of October 2016 with permission from the Ministry of Environment and Mines under the permit reference number: 242/16/MEEMF/SG/DGF/DASP/SCB.Re (Appendix 1).

Since the aim of the study is to investigate vegetation change in Madagascar prior to human settlement and expansion at ca. 2000–1350 cal years BP (Burney et al., 2004; Crowley, 2010; Anderson et al., 2018; Douglass et al., 2019), the sites were selected based on the age and level of pollen preservation within the sediment cores collected. Based on the information gained from basal radiocarbon dating and preliminary pollen analysis of the sediment cores, two study sites were chosen. The sites are represented by the grassland area of the Tampoketsa-Ankazobe wetland (TAMB$_2$ core) located near the Ambohitantely Reserve; Ankazobe district and the forest-grassland mosaic of Lake Dangovavy (DAN core) near Faratsiho (Figure 3.3).

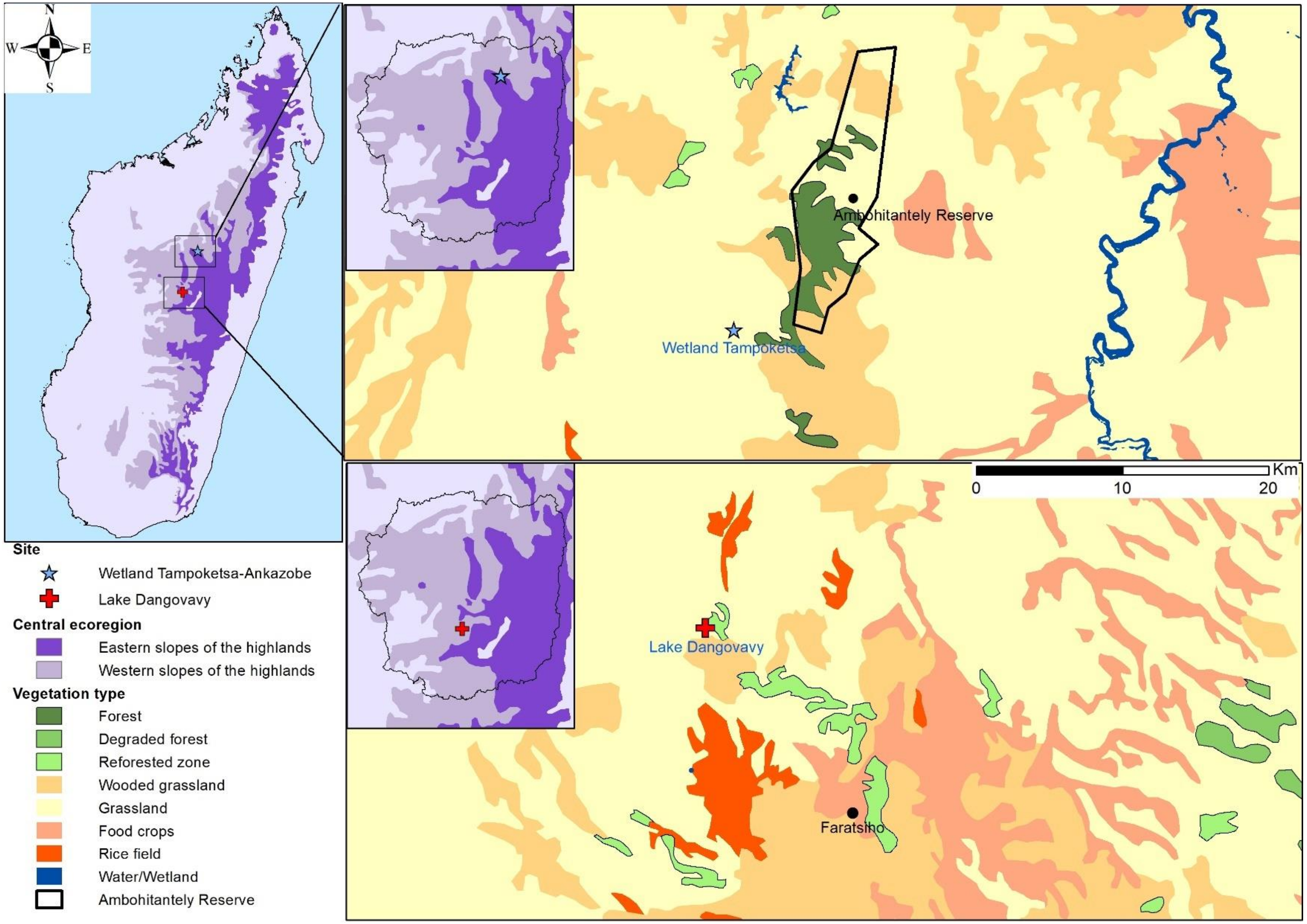


Figure 3.3: Location of the two study sites, Tampoketsa-Ankazobe wetland and Lake Dangovavy, within the eastern and western slopes of the Central Highlands of Madagascar. Ecoregion adapted from Humbert (1955) and Nusbaumer et al. (2010); Vegetation based on Moat and Smith (2007)

3.3.2 Tampoketsa-Ankazobe wetland

Tampoketsa-Ankazobe wetland is a non-disturbed wetland with less human disturbance related to agricultural practices. The site is located at -18.23195, 47.24451, 1600 m a.s.l. on the eastern slopes of the Central Highlands of Madagascar (Figure 3.3). The area is close to Ambohitantely Reserve (Figure 3.3), which is among the few terrestrial protected areas in the central ecoregion (Pareliussen, 2004; Goodman, Raherilalao & Wohlhauser, 2018). Instrumental records from Manankazo, the nearest meteorological station around the site obtained from the meteorological services in Madagascar, shows that between 2005 and 2016, the climate is marked by a five-month (May to September) cold and dry season and a seven-month (November to April) warm and rainy season. The mean annual precipitation is 1375 mm, with the wettest month in January (mean of 317 mm) and the driest in August (mean of 2 mm). The mean annual temperature is 19.8 ˚C where December is the hottest month (mean of 22.7 ˚C) and July is the coldest (mean of 15.3 ˚C), which can drop to 5.7 ˚C (Goodman, Raherilalao & Wohlhauser, 2018). The local soils in the area are, in general, ferralitic.

Contemporary vegetation in the study site and its surroundings are dominated by grassland (Figure 3.4). The most common grass species are represented by *Aristida similis*, *Hyparrhenia rufa*, *Loudetia simplex*, *Panicum glanduliferum* and *Trachypogon spicatus*. Patches of evergreen forest were also noted near the study site within the Ambohitantely Reserve (Ratsirarson & Goodman, 2000). Radimbison (1990) and (Goodman, Raherilalao & Wohlhauser (2018) described that the slopes are dominated by tree species, such as *Baronia taratana* (Anacardiaceae), *Cussonia bojeri* (Araliaceae), *Filicium decipiens* (Sapindaceae), *Homalium nudiflorum* (Salicaceae), *Ilex mitis* (Aquifoliaceae), *Nuxia capitata* (Stilbaceae), *Schefflera longipedicellata* (Araliaceae), and *Podocarpus madagascariensis* (Podocarpaceae) with some Erythroxylaceae, Gentianaceae, Myrtaceae, Gaertnera and Rubiaceae, particularly in the shrub layers. The hills, however, are dominated by tree species, such as *Uapaca densifolia* (Phyllanthaceae), *Leptolaena pauciflora* (Sarcolaenaceae) and *Weinmannia rutenbergii* (Cunoniaceae), while palm trees are represented by *Ravenea* sp., *Dypsis decipiens* and *Dypsis oropedionis* (Ratsirarson & Goodman, 2000; Goodman, Raherilalao & Wohlhauser, 2018). Some slopes of the hills in the area are characterised by an abundance of pioneer species, such as *Dodonaea madagascariensis* (Sapindaceae), *Harungana madagascariensis* (Clusiaceae), *Psiadia altissima* (Asteraceae) and *Trema orientalis*

(Cannabaceae) (Goodman, Raherilalao & Wohlhauser, 2018). Exotic trees such as *Eucalyptus* spp., *Pinus* spp. and *Acacia dealbata* are also found in the study site (Pareliussen, 2004).

People living around the Tampoketsa-Ankazobe site are mostly pastoralists and use fire as a tool for their livelihood (Pareliussen, 2004). Local people burn grassland seasonally to manage pastures for cattle grazing. Fire is also used to collect honey and hunt animals, particularly tenrec in the forest (Radimbison, 1990). Uncontrolled fire often expands from one forest patch to another, which is thought to lead to a decrease in forest cover in the area (Goodman, Raherilalao & Wohlhauser, 2018). This makes the area amongst the most heavily burned regions of the island, despite a government ban on burning (Klein, Réau & Edwards, 2008).

Figure 3.4: Grasslands of Tampoketsa-Ankazobe on the eastern slopes of the Central Highlands of Madagascar: a) Investigated wetland and b) One of the two 50 cm sediment cores collected from the lake using a Russian corer

3.3.3 Lake Dangovavy

Lake Dangovavy is situated at -19.287569, 46.857446, 1700 m a.s.l. on the western slopes of the Central Highlands of Madagascar (Figure 3.3). The lake is ca. 350 m wide and ca. 600 m long with abundance of *Eleocharis plantaginea* (Cyperaceae) in the lake (Figure 3.5). The lake is located near Faratsiho town and belongs to the Vakinankaratra region. The region receives a mean annual rainfall between 1200 and 2000 mm and has a mean annual temperature of about 20 °C (Razafindratsima, 2019). The region is dominated by ferralitic soils, but some alluvial and volcanic soils are also found (Sourisseau et al., 2016). Volcanic eruptions are the origin of the formation of some lakes in the region (Rufer et al., 2014). Vegetation surrounding the lake is dominated by grassland with an abundance of *Aristida rufescens* (Poaceae) as recorded during the field work. Some shrubs and trees were also noted on the lake margin. Shrubs were represented by *Elephantopus scaber*, *Helichrysum* sp. (Asteraceae), *Agauria polyphylla*, *Erica goudotiana*, *Vaccinium secundiflorum* (Ericaceae) and *Weinmannnia* sp. (Cunoniaceae). The trees are represented by *Ilex mitis* (Acquafoliaceae), *Aphloia theiformis* (Aphloiaceae), *Kotschya perrieri* (Fabaceae), *Syzygium jambos*, *Syzygium* sp. (Myrtaceae), *Maesa lanceolata* (Primulaceae) and *Tina striata* (Sapindaceae); as well as herbaceous species such as the fern, *Pteridium aquilinum* (Pteridaceae). It is worth noting that Lake Dangovavy was surrounded by food crop fields including corn, potato and rice. Plantations of exotic trees, such as *Acacia* spp., *Eucalyptus* spp. and *Pinus* spp., were also found in the upland with individual *Uapaca bojeri* trees.

Local people in the region practice subsistence and commercial agriculture for their livelihoods (Sourisseau et al., 2016). Farmers have transformed the landscape into rice fields to harvest crops, such as corn, potatoes, beans and cassava (Ministère de l'Agriculture, 2015). Despite reports from the Ministry of Environment indicating that farming has not been responsible for deforestation, land degradation in the region has often been associated with population growth where farmers decide to clear new lands to accommodate household expansion (Randriamanantena et al., 2020). In addition, farmers kept livestock to help with agriculture but also for commercial uses like milk production.

Figure 3.5: Lake Dangovavy (Vakinankaratra region) in the western slopes of the Central Highlands of Madagascar. a) The lake and its surrounding landscape, and b) One of the two 50 cm sediment cores collected from the lake using Russian corer

3.4 Methods

3.4.1 Sediment collection

To investigate long-term vegetation and environmental change in the Central Highlands of Madagascar, sediment cores were collected from the Tampoketsa-Ankazobe wetland and Lake Dangovavy using a Russian corer (De Vleeschouwer, Chambers & Swindles, 2010). The Russian corer is a D-section corer, which consists of a 50 cm long steel chamber with a diameter of 5 cm and 1.5 m steel rods. The core chamber has a rotating blade with a sharp end to allow the material to penetrate and collect sediments (gyttja and/or peat) in both the wetland and lake. Coring was made in 50 cm overlapping steps (0-50 cm, 50-100 cm and 100-150 cm) from two parallel holes as deep as possible using the extension steel rods. The sediment cores collected in Tampoketsa-Ankazobe (TAMB$_2$ core) (Figure 3.4b) and Lake Dangovavy (DAN core) (Figure 3.5b) were 99 cm and 110 cm long, respectively. The cores were collected as close as possible to the centre of the wetland/lake. Once collected, each core was wrapped in plastic and aluminium foil and then placed in halved PVC tubes to avoid damage, and contamination but also to maintain humidity in the field.

After fieldwork, sediment cores were kept in a 4 °C cold room to prohibit microbial activity before laboratory analysis.

3.4.2 Sediment description

The sediment description of the $TAMB_2$ and DAN sediment cores was based on a simplified Troels-Smith and sediment colour description, which has been widely used to describe sediment cores from swamps and lakes. It is based on physical features, organic content and components of the sediment cores (Troels-Smith, 1955; Kershaw, 1997). The components in the sediment cores are mainly classified into *Turfa* (plants and roots), *Detritus* (plant fragments), *Limus* (organosilicates, carbonates and iron oxides), *Argilla* (clay and silt) and *Grana* (sand and gravel). A class scale from 0 to 4 was used to characterise the value of each component in the sediments, whereby zero (0) represents the absence of components, 1 = rare, 2 = occasional, 3 = frequent and 4 indicates an abundance of component value in the sediment. Additional characters using plus (+) and minus (−) signs were added in the scale class for precise and slight changes in the value. Munsell soil color charts were used to define the sediment color (Munsell color company, 1954). Different layers of the sediment cores were visually compared between the samples and the Munsell chips with its Munsell notation. However, the Munsell colour chart is limited in that the method can be more subjective than objective (Pegalajar et al., 2020).

3.4.3 Subsampling sediment cores

Subsampling was conducted by using 3 to 5 ml plastic syringes with the tips cut off and/or razorblades. The syringes were used to subsample sediment for physical (bulk density, water and carbon contents) and proxy (pollen, charcoal, dung spores and diatoms) analyses. The syringe was inserted into the sediment cores at desired depths to collect a pre-defined volume of 1 cm^3 of sample for analyses. Razorblades were used for sampling procedures that require samples free from contamination. The method consists of collecting an amount of 1-10 g and 20-40 mg for radiocarbon dating and carbon isotope analysis, respectively, at a desired level within the core using two razorblades. The samples were then weighed and put into materials prescribed by the analysis.

3.4.4 Physical analyses of sediment

The physical analysis of the $TAMB_2$ and DAN sediment cores included measures of water and carbon content which are used to infer moisture and the amount of organic materials in the sediment (Heiri, Lotter & Lemcke, 2001). A volume of 2 cm^3 samples (wet samples) were collected every 4 cm throughout the sediment cores to obtain high-resolution in the data, using syringes. The samples were weighed in heated and pre-weighed crucibles to determine the bulk density of the sediment following the adapted equation from Berglund (1986) (Equation 1).

Equation (1):

$$Bulk\ density\ (gcm^{-3}) = \frac{(\mathrm{Mc} + \ \mathrm{WS})\ - \mathrm{Mc}}{\mathrm{Sample\ volume}}$$

Where: - Mc and WS are dry crucible mass (g) and wet sample mass (g), respectively.

- Sample volume is equal to 2 cm^3

The same wet samples were used to evaluate the amount of water and carbon content in the sediment cores by using the Loss on ignition (LoI) method (Dean, 1974; Heiri, Lotter & Lemcke, 2001; Wood, 2015). The LoI method is based on two different phases, which are successively to dry the samples and then ignite them to sequential thermal analysis (Santisteban et al., 2004; Wood, 2015). Samples were dried to evaluate the amount of water in the sediment cores. It consists of putting the wet samples in an oven at 105 °C overnight for approximately 12 hours, and then weighing them. The moisture content of samples was calculated following the formula of Wood (2015) in Equation 2.

Equation (2):

$$Moisture\ content\ (\%) = \frac{\mathrm{WS} - \mathrm{LOI}_{105}}{\mathrm{WS}} \times\ 100$$

Where: WS and LOI_{105} are wet sample mass (g) and dry sample mass (g) respectively. Once dried, samples were heated sequentially in a muffle furnace and then weighed to evaluate the carbon content in the sediment cores. Total organic carbon (TOC) was obtained by heating the dry samples at 550 °C for between 6 and 12 hours (Heiri, Lotter & Lemcke, 2001) and calculated the TOC by the Equation 3.

Equation (3):

$$Total\ organic\ carbon\ (TOC)\ (\%) = \frac{\mathrm{DS} - \mathrm{LOI}_{550}}{\mathrm{DS}} \times\ 100$$

Where: DS and LOI_{505} are dry sample mass (g) and ignited (550 °C) sample mass (g) respectively.

The estimate Total inorganic carbon (TIC) was obtained by heating the dry samples at 950 °C for 2 hours (Equation 4).

Equation (4):

$$Total\ inorganic\ carbon\ (TIC)\ (\%) = \frac{\mathrm{LOI}_{550} - \mathrm{LOI}_{950}}{\mathrm{DS}} \times\ 100$$

Where: DS, LOI_{505} and LOI_{950} are dry sample mass (g), ignited (550 °C) sample mass (g) and ignited sample (950 °C) respectively.

3.4.5 Chronology and age-depth modelling

Radiocarbon dating is now the most widely applied dating technique to provide an accurate chronology for palaeoenvironmental studies. Accelerator Mass Spectrometry (AMS) technique was used to measure radiocarbon in the sediment cores. AMS radiocarbon dating uses smaller sample sizes (1-10 g) compared to other methods (for example radiometric dating) and this allows higher temporal resolution and also suits the amount of our sediments collected by Russian corer. AMS techniques consist of measuring the residual Carbon-14 (^{14}C) activity in a sample by counting the number of ^{14}C atoms present in the sample. The ^{14}C is an unstable carbon that is absorbed by the living organism and decayed to form the stable element Nitrogen-14 (^{14}N) when the living organism dies. About half of the ^{14}C rate, known as *half-life*, decays from the dead organism every 5570±40 years (Walker, 2005). This allows calculating objective age-estimates of a sample from fossil materials by measuring the number of ^{14}C remaining in the sample and by comparing it with the modern material (Walker, 2005).

Bulk sediment samples were collected from both sediment cores (TAMB_2 and DAN), for radiocarbon dating for using razorblades. The choice of bulk sediment is based on its association with the deposition of fossil pollen which is one of the primary proxies for the present study. This is critical to better interpret and establish a clear chronology more coherent with the pollen diagrams. The individual samples were then wrapped in aluminium foil and put in a ziplock bag to be sent to the radiocarbon laboratories, mentioned below. Eight and seven samples were collected from the $TAMB_2$ and DAN sediment cores, respectively. The choice of dated levels was based on the estimated basal age of each sediment core, as well as the main important shifts of pollen results throughout the cores. Precautions were taken to avoid or minimise sample contamination following protocols prescribed by the labs. However, contamination is not excluded (e.g., root penetration, bioturbation, allochthonous input) which could be a source of older and newer deposited carbon that can lead to some spurious dates. The samples were submitted for AMS radiocarbon dating to Beta Analytic Inc., Miami (United States of America) and iThemba LABS facility in Johannesburg (South Africa). The returned radiocarbon ages from the laboratories were calibrated into calendar time using SHCal20 calibration dataset for Southern Hemisphere terrestrial samples (Hogg et al., 2020). The calibration curve SHCal20 can provide a calibration date up to 55 000 years, which is older than its predecessor SHCal13, of up to 50 000 years (Hogg et al., 2013). An age model was constructed using the Classical Age-Depth Modelling, Clam package version 2.3.9 (Blaauw, 2021) within the open-source statistical software program R version 4.0.4 (R Core Team, 2021). Clam produces an age depth model which does not overestimate the age uncertainties in the model (Trachsel & Telford, 2017). The age-depth models of both sediment cores were constructed using linear interpolations as they fit the best to the midpoints of the highest probability density ranges and the stepwise point estimates (Blaauw, 2010; MacPherson, Gillson & Hoffman, 2019). However, Bacon version of the age-depth models are provided for verification (more details in section 4.3 and 5.3). For this PhD project, calibrated dates obtained were expressed in cal years BP (Before Present).

3.4.6 Sample analyses

3.4.6.1 Pollen analysis

Pollen analysis is a globally utilised method applied to understand vegetation response to past environmental change (Bennett & Willis, 2001). It was applied to reconstruct past vegetation change during the Holocene at the Tampoketsa-Ankazobe wetland ($TAMB_2$ core) and Lake Dangovavy (DAN core) in the Central Highlands of Madagascar. The method used for the extraction of pollen in the sediment cores was based on the standard procedures by Faegri and Iversen (1989) as adapted by Bennett & Willis (2001). Subsamples (1 cm^3) were collected from the sediment cores using a plastic syringe (see section 3.4.3) at an interval divisible by 2 (Bennett & Willis, 2001) starting at 16 cm intervals, then 8 cm and finally increased to 4 cm intervals after obtaining the radiocarbon dates range. Each sample was put in 50 ml polypropylene boiling tubes and a known quantity of exotic *Lycopodium* spores was added to each tube before any chemical processing. The *Lycopodium* spores came in the form of tablets, Batch number 3862 with a concentration of 9666±671 *Lycopodium* spores per tablet. These tablets are manufactured by the Department of Geology at the University of Lund. Two tablets were added to each sample, which allowed for the calculation of pollen concentration and to measure changes in the sedimentation rate (Bennett & Willis, 2001).

The chemical and physical processing of pollen extraction in the sediment is presented diagrammatically in Figure 3.6. Each step in the chemical process is generally separated by washing the sample with deionised water, centrifuging at 3500 RPM for 5 min (or leaving overnight) and decanting. The first process involved treatment of the sample with the hydrochloric acid (HCl) 10%, which removes carbonates from the sample, and also helps to dissolve the *Lycopodium* spore tablets added to the tube. The samples were then treated with 10% sodium hydroxide (NaOH), which removed the humic acid components in the sample. Samples were then immediately sieved with a 150 µm mesh and washed with deionised water. Elements > 150 µm, including the macrocharcoal, were retained for other purposes (see macrocharcoal extraction). Samples were exposed to a washing process several times (making sure that supernatant was clear) after sieving. Once clean, samples were acidified using HCl 10% and hydrofluoric acid (HF) 60%. The HCl 10% decreased pH and prepared samples for the introduction of HF, which removed silicates in the sample. A second treatment of HF was added to the samples with abundant silicate. After HF, the samples were treated again with HCl (10%) to remove colloidal silicates. Glacial acetic acid was then added to the samples to dehydrate them. An acetolysis mixture (1 part concentrated sulphuric acid and 9 parts acetic anhydride) were added to the samples to remove polysaccharides from the pollen (Erdtman, 1960). Glacial acetic acid was then added to the samples to stop the acetolysis reaction, before washing them several times with deionised water to make the pH neutral. Finally, samples were coloured with a Safranin solution, dehydrated by tertiary butyl alcohol (TBA), and mounted with silicone on glass slides to be counted on the microscope.

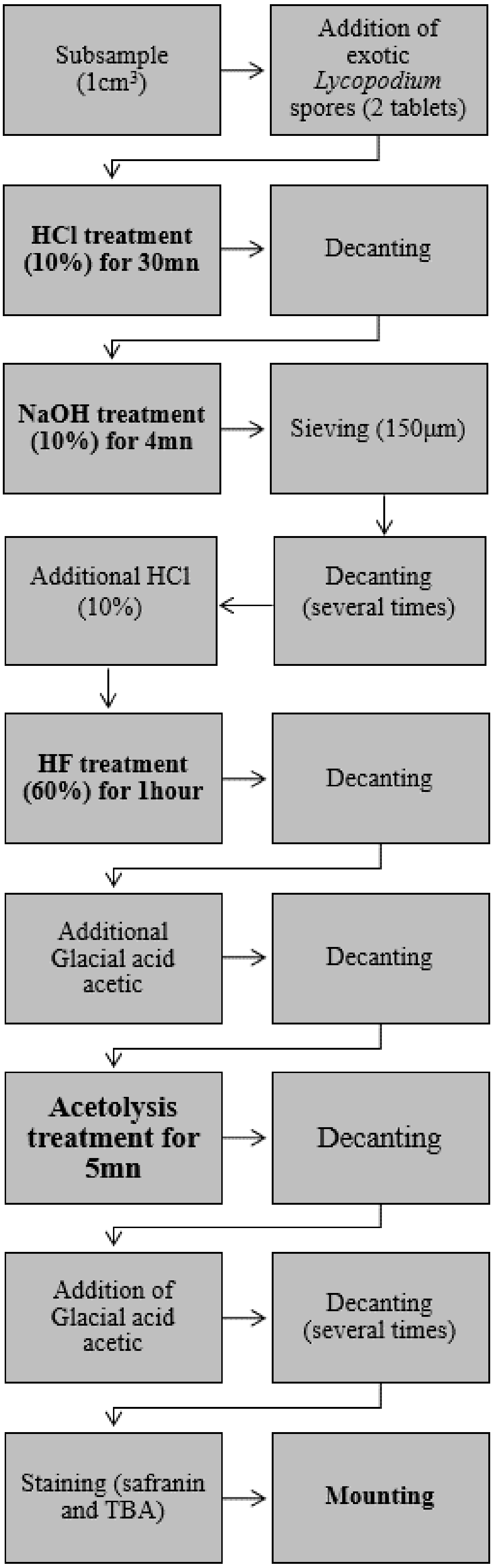


Figure 3.6: Palynomorph extraction (pollen, coprophilous spores and microcharcoal) process used during the study adapted from Bennett and Willis (2001)

Pollen counting was conducted by using a digital Nikon Eclipse 50i microscope with four objectives lenses (10x, 20x, 40x, 100x). The major counting was done at magnification 400x and at 1000x for some pollen taxa which needed particular attention. An independent pollen counting software based on Java established by Froyd Lab Tools Version 1.1 copyright © 2015 was used to facilitate the counting. By using the software, we could classify the pollen taxa immediately with respect to their ecological affiliation while taking into account the total sum of the pollen grain. A minimum standard count of 300 pollen grains (excluding Cyperaceae and other aquatic types) per level were counted to improve statistical confidence (Bennett & Willis, 2001; Keen et al., 2014).

Pollen identification was based on the reference slide collection from the Palynology Unit of the Department of Ecology and Plants Biology at the University of Antananarivo. Unpublished theses focusing in the Central Highlands investigating pollen rain on samples from spore Brutayert traps were also used as they present a description of abundant taxa in the region(e.g., Ramiaramanana, 2011; Andriamahery, 2014). Pollen described from melissopalynology studies on the island, such as Rasoloarijao et al. (2019) and Vololona et al. (2019) were also used to strengthen and confirmed the identification as yet available pollen data is still very limited for Madagascar. In addition, some known published pollen data reference like the Australian pollen database (Australasian Pollen and Spore Atlas [APSA], 2007), and some published atlases of pollen like Gosling, Miller and Livingstone (2013), and Schüler and Hemp (2016), were used to identify pollen not described by modern pollen rain studies in the region.

Pollen data from the $TAMB_2$ and DAN sediment cores were converted to percentages. Relative abundance was used in this research because it considers the relative abundance of taxa to one another and shows well the dynamism of each pollen taxa over time. Pollen value was expressed as a percentage of total pollen counted (pollen sum). The total pollen sum contained all terrestrial taxa, including undifferentiated pollen, which incorporates broken and rare undefined pollen, but excluded Cyperaceae and other aquatic plants (Equation 5).

Equation (5):

$$Pollen\ abundance\ (\%) = \frac{ni}{N} \times\ 100$$

Where:

ni and N are the absolute frequency of the taxa i and N the total pollen sum for the sample, respectively.

3.4.6.2 Stable carbon and nitrogen isotope measurement

Measurements of the stable carbon isotope ($\delta\ ^{13}C$), and the C:N stable isotope ratio were conducted in Tampoketsa-Ankazobe wetland and Lake Dangovavy sediment cores. Stable carbon isotope analysis was used to evaluate past vegetation change in both sites alongside the pollen analysis previously prescribed. The analysis is based on the ratio of ^{12}C and ^{13}C composition of C_3 (trees) and C_4 (grasses) plants preserved in the sediment cores (Pessenda et al., 2004). Photosynthetic pathways of C_3 and C_4 plants differ and therefore contribute to different stable carbon isotope ($\delta\ ^{13}C$) values. The $\delta^{13}C$ values of C_3 plants mostly dominated by trees and shrubs range between -33‰ and -22‰ PDB (Deines, 1980), while for C_4 plants (mostly grass) it ranges between -17‰ and -9‰ PDB (Boutton et al., 1998). The C-N stable ratio i.e., $\delta\ ^{13}C$ and $C{:}N$ was used for tracing the origin of organic matter (Cloern, Canuel & Harris, 2002) whether it was a more aquatic with low C/N ratio (<12) or terrestrial with highest ratio (Bonn & Rounds, 2010).

To process, 20 to 40 mg subsamples of sediment were taken at the same level as pollen (every 4 cm) throughout the sediment cores collected in the Central Highlands using razorblades. Samples were acidified, washed, and dried before sending them to the Stable Light Isotope Laboratory at the Department of Archaeology, University of Cape Town. The acidification process removes carbonates by adding HCl 10% and leaving it overnight to react. Samples were then washed several times to remove the acid and then dried in the oven at 60 °C. Once the pre-treatment was finished, samples were weighed and ready to be combusted in a mass spectrometer for carbon isotopes measurement.

3.4.6.3 Charcoal analysis

Charcoal analysis from sediment cores has proven to be a powerful tool in reconstructing fire history over time (e.g., Whitlock & Larsen, 2001; Hawthorne et al., 2018). The mode of analysis differed depending on charcoal size, where microcharcoal (< 150 μm) was analysed on pollen slides, while macrocharcoal (> 150 μm) was counted in a petri-dish. The charcoal size classification is determined by taking into account the distance traveled from the source, as indicated in the literature (Whitlock & Larsen, 2001). The microcharcoal is supposed to be easily dispersed by wind and water and supposed to represent a regional signal, while macrocharcoal, being heavier, is supposed to reflect local fire (Carcaillet et al., 2001).

Microcharcoal and macrocharcoal analysis were conducted to understand fire history and its impact on vegetation change in the Central Highlands of Madagascar. The same sample for pollen analysis was used for charcoal analysis. Microcharcoal extraction followed the same process as the pollen used by Bennett and Willis (2001). For macrocharcoal, after sieving samples with a mesh 150 μm (Figure 3.6), elements > 150 μm were collected into a test tube in water and then washed and decanted. Once cleaned, samples were suspended overnight in hydrogen peroxide (H_2O_2) 6% to bleach the organic matter and highlight only the charcoal (Stevenson & Haberle, 2005). Macrocharcoal samples were then processed by a final wash, decanted and then stored until counting was done. Microcharcoal counting and concentration in the TAMB$_2$ and DAN sediment cores were based on the charcoal point count method of Clark (1982) (see Equation 6 and 7). Within the pollen slides, at least 200 particles of black compact charcoal fragments and *Lycopodium* spores were counted per sample (Finsinger & Tinner, 2005; MacPherson, Gillson & Hoffman, 2019). Macrocharcoal was counted directly under a Leica EZ4 stereomicroscope using the petri-dish technique (Stevenson & Haberle, 2005). The petri-dish was subdivided into eight equal sectors. Four of the eight were tallied at random, and the total macrocharcoal count was calculated by multiplying the total proportions by the value. For both sediment cores, macrocharcoal and microcharcoal were expressed as a function of concentration i.e. particles.cm^{-3} and cm^2.cm^{-3}, respectively.

<u>Equation (6):</u>

$$Ca = \frac{(Area\ of\ field\ of\ view)\ \times (number\ of\ charcoal\ hits)}{Number\ points}$$

Where: Ca represents charcoal area counted (cm^2)

Equation (7):

$$Mc = \frac{Ca \times \frac{Lycopodium\ added\ to\ sample}{Lycopodium\ counted}}{Sediment\ volume}$$

Where: Mc represents microcharcoal concentration ($cm^2.cm^{-3}$)

3.4.6.4 Coprophilous spore analysis

Worldwide, analysis of coprophilous spores in sediment cores have been used to reveal past herbivore abundance, decline and extinction (e.g., Burney, Robinson & Burney, 2003; Ekblom & Gillson, 2010; Feranec et al., 2011). It was most commonly used to reflect herbivore activities from animals that defecates in water. For instance, it was used to to reconstruct abundance of giant tortoise in Galápagos Islands (Froyd et al., 2014) and megafaunas and pastoralism in Madagascar (Burney, Robinson & Burney, 2003). It was, therefore, applied at our two highland sites to reconstruct herbivory activity and to evaluate its link to the vegetation change over time. The method of extraction of coprophilous spores in the sediment was the same as the pollen method (Bennett & Willis, 2001; Figure 3.6). Coprophilous spores counting was done on the same slides as pollen and was based on Ekblom and Gillson (2010), who counted spores alongside the pollen grains until the minimum pollen count of 300 was reached. Spore value was expressed as concentration (spores. cm^{-3}) calculated as a function of the *Lycopodium* added to the sample (Stockmarr, 1971) following the Equation (8). Coprophilous spores identification was based on published literature and photos (Van Geel, 2001; Prager et al., 2006; Cugny, Mazier & Galop, 2010; Ekblom & Gillson, 2010). The coprophilous spores counted are represented by *Sporormiella*, Sordariaceae, *Coniochaeta* and *Podospora* taxa as they have been used with studies of megafauna extinction (Burney, Robinson & Burney, 2003; Baker, Bhagwat & Willis, 2013) and introduction of livestock particularly in Madagascar with the genus *Sporormiella* (Burney, Robinson & Burney, 2003).

Equation (8):

$$\text{Coprophilous spores concentration } = \frac{\text{Spore counted}}{Lycopodium \text{ counted}} \times Lycopodium \text{ added}$$

3.4.6.1 Diatom analysis

Diatom analysis has been used worldwide, including a few studies in Madagascar, to reconstruct past hydrological and environmental change (Gasse & Van Campo, 1998, 2001; Virah-Sawmy, Willis & Gillson, 2010) . Diatoms are very sensitive to habitat variation and diatom assemblages are linked to the biological, chemical, and physical characteristics of their environment (Fritz *et al*., 1999). The extraction of diatoms from the $TAMB_2$ and DAN sediment cores was based on Battarbee (1986) adapted by Kirsten (2014). 1 cm^3 subsamples were initially taken with a plastic syringe at 8 cm intervals down the length of both sediment cores for pre-analysis of diatom presence and abundance in the sediments. Only one site (Lake Dangovavy) had notable diatom preservation which was then used to conduct analysis at the same intervals as the pollen analysis (4 cm intervals) and even increased to 2 cm intervals in the section that showed significant changes (DAN core from 30 to 0 cm). Samples were then chemically and physically treated to remove extraneous materials so as to concentrate the diatoms in the sample. The process consisted of first removing organic matter and carbonates in the samples by using hydrogen peroxide (H_2O_2) 30%, and hydrochloric acid (HCl) 10%, respectively. Coarse organic (roots) and mineral matter were then removed by sieving the sample with a 300 μm mesh. Following which, samples were swirled for a few seconds in the beaker before being decanted to remove fine mineral and sand. The final process consisted of removing clays and finer mineral matter in the samples. Samples were decanted, refilled, suspended and settled overnight (8 hours) with the process being repeated several times until they were clean (supernatant clear). Diatom slides were mounted in Pleurax which allows for observing characteristic details of diatom taxa under an optical microscope (Vojíř, 2017). The Pleurax used was characterised with Retractive Index (R.I.) equal to 1.73.

Diatoms were counted at magnification 1000x with a minimum standard count of 300 valves (Battarbee, 1986). Diatom value was expressed as a percentage of total diatoms counted including fragments with the valve central area or a single characteristic feature of the valve present (e.g. Gordon, García-Rodríguez & Adams, 2012) (Equation 9). The relative abundance data was used because it provide an optimal tracking of environmental stress (Kireta et al., 2012). The identification of diatom species was based on the key and photos from Metzeltin & Lange-Bertalot (2002). Other published literature including some dataset of modern diatom in Africa associated with their environmental information were used, such as

Gasse, Juggins and Khelifa (1995) and Taylor, Harding and Archibald (2007). In addition, known and published diatom data catalogues were used, including *Diatoms of North America* (https://diatoms.org/) and Digital herbarium hosted by the Academy of Natural Sciences of Drexel University (ANS) in Philadelphia, PA, USA (http://dh.ansp.org/dntf). Diatoms were classified into two ecological groups, namely planktonic and benthic. Planktonic species are defined as diatom taxa that float freely in open water often interpreted and associated with a deep water (Wolin & Stone, 2010). Benthic species are composed of taxa that are fixed in specific substrates (Julius & Theriot, 2010) and are further divided into two main sub-groupings which are periphytic and aerophilic. Periphytic diatom describes community taxa that reside on the lake's bottom and dominate shallow water (Vannote et al., 1980), while aerophilic taxa are found in subaerial habitats commonly used to indicate shallower waters and even drought events (Gaiser & Rühland, 2010).

Equation (9):

$$Diatom\ abundance\ (\%) = \frac{ni}{N} \times\ 100$$

Where: *ni* and *N* are the absolute frequency of the taxa *i* and *N* the total diatom

3.5 Data handling

Palynomorph data in sediment cores collected in the Central Highlands of Madagascar were plotted in a diagram against age using C2 software version 1.5 (Juggins, 2003). Pollen and diatom results were expressed as relative frequency which considers the abundance of taxa relative to one another and shows well the dynamism of each pollen/diatom taxa over time. Taxa with relative abundance higher than 2% were used to assess changes in pollen and diatom assemblage over time. This is particularly important for pollen where there was a need to exclude rare taxa and the influence of long-distance pollen that might cause a misinterpretation of the local plant community (Sugita, 1994). Pollen data were grouped according to their ecological affiliation such as forest, heathland and grassland to evaluate the relative abundance changes of each ecosystem over time as the nature of the landscape is poorly understood. The identified pollen taxa were grouped based on current vegetation distribution in the region and also referring to vegetation surveys that have been conducted during the initial fieldwork around the study site. On the other hand, diatoms were grouped as a function of their habitat to represent hydrological changes in the landscape in order to better understand climate variability in the region over time. Planktonic diatoms represent the taxa abundant in deeper water while benthic, particularly aerophilic taxa, represent diatoms in more shallow water environments (Vos & de Wolf, 1993; Gaiser & Rühland, 2010).

Charcoal and coprophilous spore data were both expressed as a concentration in particles.cm^{-3} and spores.cm^{-3}, respectively. This was done to allow comparison between proxies but also to avoid biases linked to the variable sediment accumulation and the uncertainties associated with the chronology of the analysed core. On the other hand, coprophilous spores were expressed as a concentration because the abundance of one coprophilous spore taxon relative to another is unimportant as all spores indicate the dynamism of herbivore activities over time regardless of particular taxa.

3.6 Numerical analyses

3.6.1 Zonation techniques

Data analyses of the TAMB$_2$ and DAN sediment cores were conducted in the open-source statistical software program R version 4.0.4 (R Core Team, 2021). Palynomorph data were transformed using the function “decostand” in the Hellinger method to consider the zero values in the data (e.g. Razanatsoa et al., 2021). To identify the significant stratigraphic changes in the pollen assemblage, zonation techniques based on cluster analyses were used. (Legendre & Birks, 2012), particularly to identify major shifts in vegetation in the study sites over time. This was based on the stratigraphy constrained cluster analysis using the function “chclust” in CONISS method with Euclidean distance (Grimm, 1987; Bennett, 1996) through the “Analogue” package (Simpson, 2007).

3.6.2 Rarefaction analysis and Beta diversity

Diversity changes of the vegetation in the Central Highlands of Madagascar was evaluated by rarefaction and beta diversity analyses using the “vegan” package in R. Changes in taxonomic richness over time were measured using rarefaction analysis (Birks & Line, 1992). It was done using the function “rarefy”, commonly used in palaeoecological studies (e.g., Berglund et al., 2008; Meltsov et al., 2011; Giesecke et al., 2012).Numbers of pollen taxa can be influenced by a few dominant taxa. The measurement of pollen evenness considers the presence of rare taxa along with abundance of certain dominant taxa by taking in account the equality of distribution of taxa abundances (Magurran, 2004).

In addition to that, beta diversity was analysed in the sediment cores to measure compositional change over time, using the "decorana" function. The value obtained from detrended canonical analysis first axis (DCA axis 1, as described below) is then transformed using Hill's transformation to evaluate the change on a positive axis (Birks, 2007).

3.6.3 Multivariate analysis

Pearson (standard correlation coefficient) was used to measure the relationship between microcharcoal and macrocharcoal informing the charcoal source either regional or local (Florescu, Vannière & Feurdean, 2018). In the context of the present study, we are expecting a more local signal from the small wetlands in Tampoketsa-Ankazobe (TAMB2) with a relevant source area estimated at 50-100 m from the wetland/lake edge and a more regional signal from the Lake Dangovavy (DAN) between 600 and 800m (Sugita, 1994). Pearson correlation was also conducted between charcoal and coprophilous spore data to evaluate relationship between fire and herbivory activities over time. Statistical analyses were considered significant at a level of 0.05.

Pollen data were square-root transformed to stabilise variances and optimise the signal-to-noise ratio (Marquer et al., 2017). The length of the gradient of the first Detrended Correspondence Analysis (DCA) axis was initially extracted to assess whether pollen data fit a linear or unimodal model (Birks & Gordon, 1985). With our sediment cores, the gradient lengths of the pollen data were less than three (03) standard deviations (SD) of compositional turnover, which justified the use of the linear-based method for our datasets (Smilauer & Leps, 2014).

The linear method used includes a Principal Component Analysis (PCA) and Redundancy Analysis (RDA). The PCA was used to analyse the distribution of pollen and their supposed environmental parameters such as altitudes, water availability and openness of the vegetation in the study sites over time. It was done using the function "prcomp" in the "factorextra" package (Kassambara, 2017) to highlight the contribution of variables in the principal component. On the other hand, the RDA was used to test and quantify the impact of fire, herbivory activities, and climate on the Holocene vegetation composition in the Central Highlands of Madagascar.

The RDA summarises linear relationships between components of response variables that are "redundant" with a set of explanatory variables. The RDA explains how much of the variances can be explained by the explanatory variables. The RDA method generates two ordinations, one in the space defined by the response variables matrix, and the other in the space defined by the explanatory variable matrix. Within our dataset, charcoal, coprophilous spores and diatoms, which indicate fire, herbivory activities and hydrological change, respectively, were classified as explanatory variables while pollen (vegetation) represented response variables. The analysis was done using “rda” function in the “vegan” package.

Chapter 4 TAMPOKETSA-ANKAZOBE WETLAND RESULTS

4.1 Introduction

This chapter presents the results of palaeoecological analyses conducted on the sediment core from the Tampoketsa-Ankazobe wetland (TAMB$_2$ core) collected in the eastern slopes of the Central Highlands of Madagascar. Results are structured as follows: description of the stratigraphy and sedimentology, chronology of the sediment core, fossil pollen and stable carbon isotopes results for vegetation dynamics, charcoal (macro- and microcharcoal) for fire history (local and regional) and coprophilous spores for herbivory activities. It also includes the statistical and multivariate analyses to assess the relationship between pollen, charcoal and coprophilous spore data.

4.2 TAMB$_2$ stratigraphy and sedimentology

4.2.1 TAMB$_2$ Troels-Smith

The description of sediment was based on the modified description of Troels-Smith (1955). The sediment generally consisted of organic clay with the presence of detritus plants through the entire core. Eleven layers (named TAMB$_2$-I to TAMB$_2$-XI) were observed through the length of the 99 cm sediment core. Each section was characterised by the type and size of mineral particles and plant fragments present as well as the colour of sediment. These lithological information, and the raw ages from radiocarbon dates (see details in section 4.3), are provided in Table 4.1 and Figure 4.1. Starting from the bottom of the core, TAMB$_2$-I (99-91.5 cm) was dark grey with an abundance of fine sand and more visible plant detritus. TAMB$_2$-II (91.5-87.5 cm) and TAMB$_2$-III (87.5-77 cm) were lighter and clayey, with a decrease in plant fragment size (< 2 mm) in TAMB$_2$-III. The following layer, TAMB$_2$-IV (77-71 cm) was dominated by fine sand and more visible plant fragments. The colour of the sediment became darker in colour and was maintained from this section towards the top of the sediment core. In the following two layers, TAMB$_2$-V (71-58.5 cm) and TAMB$_2$-VI (58.5-49 cm) the sediment became more clay-rich containing some detritus of plants which was less and more than 2 mm, respectively. However, TAMB$_2$-VII (49-43.5 cm) was characterised by the dominance of fine sand with smaller sized plant detritus. The next layer, TAMB$_2$-VIII (43.5-32.5 cm), was clay-rich containing fragments of plants less than 2 mm.

An abundance of sand was noted in TAMB$_2$-IX (32.5-19 cm) with a small size (< 2 mm) of plants fragments. The last two layers TAMB$_2$-X (19-4 cm) and TAMB$_2$-XI (4-0 cm) were clay-rich with small plant fragments (< 2 mm) and roots. Apparent charcoal fragments were visible on the top layer. Most of the changes in the physical description of the sediment were noted in TAMB$_2$-I, TAMB$_2$-IV, TAMB$_2$-VII and TAMB$_2$-IX, which were characterised by an abundance of sand rather than clay as compared to the rest of the core. The layers TAMB$_2$-IV and TAMB$_2$-IX coincided with the main pollen zone transition which is discussed in detail in section 4.4.1).

Table 4.1: Lithological description of the sediment core collected at Tampoketsa-Ankazobe in the eastern slopes of the Central Highlands of Madagascar

Depth (cm)	Layer	Troels-Smith	Description	Munsell colour name
0-4	TAMB$_2$-XI	As2, Ld^{2}1, Th^{2}1	Clayey, strongly humified with roots and rootlets of herbaceous plants. Presence of charcoal debris.	5Y 2.5/1 Black
4-19	TAMB$_2$-X	As2, Dg2, Ld^3	Clayey, strongly humified with detritus or fragments of ligneous and herbaceous plants < 2 mm.	2.5Y 2.5/1 Black
19-32.5	TAMB$_2$-IX	Ga2, As1, Dg1,	Sandy with detritus or fragments of ligneous and herbaceous plants < 2 mm.	10YR 2/1 Black
32.5-43.5	TAMB$_2$-VIII	As2, Dg1, Ga1, Ld^1	Clayey, medium humified with detritus or fragments of ligneous and herbaceous plants < 2 mm and fine sand.	10YR 2/1 Black
43.5-49	TAMB$_2$-VII	Ga2, As1, Dg1	Sandy with detritus or fragments of ligneous and herbaceous plants < 2 mm.	10YR 3/1 Very dark grey
49-58.5	TAMB$_2$-VI	As2, Ld^{0}1, Th^{2}1	Clayey, strongly humified with roots, rootlets and detritus plants and maybe animals.	5Y 2.5/1 Black
58.5- 71	TAMB$_2$-V	As2, Ga1, Dg1, Ld^1	Clayey, medium humified with detritus of ligneous and herbaceous plants < 2 mm and fine sand.	5Y 3/1 Very dark grey
71-77	TAMB$_2$-IV	As2, Ga2, Tl^2	Sandy with rootlets of ligneous plants.	5Y 4/1 Dark grey
77-87.5	TAMB$_2$-III	As3, Dg1	Very clayey, weakly humified with detritus of ligneous and herbaceous plants < 2mm.	2.5Y 5/2 Greyish brown
87.5-91.5	TAMB$_2$-II	As3, Ga1, Tl^2	Clayey, weakly humified with some fine sand and detritus of rootlets of ligneous plants.	2.5Y 4/1 Dark grey
91.5-99	TAMB$_2$-I	As1, Ga2, Dg1	Sandy with fragments of ligneous and herbaceous plants.	2.5Y 3/1 Very dark grey

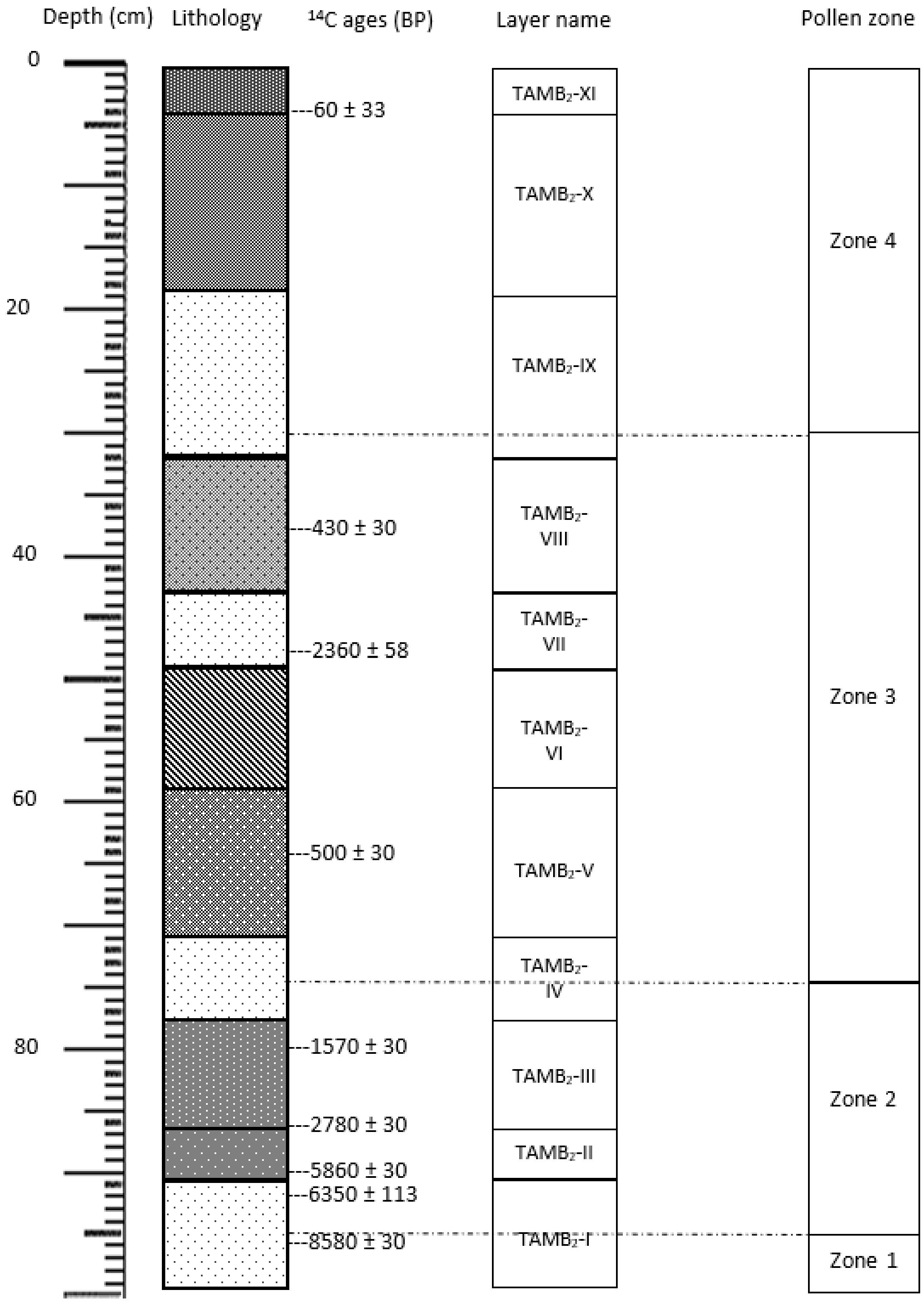


Figure 4.1: Tampoketsa-Ankazobe wetland lithology based on Troels-Smith classification with uncalibrated dates, layer name and main pollen zones. The graphical symbols are a representation used to differentiate the various layers and do not conform to Troels-Smith (1955)

4.2.2 TAMB$_2$ Loss on Ignition

The Loss on Ignition (LoI) estimates the bulk density, water content, total soil organic carbon (TOC) and inorganic carbon (TIC) content in the sediment (see Chapter 3). Results from the TAMB$_2$ core indicated a mean± standard deviation (SD) bulk density of 1.2±0.1% g.cm^{-3} of wet weight per unit volume of fresh sediment. The bulk sediment was abundant at the bottom and low toward the top of the core (Figure 4.2). However, moisture content tended to increase towards the top through the entire sediment core. A slight peak in the water content was noted at 56 cm with a value of 54.5%, but the highest value of water content was recorded at the top of the core (80.6%). Furthermore, the TAMB$_2$ core contained a high TOC) with a mean±SD of 17.1±1.8% compared to the TIC, of 2.3±0.2%. Both TOC and TIC tended to increase towards the top of the core with a slight peak at 56 cm (19.5% TOC and 3.5% TIC). Carbon content increased from 8 cm for TOC and 12 cm for TIC toward the top, reaching maximums of 50% and 5.3%, respectively.

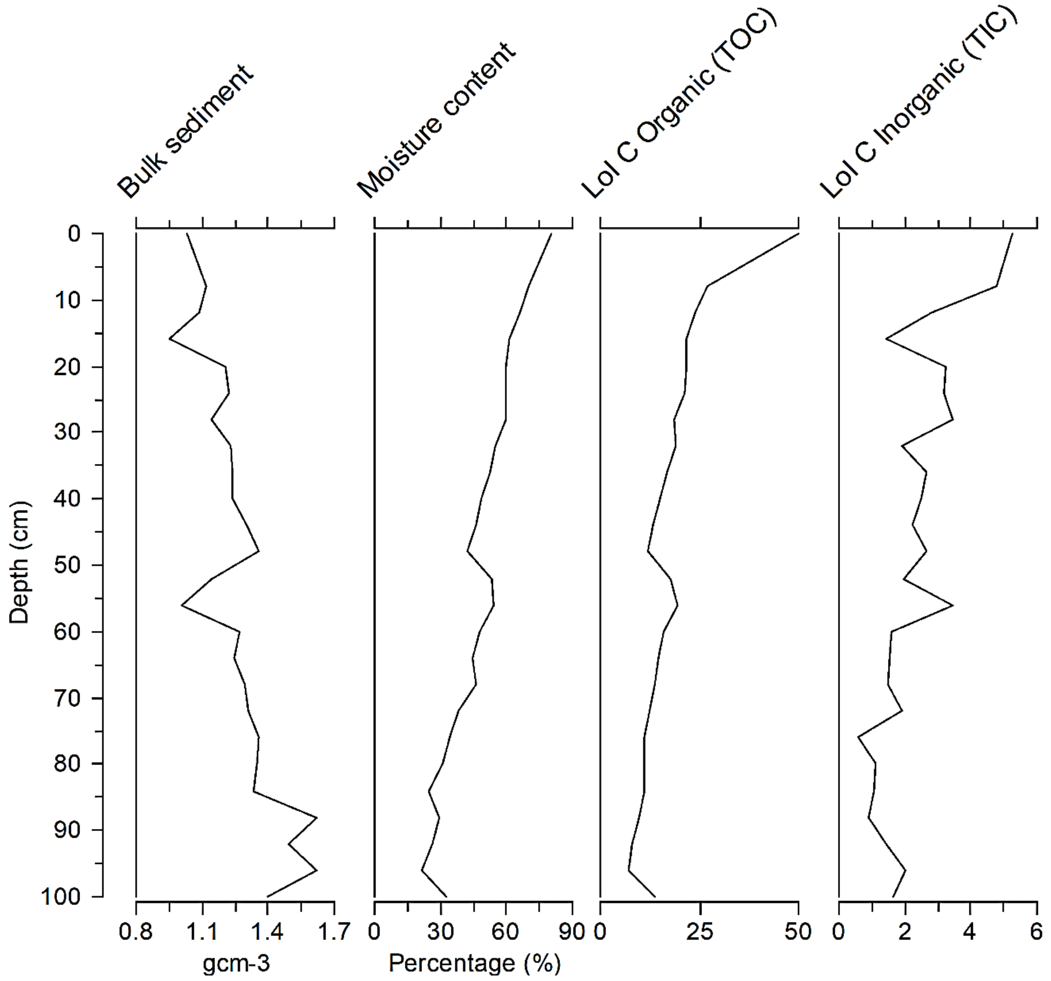


Figure 4.2: Tampoketsa-Ankazobe Loss on Ignition (LoI) results indicating the bulk density, water content and the carbon content namely Total Organic Carbon (TOC) and Total Inorganic Carbon (TIC).

4.3 TAMB2 chronology and sediment accumulation

Nine samples taken from the TAMB2 sediment core were AMS radiocarbon dated, (Table 4.2). From the Clam age-depth model, the bottom of the sediment core (99 cm) was dated to ca. 11 200 cal years BP (Figure 4.3). The depth 48 cm (IT–C–1487) uncalibrated date 2 360±58 showed a reversal age relative to the other ages. In addition, based on the appearance of exotic taxa in the pollen record, this age was too old and therefore considered as an outlier and excluded from the age-depth model. This was also verified by the Bayesian model run in Bacon (Appendix 2). The modelled accumulation rate varied from ca. 3 to 600 yrs.cm^{-1} in the TAMB2 core over time (Figure 4.3). Accordingly, six successive phases were recorded from the bottom to the top of the sediment core. A very low sediment accumulation rate was observed (ca. 600 yrs.cm^{-1}) from ca. 11 200 to 7000 cal years BP.

A slight increase of ca. 300 $yrs.cm^{-1}$ was recorded between ca. 7000 to 6000 cal years BP and the accumulation rate then slowed again between ca. 6000 to 1400 cal years BP, with a value of ca. 500 $yrs.cm^{-1}$. From ca. 1400 cal years BP to the present period, a massive increase in the sediment accumulation rate was noted in the $TAMB_2$ core with 50 $yrs.cm^{-1}$ (ca. 1400-500 cal years BP), 3 $yrs.cm^{-1}$ (ca. 500-400 cal years BP), 10 $yrs.cm^{-1}$ (ca. 400 to 100 cal years BP) and 30 $yrs.cm^{-1}$ from ca. 100 cal years to the top.

*Table 4.2: Tampoketsa-Ankazobe uncalibrated and calibrated radiocarbon dates obtained from bulk sediment samples. Upper and lower calibrated ages are provided in cal years BP. * indicates date that has been excluded from the age model and considered as an outlier.*

Depth (cm)	Sample label	Laboratory ID	C14 age (yr BP)	1 sigma error	95% calibrated age range (cal years BP)	Probability (%)
04	AMB2_3-5	IT–C–1513	60	33	33-139	68.4
37	AMB2_36-38	Beta – 554610	430	30	452-526	90.8
48	AMB2_47-49	IT–C–1487	2360*	58	2305-2539	75.8
64	AMB2_64	Beta – 476891	500	30	502-550	95
80	AMB2_80	Beta – 480141	1570	30	1387-1524	95
86	AMB_86	Beta – 554611	2780	30	2784-2956	75.5
90	AMB2_90	Beta – 495512	5860	30	6620-6747	90.5
92	AMB2_91-93	IT–C–1486	6350	113	6989-7433	93.2
96	AMB2_96	Beta – 463279	8580	30	9521-9557	90.8

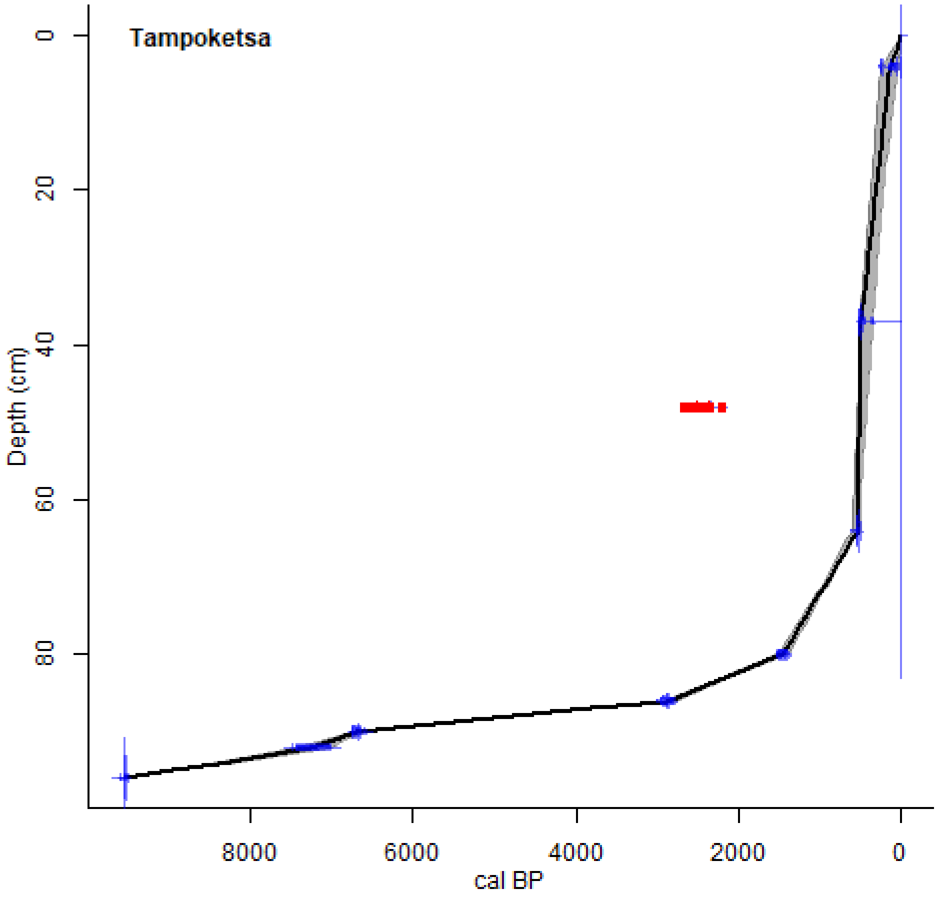


Figure 4.3: Tampoketsa-Ankazobe (TAMB2) age-depth model. Blue represents measured AMS radiocarbon ages, grey indicates the calibration range and red represents the outliers, which were subsequently excluded from the analysis.

4.4 TAMB$_2$ pollen and stable isotope (carbon δ^{13}C and C-N ratio) results

Pollen and stable isotope analyses in the Tampoketsa-Ankazobe sediment core were conducted every 4 cm throughout the core. The total pollen sum (TPS) included terrestrial taxa and undifferentiated pollen i.e. broken and rare undefined pollen. Therefore, aquatic pollen was excluded from the TPS, and discussed separately, as their abundance does not reflect changes in terrestrial vegetation. A minimum of 300 pollen grains per level in each sample provided a total of 8499 terrestrial pollen counted in TAMB$_2$ sediment core, equivalent to a mean±SD of 326±1 pollen per level. The stable isotope including carbon (δ^{13}C) and C-N ratio were analysed in the same level as pollen and had a mean±SD of -16.6±0.4‰ and mean±SD of 20.4±1, respectively.

4.4.1 TAMB$_2$ pollen zones

Based on the stratigraphy constrained cluster analysis, four statistically significant cluster zones (TAMB$_2$-01 to TAMB$_2$-04; Figure 4.4), were identified in the pollen assemblage of the Tampoketsa-Ankazobe sediment core. These zones represent the major grouping of the pollen assemblage representing the vegetation in the region over the last ca. 11 200 cal years BP based on the ecological affinities and abundance of taxa recorded in the sediment. The first pollen zone, TAMB$_2$-01, represents the age interval between ca. 11 200 to 8300 cal years BP. The second and third, TAMB$_2$-02 and TAMB$_2$-03 span the periods from ca. 8300 to 1000 cal years BP and 1000 to 350 cal years BP, respectively. The last zone TAMB$_2$-04, is recorded from 350 cal years BP to the present period.

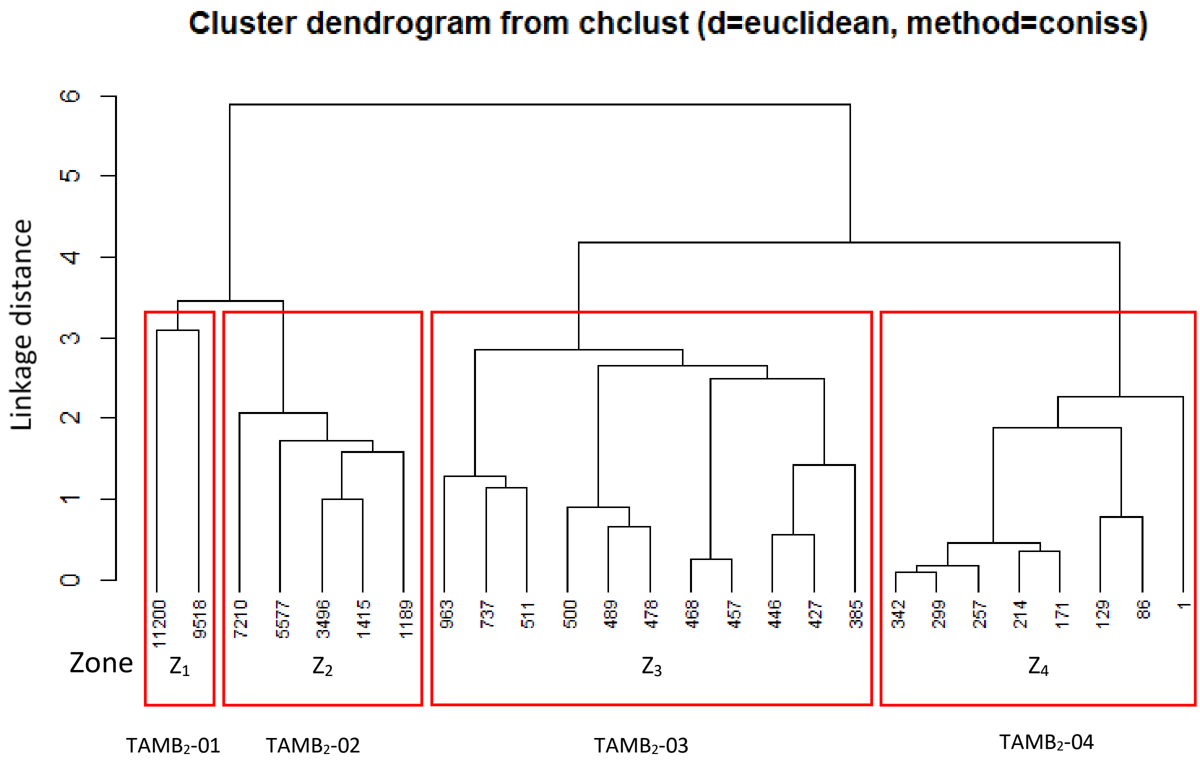


Figure 4.4: Tampoketsa-Ankazobe hierarchical clustering analysis based on Euclidean distance and the coniss method of the pollen taxa assemblages. The red rectangles indicate the boundaries between each cluster or pollen zone.

4.4.2 TAMB$_2$ pollen diagram: pollen abundance and stable isotopes (carbon δ^{13}C and C-N ratio)

Pollen and stable carbon isotope results reflected the vegetation dynamics in Tampoketsa-Ankazobe wetland and its surroundings over the last ca. 11 200 cal years BP. Based on the TAMB$_2$ pollen zones (Figure 4.4), four major shifts in vegetation occurred in the landscape over time. Figure 4.5 represents the pollen diagram of abundant terrestrial pollen ($\geq 2\%$) in each zone, together with the stable carbon isotope results and the C/N ratio, justifying the source of δ^{13}C value (Bonn & Rounds, 2010). The relative abundances of some rare and exotic taxa, are presented in section 4.4.3.

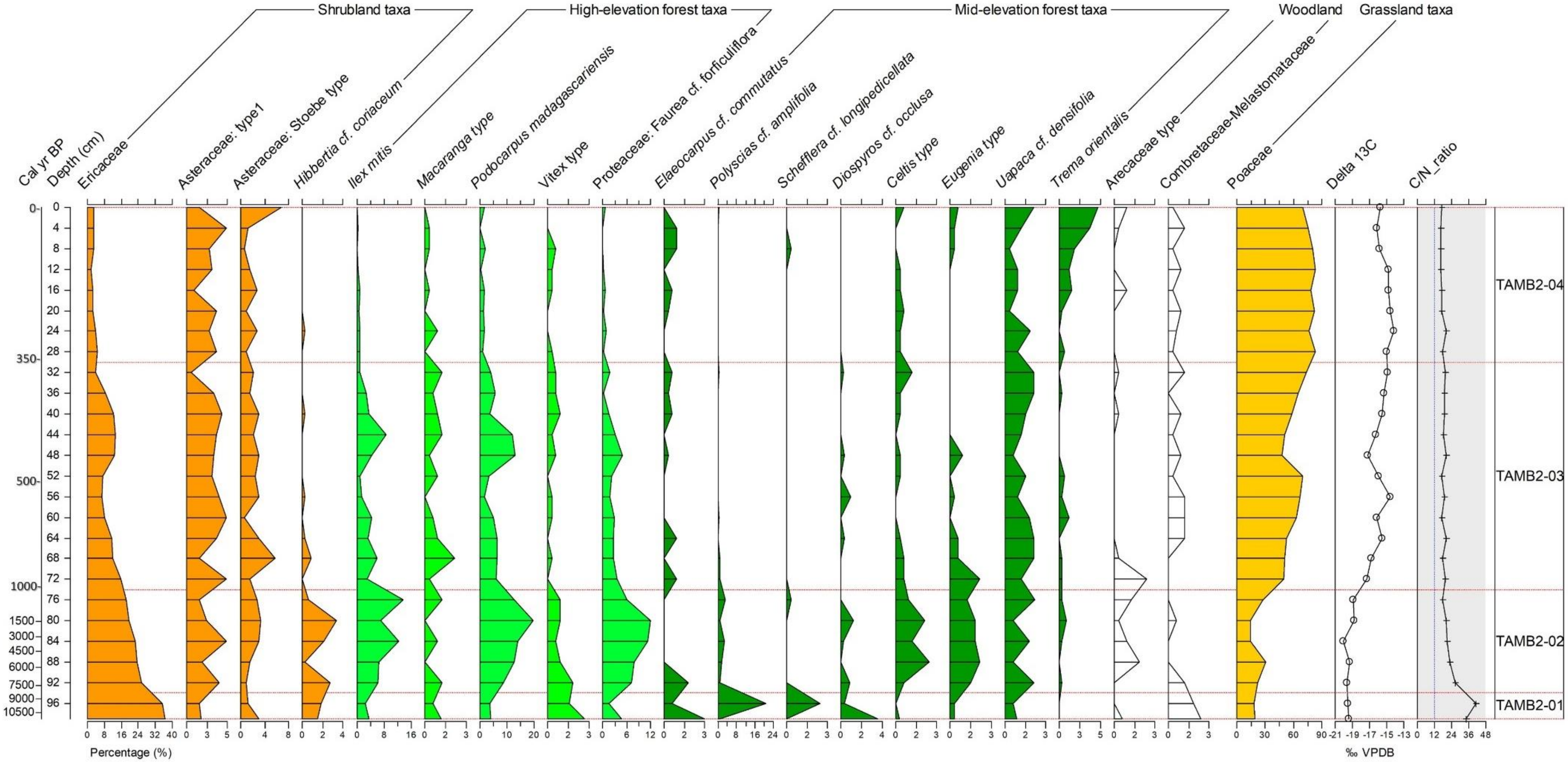


Figure 4.5: Tampoketsa-Ankazobe pollen diagram with pollen taxa ≥2% grouped in their ecological affiliations. Shrubland taxa in orange, High-elevation forest taxa in lawn green, Mid-elevation forest taxa dark green, Wooded grassland in white, and Grassland in yellow. The $\delta^{13}C$ stable isotope results are represented by the graph line with circle symbol, while the C/N ratio is displayed in the grey box

- **TAMB$_2$-01 pollen zone: From 11 200 to 8300 cal years BP:**

The pollen signal of the first zone was characterised by the high abundance of pollen identified as within the Ericaceae family and some arboreal forest taxa. The Ericaceae pollen presented a mean±SD value of (36±0.5%) of pollen abundance and reached its maximum (36.4%) during the Early Holocene (ca. 11 000 cal years BP). The arboreal taxa were mostly characterised by an abundance of mid-elevation forest taxa particularly the species *Polyscias* cf. *amplifolia* pollen with a peak relative abundance of 20.7% observed at ca. 9500 cal years BP. Also, some mid-elevation species like *Elaeocarpus* cf. *commutatus*, *Diospyros* sp. and *Schefflera* cf. *longipedicellata* characterised the period, giving the mid-altitude taxa a total pollen sum (TPS) of 17.7%. The woodland and grassland taxa were low during the period with TPS of 2.4% and 18.7%, respectively. The woodland was characterised by Combretaceae-Melastomataceae pollen with a mean±SD relative abundance of 2.1±0.3%. The grassland vegetation was comprised by the Poaceae pollen (mean±SD, 18.7±0.5%). Grass pollen was relatively low in abundance during this period compared to the pollen rain from surface samples pre-dominantly covered with grasslands on the island (Burney, 1988; Straka, 1991; Razafimanantsoa, 2015). The stable carbon isotopes ($\delta^{13}C$) results had a mean±SD value of -19.5±0.1‰ and the ratio carbon-nitrogen (C/N) had mean±SD value of 37.5±3.7.

- **TAMB$_2$-02 pollen zone: From 8300 to 1000 cal years BP:**

This period was still characterised by the dominance of Ericaceae pollen, and some arboreal forest taxa compared to woodland and grassland taxa. In contrast to the previous period, Ericaceae pollen decreased with a mean±SD value of 21.9%, while the arboreal forest taxa increased, particularly high-elevation taxa with a TPS of 32.5%. The relative abundance of high-elevation arboreal taxa was exemplified by peaks of *Podocarpus madagascariensis* (19.5%) and Proteaceae: *Faurea* type (11.9%) around 1400 cal years BP. An increase in Asteraceae pollen was also recorded during the period with a mean±SD value of 5.3±1.1%. The woodland taxa remained low with 1.2% of the TPS during this period. Grassland taxa were characterised by a slight increase compared to the previous period but remained low with a mean±SD of 21.9±3.3%. However, it is worth noting that a slight increase of Poaceae was recorded at ca. 4000 cal years BP. The stable carbon isotope results did not change too much compared to the previous period with a mean±SD value of -19.4±0.2‰. The C/N ratio value was high with a mean±SD value of 21.8±1.5.

- **TAMB$_2$-03 pollen zone: From 1000 to 350 cal years BP:**

The period was characterised by a decrease relative abundance of Ericaceae pollen and arboreal forest taxa with 10.2% and 16.6% of the TPS, respectively, and a massive increase of grassland taxa with a mean±SD value of 59±2.8%. In the shrubland, Ericaceae pollen was half of the previous period, while the Asteraceae pollen remained almost the same (mean±SD 5.9±0.7%). For the forest taxa, high- and mid-elevation arboreal taxa were reduced to 12.5% and 4.1% of the TPS, respectively. The woodland taxa remained low as in the previous period. Grassland taxa, characterised by Poaceae pollen, increased enormously during this period with a first peak recorded at ca. 480 cal years BP characterised by a relative abundance of 70%. The abundance of grassland taxa during this period was correlated with a shift to more enriched carbon isotope value with a mean±SD value of -15.9±0.3‰. The C/N ratio value was still relatively high and presents a mean±SD of 18.8±0.3.

- **TAMB$_2$-04 pollen zone: From 350 cal years BP to the present period:**

This last period was characterised by a very low relative abundance of shrubland, forest and woodland taxa, but a high relative abundance of grassland taxa. The Ericaceae dropped dramatically with a mean relative abundance of 3±0.3%, while Asteraceae pollen remained the same as during the previous period (5.1±1.2%). However, the forest taxa i.e., high- and mid-elevation taxa, were both very low and represented 2.2% and 3.9% of the TPS, respectively. It is worth noting that *Trema* cf. *orientalis* pollen started to increase in the pollen record from ca. 150 cal years BP and reached its maximum at the present period with a relative abundance of 4.6%. Woodland taxa (Combretaceae and Arecaceae) remained low as during the previous periods. Grassland taxa, characterised by Poaceae pollen, was very dominant with a mean±SD relative abundance of 79±1.6% reaching a peak (82.8%) at ca. 150 cal years BP. The high abundance of grass pollen taxa was associated with a more enriched value of the stable carbon isotope results with a mean±SD value of -15.1±0.3‰. The C/N ratio value was as high as the previous period with a mean±SD value of 17.4±0.4.

4.4.3 TAMB2 aquatic and rare terrestrial pollen and exotic taxa

The abundance of aquatic, rare terrestrial and exotic pollen taxa recorded in the Tampoketsa-Ankazobe wetland during the Holocene is provided in Figure 4.6. Pollen of aquatic plants was represented by Cyperaceae and *Myriophyllum* type in the $TAMB_2$ sediment core. The rare terrestrial pollen (relative abundance < 2%) was composed of some characteristic pollen taxa in the area (Ratsirarson & Goodman, 2001). Exotic pollen are represented by *Eucalyptus* and *Pinus* currently observed in the landscape. According to the pollen zone (section 4.4.1), from ca. 11 200 to 1000 cal years BP ($TAMB_2$-01 and $TAMB_2$-02) the aquatic and exotic pollen were negligible and even absent, respectively. However, some arboreal tree rare characteristic taxa were present, such as Anacardiaceae and Flacourtiaceae family represented by *Eugenia* and *Homalium* type pollen, respectively. The next pollen zone ($TAMB_2$-03) showed an increase of aquatic pollen taxa reaching a peak at ca. 450 cal years BP with 4.9% of the TPS. The exotic tree taxa remained negligible (~0.3%), but some fire resistant or adaptive rare taxa increased, such as *Weinmannia*, *Dombeya* and *Justicia*. The last pollen zone, from 350 cal years BP to the present period ($TAMB_2$-04), was characterised by the highest value of aquatic pollen in the region with a mean±SD value of 4.3±0.8%, reaching its maximum at ca. 100 cal years BP (7.7% of the TPS). This zone was also marked by slight presence of exotic tree taxa in the pollen diagram with a maximum TPS value of 1.5% at the present period. However, the shrub and rare characteristic tree taxa decreased toward the present period.

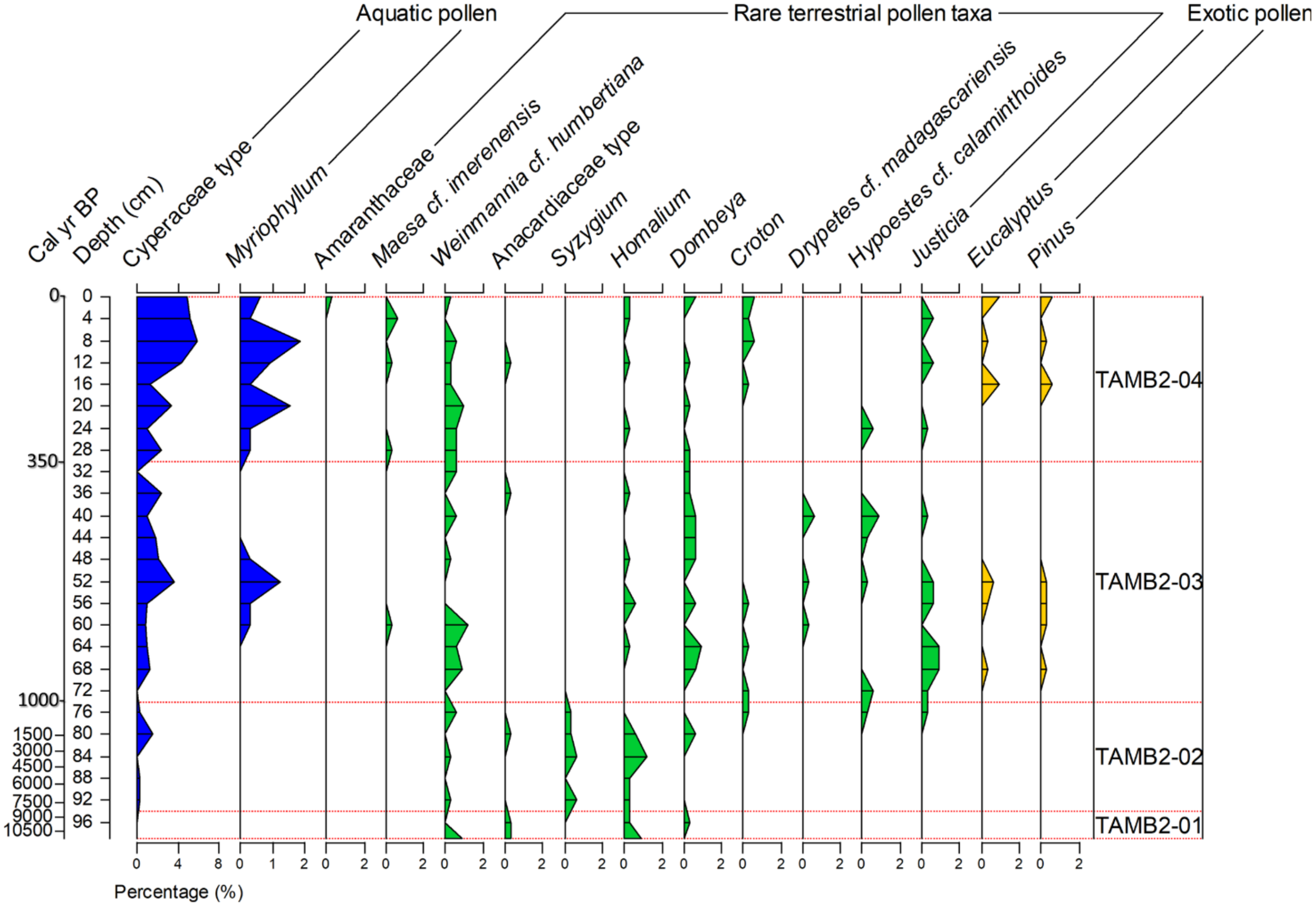


Figure 4.6: A pollen diagram illustrating the mean relative abundances (%) of aquatic (blue), rare (green) and exotic (yellow) pollen taxa over the last ca. 11 200 cal years BP from a sediment core extracted at the Tampoketsa-Ankazobe wetland.

4.4.4 TAMB$_2$ pollen richness, evenness and beta diversity

The rarefaction analysis of the Tampoketsa-Ankazobe pollen data showed a pattern of decreasing pollen richness over time (see Figure 4.7). TAMB$_2$-01 presented the highest pollen richness recorded with a mean±SD of 33±4 pollen types reaching its maximum at ca. 11 200 cal years (37 pollen types). TAMB$_2$-02 and TAMB$_2$-03 indicated moderate pollen richness with a mean±SD value of 29±2 and 28±1 pollen types, respectively. Two main peaks were recorded during those zones, which were at ca. 7200 and 480 cal years BP. The last zone (TAMB$_2$-04) was characterised by the lowest pollen richness recorded over time with a mean±SD value of 25±1 pollen types. It is worth noting that a slight peak was recorded at ca. 200 cal years BP with a value of 29 pollen types. Pollen richness and evenness showed the same trend which decreased toward the present period. The pollen evenness in Tampokesta-Ankazobe was very low during the last ca. 350 cal years BP.

The beta diversity analysis revealed two main compositional changes over time (Figure 4.7). The first one was recorded between TAMB$_2$-02 and TAMB$_2$-03 at ca. 1000 cal years BP with the highest value over time, which was 2.9 SD (Standard Deviation). This was associated with the pollen and stable carbon isotope results, which indicated a shift in the vegetation from a C_3 dominated to a C_4 dominated landscape in the pollen and carbon isotope results. A second moderate change occurred at 350 cal years BP between TAMB$_2$-03 and TAMB$_2$-04 with a value of 1.6 SD, characterised by the abundance of Poaceae pollen in the record (see section 4.4.2).

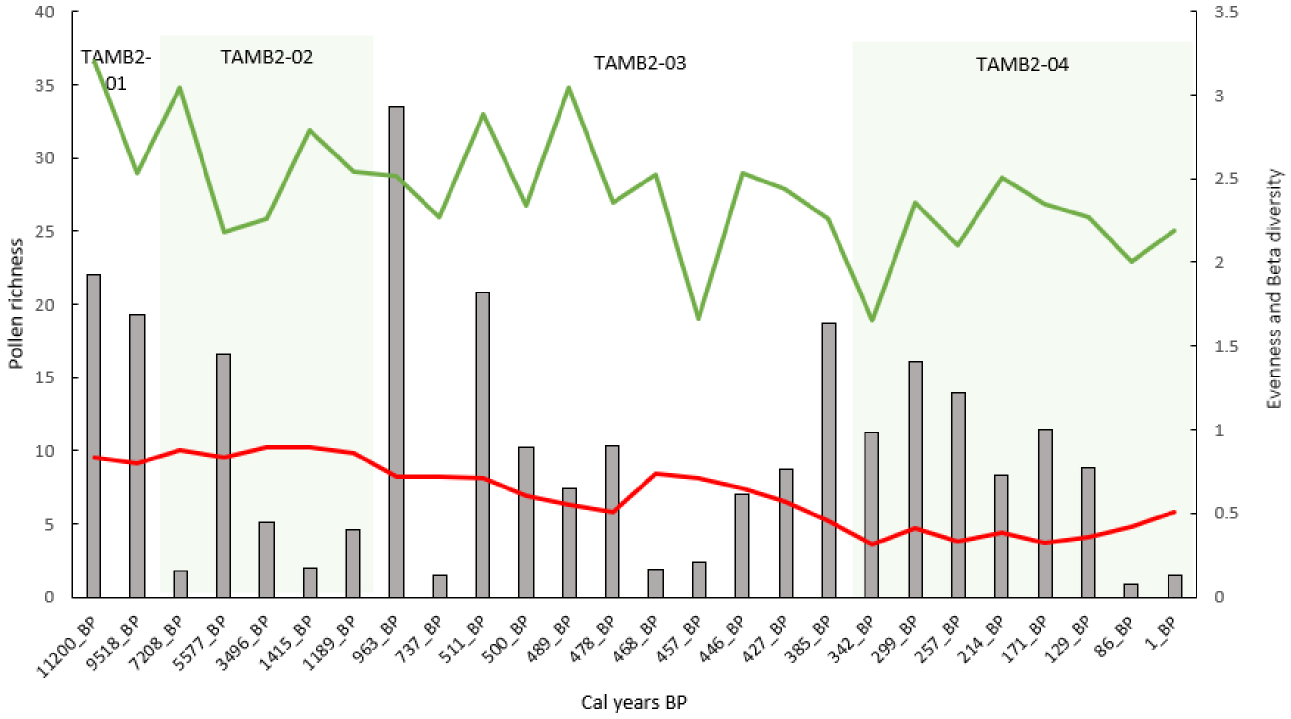


Figure 4.7: Tampokesta-Ankazobe pollen richness, evenness, and the compositional change (Beta diversity) over the last ca. 11 200 years. The green line represents pollen richness while the red represents pollen evenness. Grey bar represents the beta diversity.

4.5 TAMB$_2$ charcoal and coprophilous spores results

This section presents the charcoal i.e. macro- and microcharcoal, and coprophilous spores results in the Tampoketsa-Ankazobe wetland over the last ca. 11 200 cal years BP. Analyses of charcoal and coprophilous spores concentration were conducted at the same temporal resolution as the pollen (every 4 cm) and were used to understand fire history and herbivory activities, respectively.

4.5.1 TAMB$_2$ charcoal results

Macro- and microcharcoal analysis of the Tampoketsa-Ankazobe wetland showed an increasing rate of charcoal concentration in the area towards the present period. Regarding the macrocharcoal results, a total of 6024 charcoal particles were counted, equivalent to a mean±SD of 232±44 charcoal particles.cm^{-3}. Meanwhile, a total volume of 16 797.5 cm^{2}.cm^{-3} of microcharcoal was counted, equivalent to a mean±SD of 646±75.5 particles charcoal.cm^{-3}, were counted with the macrocharcoal.

Macrocharcoal and microcharcoal were present with very low values in the first two pollen zones but increased substantially in the last two zones (Figure 4.8). For $TAMB_2$-01, the mean±SD concentrations of macro and microcharcoal values were 34±6 particles.cm^{-3} and 56.1±8.3 cm^{2}.cm^{-3}, respectively. A slight increase in the concentration of macrocharcoal, but still low, was present in the $TAMB_2$-02 layer with a mean±SD value of 66±20 particles.cm^{-3} while a slightly larger increase in the concentration of microcharcoal was evident (157 ± 46.9 cm^{2}.cm^{-3}). However, $TAMB_2$-03 was characterised by an apparent increase of charcoal in the region with mean±SD values of 234±67 particles.cm^{-3} (macrocharcoal) and 702.6±90.9 cm^{2}.cm^{-3} (microcharcoal). Two peaks of charcoal concentration were recorded in the Tampoketsa-Ankazobe sediment core during the period. The first peak was recorded at ca. 1000 cal years BP, starting with the microcharcoal (1111.8 cm^{2}.cm^{-3}), and the second peak at ca. 500 and 350 cal years BP for macrocharcoal with a value of 450 and 516 charcoal particles.cm^{-3}, respectively. The last zone ($TAMB_2$-04) was dominated by an abundance of charcoal in the area with a mean±SD macrocharcoal concentration value of 382±145 particles.cm^{-3} and a mean microcharcoal concentration of 1021.4±61.7 cm^{2}.cm^{-3}. The current period was characterised by peaks in concentrations of the mean±SD values of macrocharcoal (1072 particles.cm^{-3}) and microcharcoal (1281.9cm^{2}.cm^{-3}), which are indicative of an increase in fire occurrence at the local and regional scales, respectively.

4.5.2 $TAMB_2$ coprophilous spores results

The concentration of coprophilous spores in the Tampoketsa-Ankazobe wetland core displayed a similar increasing trend towards the present period, as for charcoal concentration. A total of 2100 coprophilous spores were counted in the entire sediment core, equivalent to a mean±SD spore concentration of 31.1±4.4x10^{3} spores.cm^{-3}. Results showed that the concentration of coprophilous spores was very low for the first two- pollen zones i.e., $TAMB_2$-01 and $TAMB_2$-02 at ca. 11 200 to 1000 cal years BP, with a mean±SD value of 1.16±0.4x10^{3} and 3.9±0.9x10^{3} spores.cm^{-3}, respectively (Figure 4.8). Between ca. 1000 and 350 cal years BP ($TAMB_2$-03), coprophilous spores increased moderately in concentration with a mean value of 7.7±1x10^{3} spores.cm^{-3}. This increase was mostly evident by *Coniochaeta* sp., which presented a mean value of 4.4±0.6 spores.cm^{-3}. During the last ca. 350 cal years BP ($TAMB_2$-04 pollen zone), a very high concentration of coprophilous spores were recorded in Tampoketsa-Ankazobe with a mean±SD value of 18.2±2.1 spores.cm^{-3}.

Two peaks of coprophilous spores were recorded during this last period. The first peak was recorded at ca. 300 cal years BP with a value of 18.4×10^3 spores.cm^{-3}. The second peak, which was the highest value recorded throughout the entire sediment core, had a value of 29.4×10^3 spores.cm^{-3} at the present period.

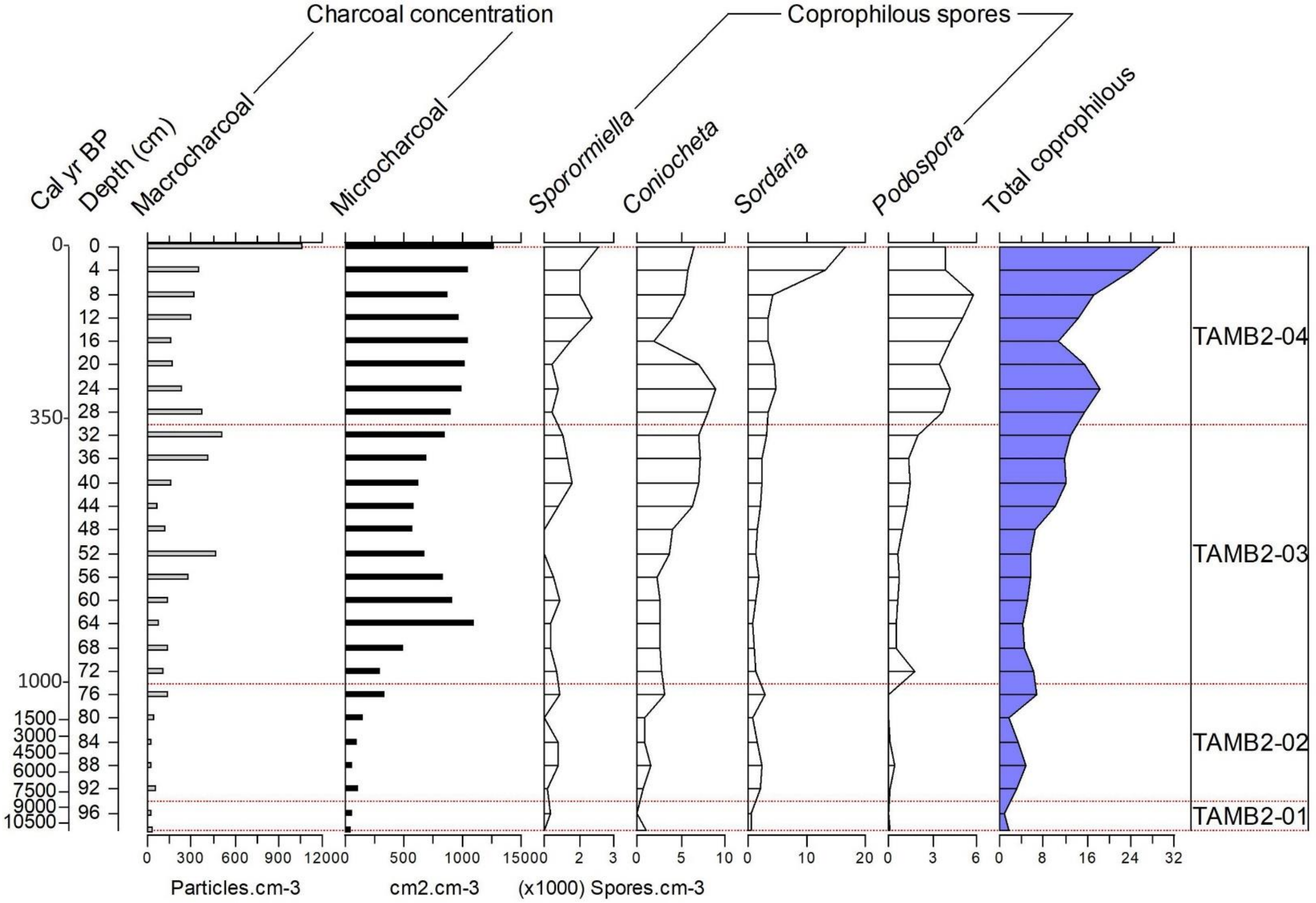


Figure 4.8: Charcoal and coprophilous spores concentration in the Tampoketsa-Ankazobe wetland over time. Macro- and microcharcoal concentration are represented in in grey and black, respectively. Coprophilous spores are represented in white and violet

4.6 TAMB$_2$ multivariate analyses

The gradient length of the first axis of the Detrended Correspondence Analysis (DCA) of pollen taxa was 1.4 SD. This value is less than the 3 SD limits that justify the use of the linear approaches including the Principal Component Analysis (PCA) and Redundancy Analysis (RDA) for Tampoketsa-Ankazobe dataset.

4.6.1 Distribution of pollen in the TAMB$_2$ sediment core

The distribution of the abundant and characteristic rare pollen taxa in the TAMB$_2$ sediment core over time was shown in the PCA (Figure 4.9). Four distinct vegetation types were identified over time: grassland, high- and mid-elevation forest taxa and ericoid shrubland. The first two principal components denoted as PC1 and PC2 explained 71.2% of the variation in the abundance of pollen taxa of the Tampoketsa-Ankazobe core. PC1, which explained 61.5% of the variation, was characterised by a high contribution of Poaceae (grassland), Ericaceae (ericoid shrubland), *Faurea*, *Podocarpus*, *Ilex* cf. *mitis* (high-elevation forest) and *Polyascias* (mid-elevation forest ; Figure 4.10). This component had high negative loadings for Poaceae, which are representative of open grassland, and positive loadings on ericoid shrubland and forest taxa. Based on these findings, PC1 is suggested to represent openness of the vegetation where fire disturbance might be an important environmental variable in the area over time, which has influenced the transition of the vegetation from a more closed-canopy (forest taxa) towards a more open, grassland-dominanted ecosystem. The second component (PC2) explained 9.7% of the variance. PC2 was characterised by a high positive contribution of *Podocarpus*, *Ilex* cf. *mitis* and *Faurea* species that are representative of high elevations (≥ 2000 m a.s.l.; Madagascar Catalogue, 2021). PC2 was also characterised by a high negative contribution of *Polyscias*, Combretaceae and *Schefflera*, which are classified as mid-elevation forest taxa (800-1300m a.s.l.; Figure 4.9 and 4.11). PC2 might reflect the elevation range which could potentially be linked to the indirect climate fluctuation and its contribution to the distribution of taxa in Tampoketsa-Ankazobe.

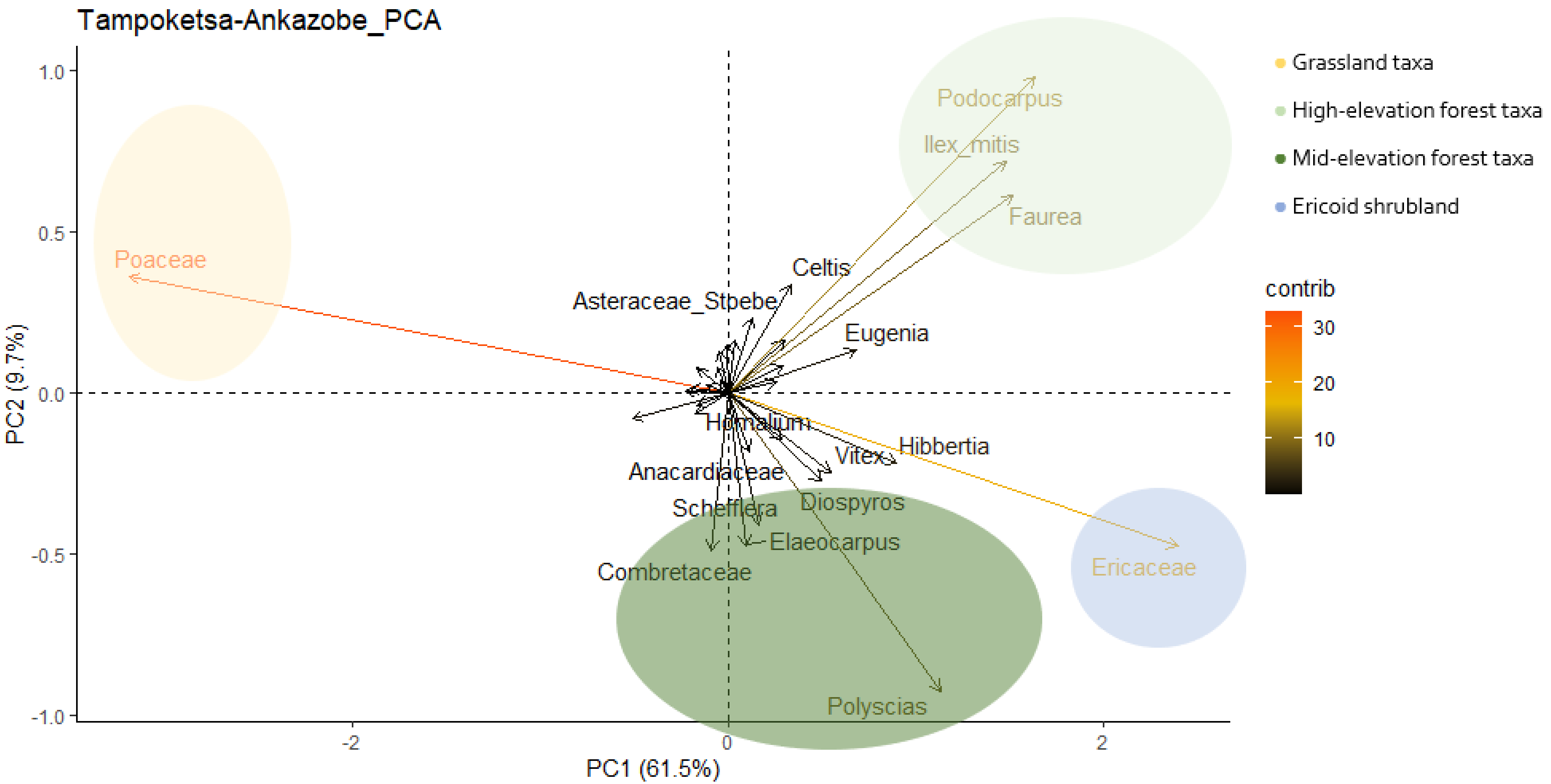


Figure 4.9: A Principal Component Analysis (PCA) determining the distribution of pollen taxa in a sediment core sampled from the Tampoketsa-Ankazobe wetland. The colour gradient represents the contribution of each taxa to the axis components: (Lowest contribution=black to high contribution=orange).

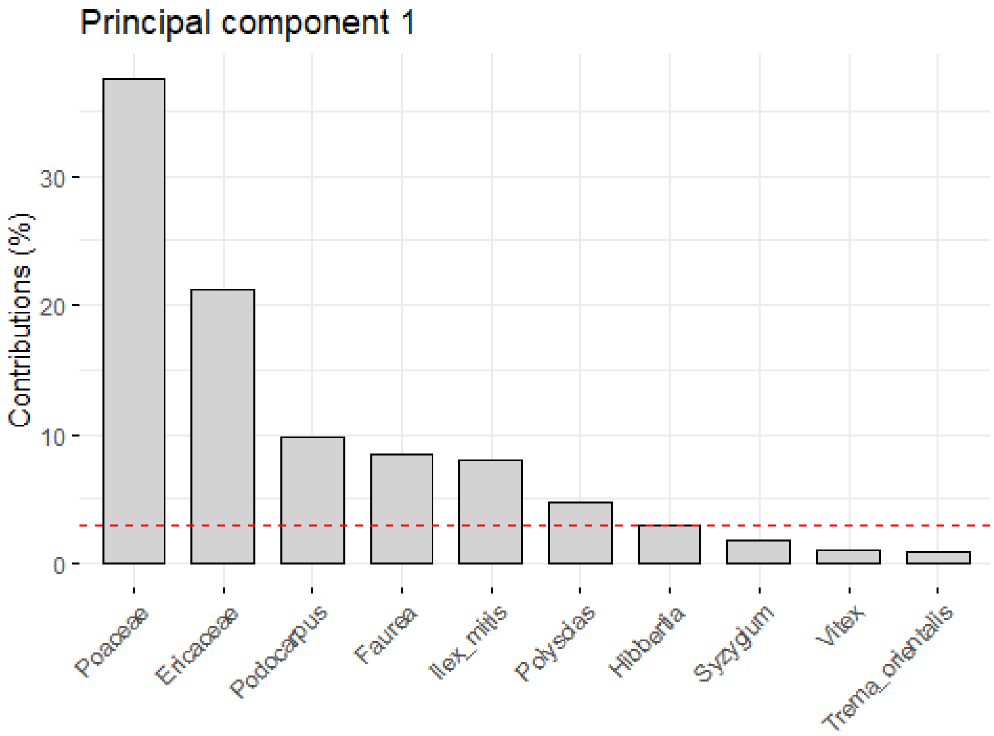


Figure 4.10: Contributions of individual pollen taxa from Tampoketsa-Ankazobe record on the first principal component (PC1). Variables above the red dashed line contributed considerably towards explaining the variation in pollen abundance (61.5%).

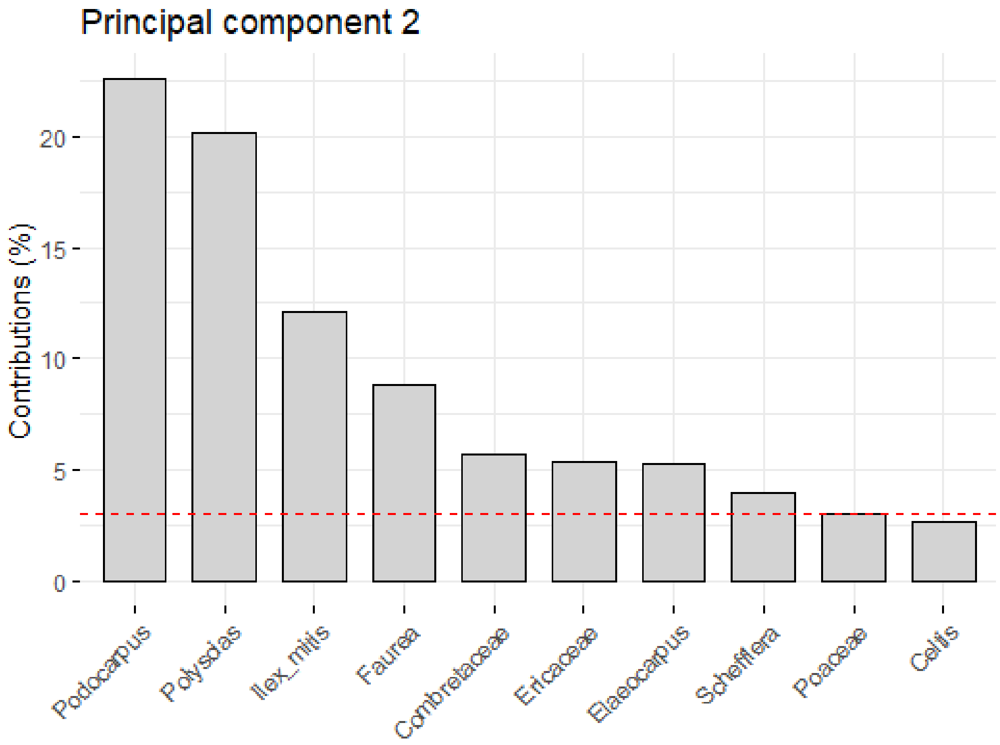


Figure 4.11: Contributions of individual pollen taxa from Tampoketsa-Ankazobe record on the second principal component (PC2). Variables above the red dashed line contributed considerably towards explaining the variation in pollen abundance (9.7%).

4.6.2 Univariate relationships between pollen, charcoal and coprophilous spores

4.6.2.1 Relationship between macrocharcoal and microcharcoal

There was a significant positive correlation between macrocharcoal and microcharcoal concentration sampled from the sediment core at *Tampoketsa-Ankazobe* sediment core ($p < 0.001$; $r = 0.6$; $R^2 = 0.4$; $n = 26$; Figure 4.12) and this still the same even if the sample at the top (0cm) was considered as an outlier and therefore removed from the analysis (see Appendix 4).

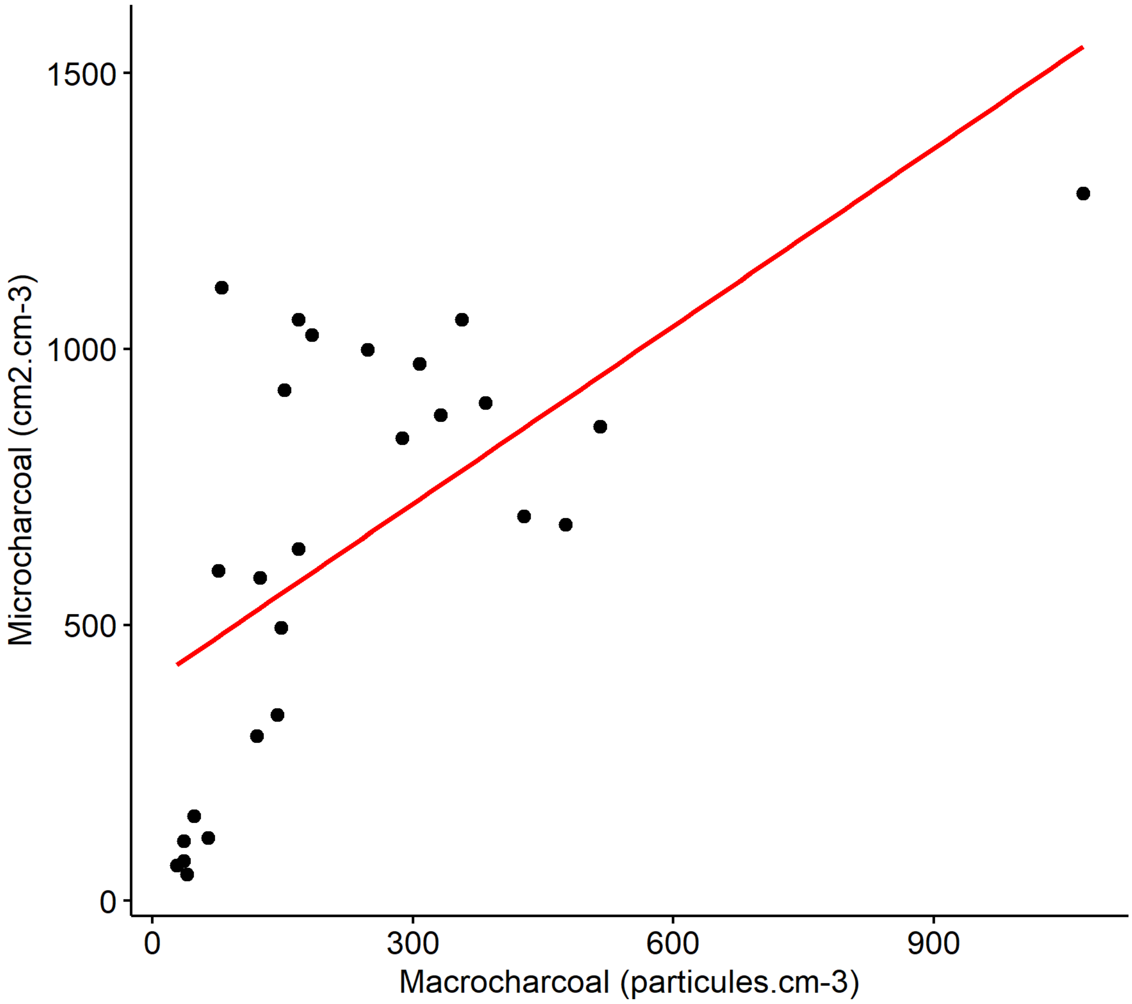


Figure 4.12: Pearson correlation and linear regression between macrocharcoal and microcharcoal particles from the Tampoketsa-Ankazobe core spanning from ca. 11 200 cal years BP to the present time (n=26).

An R^2 value of 0.4 means that only ca. 40% of the observed variation can be explained by the model's inputs. By considering this, and the pollen zone, we analysed a separate correlation between microcharcoal and macrocharcoal before and after ca. 1000 cal years where charcoal was low and high, respectively. Results showed that before ca. 1000 cal years BP ($TAMB_2$-01 and $TAMB_2$-02), there was a strong significant positive correlation between macrocharcoal and microcharcoal ($n = 7$; $r = 0.9$; $R^2 = 0.9$; $p < 0.001$; Figure 4.13a). However, after ca. 1000 cal years BP ($TAMB_2$-03 and $TAMB_2$-04), where charcoal values were high, the correlation between macrocharcoal and microcharcoal was positive but not significant ($n = 19$; $r = 0.5$; $R^2 = 0.2$; $p = 0.05$) (Figure 4.13b).

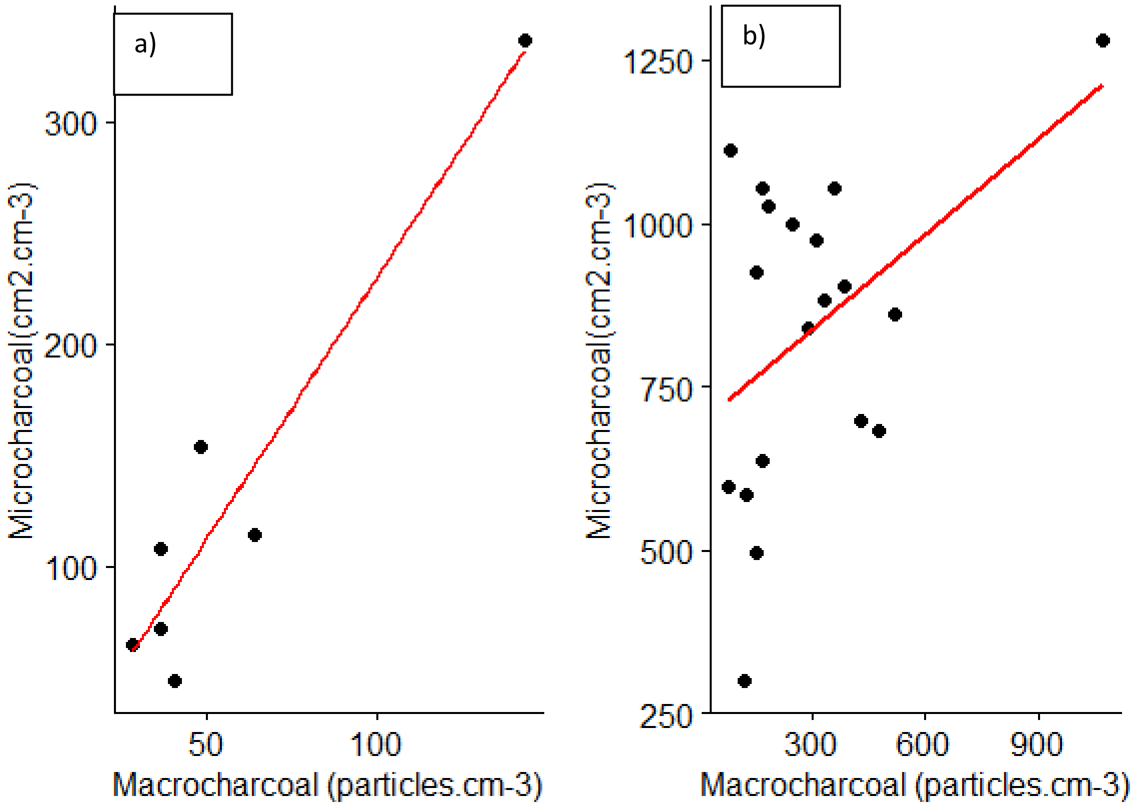


Figure 4.13: Pearson correlation and linear regression between macrocharcoal and microcharcoal particles from the Tampoketsa-Ankazobe core: a) before (n=7) and b) after (n=19) ca. 1000 cal years BP

4.6.2.2 Relationship between coprophilous spores and charcoal

There were positive and significant correlations between coprophilous spores and macrocharcoal ($n = 26$; $r = 0.8$; $R^2 = 0.6$; $p < 0.001$) and microcharcoal ($n = 26$; $r = 0.7$; $R^2 = 0.6$; $p < 0.001$) data in the Tampoketsa-Ankazobe core (Figure 4.14). The mean increase in macrocharcoal and microcharcoal for every additional one coprophilous spores.cm^{-3} is 0.5 particles.cm^{-3} and 0.3 cm^{2}.cm^{-3}, respectively.

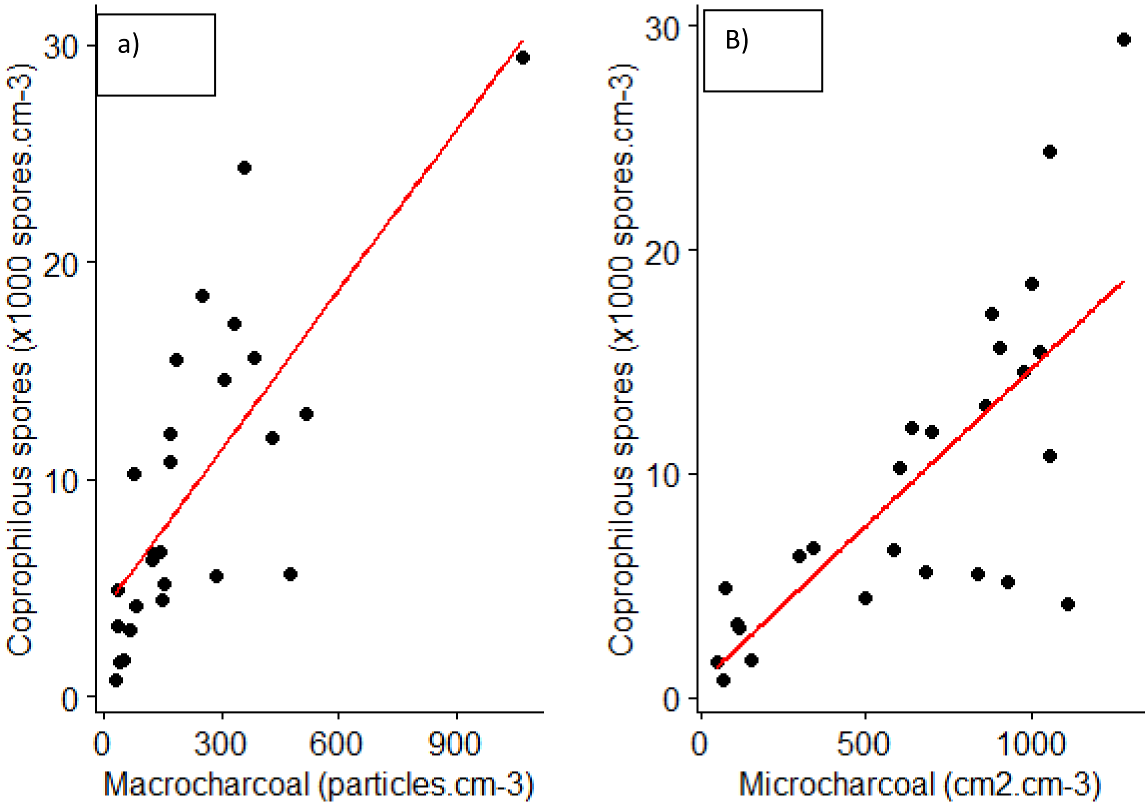


Figure 4.14: Pearson correlation and linear regression between charcoal and coprophilous spores from the Tampoketsa-Ankazobe core: a) Microcharcoal and coprophilous spores (n=26)and b) Macrocharcoal and coprophilous spores (n=26).

4.6.2.3. Relationship between pollen, charcoal and coprophilous spores

The Redundancy Analysis (RDA) showed the impact of predictor variables (macro-, microcharcoal and coprophilous spores) on the variation of pollen data in Tampoketsa-Ankazobe wetland over time. The result showed that the three variables explained 57.4% of the variance by dividing the constrained value with the total variance (inertia) (25/43.5) from the RDA output (Table 4.3). The first constrained axis (RDA1) explained 54.7% (23.8/43.5) of the variance while RDA2 and RDA3 explained 1.8% and 0.9%, respectively.

Table 4.3: The Redundancy Analysis (RDA) output for the variation of pollen explained by charcoal (macro- and microcharcoal) and coprophilous spores in Tampoketsa-Ankazobe wetland

	Inertia	Proportion
Total	43.5150	1
Constrained	25.0435	0.5755
Unconstrained	18.4715	0.4245

Eigenvalues for constrained axes		
RDA1	RDA2	RDA3
23.849	0.818	0.376

By projecting the RDA results with the pollen zones (Figure 4.15), it was noted that these predictor variables were associated to the openness of the ecosystem noted in pollen zone 4 (TAMB$_2$-04) and zone 3 (TAMB$_2$-03) characterised particularly by the abundance of Poaceae. Pollen zone 2 (TAMB$_2$-02) and zone 1 (TAMB$_2$-01) were not explained by the predictor variables, suggesting that other environmental variables different than charcoal (macro- and microcharcoal) and coprophilous spores in the area before ca. 1000 cal years BP.

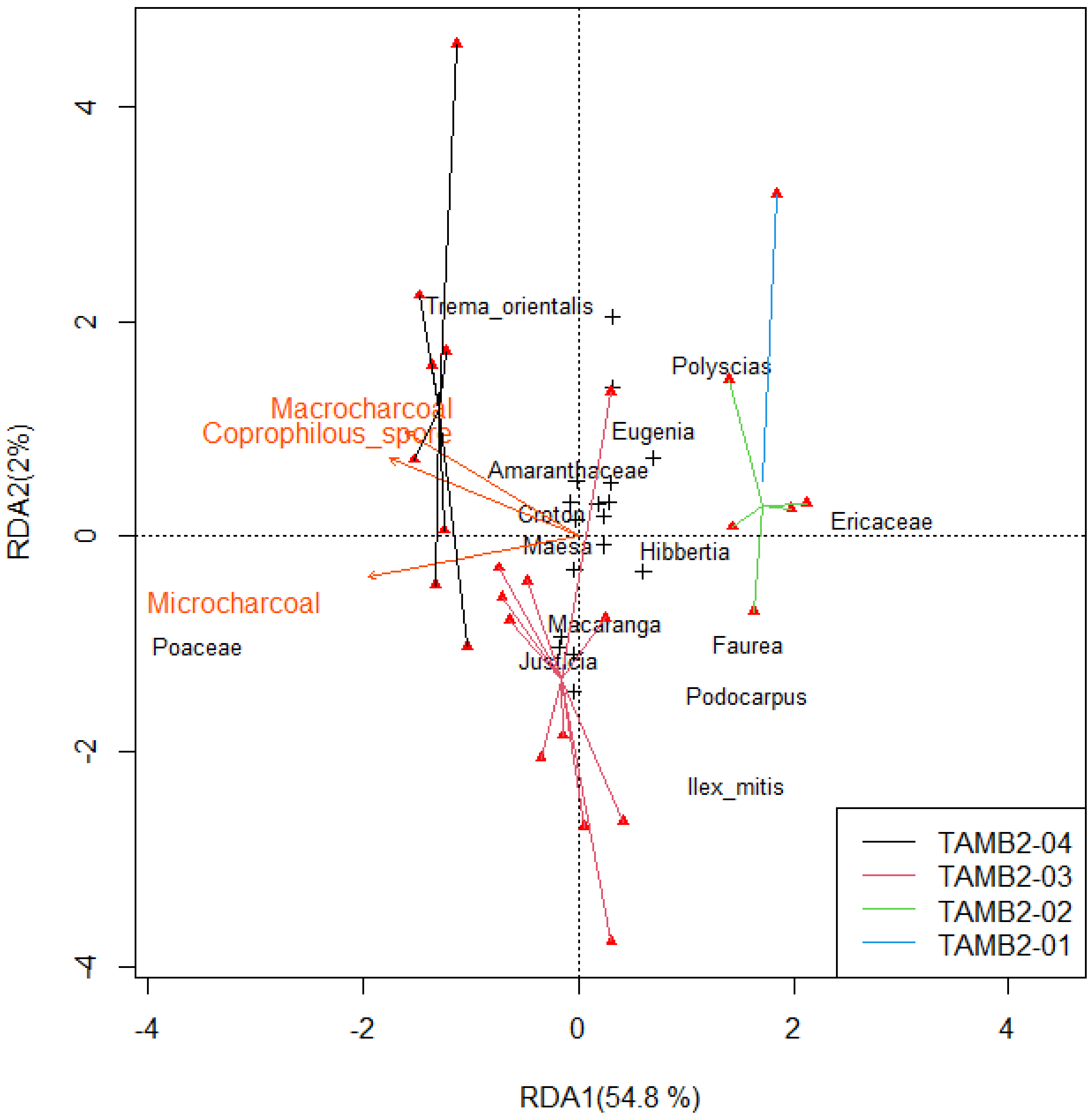


Figure 4.15: Redundancy Analysis (RDA) ordination plot of abundant and selected rare pollen taxa against macro- and microcharcoal and coprophilous spores from the Tampoketsa-Ankazobe core. Pollen zones are represented by blue, green, red and black ordispider for zone_1 to zone_4, respectively.

4.7 TAMB$_2$ overall synthesis of pollen, stable carbon isotopes, charcoal and coprophilous spores results

During the last ca. 11000 cal years BP in Tampoketsa-Ankazobe wetland, the abundance of Ericaceae pollen decreased while grass pollen increased over time. In general, forest pollen taxa decreased except *Uapaca* cf. *densifolia* species which remained more stable with the Asteraceae during the entire period. Pollen richness and evenness decreased over time and it coincided with general trend from C_3 to C_4 plants dominated. Macro- and microcharcoal data increased towards the present period, and it correlated to each other’s and also to the increase of coprophilous spores over time.

Chapter 5 LAKE DANGOVAVY RESULTS

5.1 Introduction

This chapter provides palaeoecological analyses conducted on the sediment core collected from Lake Dangovavy (DAN core) situated on the western slopes of the Central Highlands of Madagascar. It starts with a description of the stratigraphy, sedimentology and chronology of the sediment core. It is then followed by a description of the pollen and stable carbon isotope results for vegetation dynamics, microscopic charcoal (macro- and microcharcoal) for fire, coprophilous spores for herbivory activities and diatoms for hydrological change over time. Finally, statistical and multivariate analyses are conducted to evaluate the distribution of pollen taxa, and their relationship with the predictor variables.

5.2 DAN stratigraphy and sedimentology

5.2.1 DAN Troels-Smith

Based on a modified version of Troels-Smith (1955), the 110 cm core collected from Lake Dangovavy was composed by 10 different stratigraphic layers, named DAN-I to DAN-X from the bottom (110 cm) to the top (0 cm). In general, the DAN core contained organic clay mud with plant fragments, pieces of charcoal, coarse fine sands, and gravel in some layers. The abundance of these components, and the variation in colour of the sediment through the length of the core, characterised each layer (Table 5.1; Figure 5.1). The base of the core, as defined by the layer, DAN-I (110-93.5 cm), was brown and clayey containing some plant fragments. DAN-II (93.5-86 cm) was still clayey but became grey and contained some fine sands in addition to plant fragments. The next layer, DAN-III (86-82.5 cm), was still grey but was characterised by an abundance of coarse sand and gravel. DAN-IV (82.5-60.5 cm) was darker grey and characterised by the presence of rootlets, fine plant fragments and coarse sand. DAN-V (60.5-47.5 cm) was similar to the first layer (DAN-I), and DAN-VI (47.5-38 cm) to the third layer (DAN-III). A high calcareous component dominated the DAN-VII (38-29.5 cm) and DAN-VIII layers (29.5-18 cm). DAN-VII was grey and had more abundant plant fragments compared to DAN-VIII, which was darker. From 18 cm to the top, the sediment was darker and contained more clayey with a presence of plant fragments. DAN-IX (18-4.5 cm) and DAN-X (4.5-0 cm) differed by the presence and absence of fine sands, respectively.

Most notable changes in the physical properties of the sediment occurred in the layers DAN-III (86-82.5 cm) and DAN-VI (47.5-38 cm), which were dominated by coarse sand and gravel, rather than soils. A major change was also noted between DAN-VIII and DAN-IX (ca. 18 cm) where the sediment changed from a high calcareous component to a clay-rich sediment. These changes were in agreement with the transition between pollen zones (Figure 5.1; refer to section 5.4).

Table 5.1 : Lithological description of the sediment core collected at Lake Dangovavy in the western slopes of the Central Highlands of Madagascar

Depth (cm)	**Layer**	**Troels-Smith**	**Description**	**Munsell colour name**
0-4.5	DAN-X	As2, Lf1, Ld^{1}1	Clayey, ferruginous and fine fragments of herbaceous and ligneous plants.	2.5Y 3/1 Very dark grey
4.5-18	DAN-IX	As1, Lf1, Th^{3+}1 Ga1	Clayey, ferruginous with plant fragments and fine sand.	5Y 3/1 Very dark grey
18-29.5	DAN-VIII	Lc1, Gg1, Gs1, Th^{2+}1	Calcareous with a few plant fragments and some coarse sand and gravel. Visible charcoal fragments noticed.	10YR 3/2 Very dark greyish brown
29.5-38	DAN-VII	Lc1, Gg1, Gs1, Th^{3+}1	Calcareous with fragments of herbaceous and ligneous plants and coarse sand and gravel present. Presence of visible charcoal fragments.	2.5Y 5/1 Grey
38-47.5	DAN-VI	As2, Gg1, Gs1	Clayey with an abundance of coarse sand and gravel.	2.5Y 5/1 Grey
47.5-60.5	DAN-V	As3, Dg1	Very clayey and ferruginous with fragments of ligneous and herbaceous plants.	10YR 4/3 Brown
60.5-82.5	DAN-IV	Ld^{3+}1, Gs1, Th^{4+}1, Tl^{4+}1	Clayey with rootlets and very fine fragments of ligneous and herbaceous plants. Presence of coarse sand.	5Y 3/1 Very dark grey
82.5-86	DAN-III	As2, Gg1, Gs1	Clayey with an abundance of coarse sand and gravel.	2.5Y 5/1 Grey
86-93.5	DAN-II	As3, Ga1	Very clayey with fine sand and few plant fragments.	5Y 5/1 Grey
93.5-110	DAN-I	As3, Dg1	Very clayey and ferruginous with fragments of ligneous and herbaceous plants.	10YR 4/3 Brown

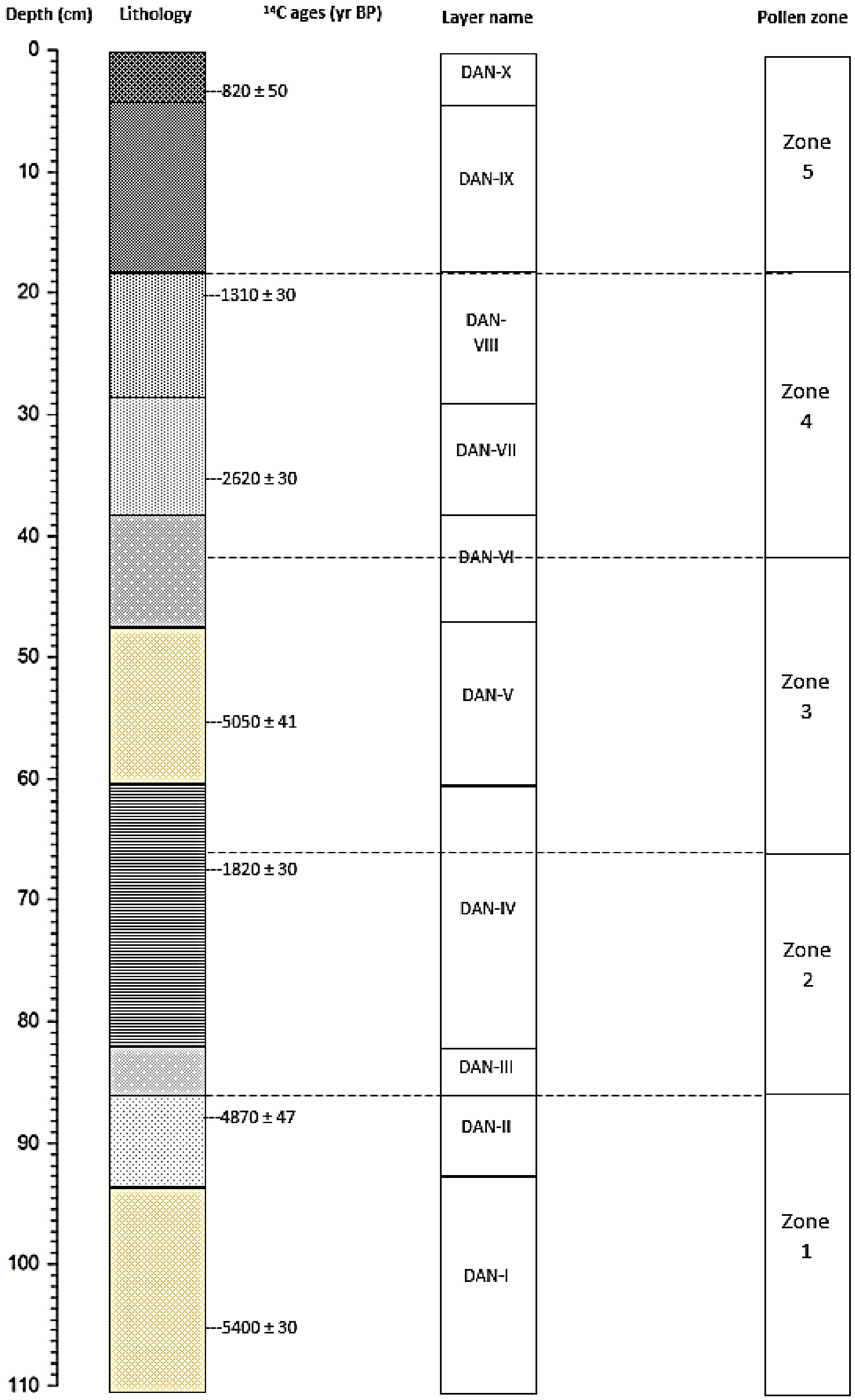


Figure 5.1: Lake Dangovavy lithology based on Troels-Smith classification with uncalibrated dates, layer name and main pollen zones. The graphical symbols are a representation used to differentiate the various layers and do not conform to Troels-Smith (1955).

5.2.2 DAN Loss on Ignition

Results from DAN sediment core showed a mean±standard deviation (SD) bulk density of 1.1±0.1% g.cm^{-3} of wet weight per unit volume of the fresh sediment, with a maximum of 1.5 g.cm^{-3} at 72 cm and a minimum of 0.6 g.cm^{-3} at 24 cm (Figure 5.2). The moisture content in the sediment ranged from 73.8% at72 cm to 25.7% at 40 cm, with a mean±SD of 42.1±4.1%. The total soil organic carbon (TOC) was higher than the total inorganic carbon (TIC) with a mean ±SD of 21.4±2.9% and 2.9±0.4%, respectively. In general, the carbon content (organic and inorganic) was low from the bottom of the core until 32 cm. From 32 cm to the top, carbon content increased and peaked at 24 cm (50%) for TOC and at 16 cm (6.9%) for TIC, respectively. A peak of TOC was also observed at 72 cm with a value of 33.3%.

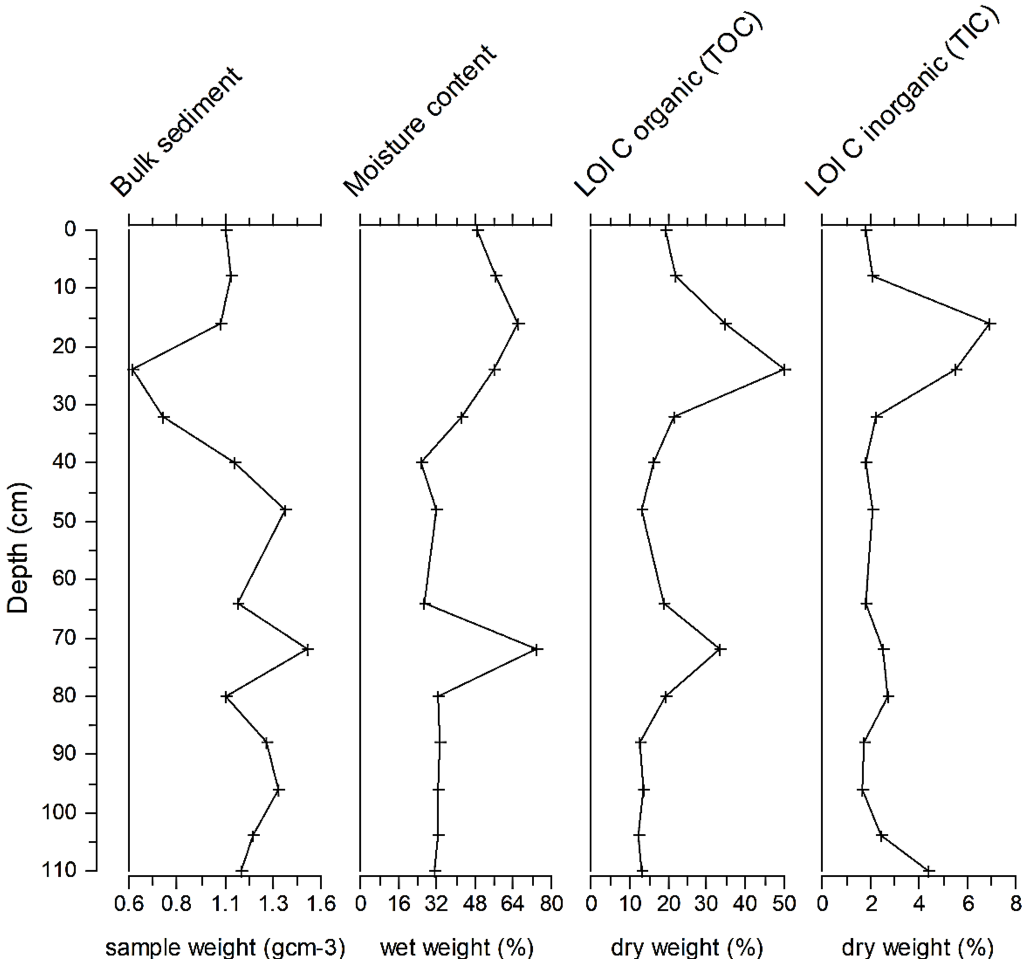


Figure 5.2: Lake Dangovavy Loss on Ignition (LoI) results indicating the bulk density, water content and the carbon content namely Total Organic Carbon (TOC) and Total Inorganic Carbon (TIC).

5.3 DAN chronology and sediment accumulation

Seven samples taken from the DAN sediment core were radiocarbon dated (Table 5.2). Three dates were considered as outliers and were subsequently excluded from the clam age-depth model. Beta–554609 (68 cm) and IT–C–1710 (56 cm) samples showed a reversal age which was possibly due to root contamination. The third outlier, IT–C–1591 (4 cm), was excluded because it was very close to the surface where there was no consolidation of the sediment (Gillson, personal communication 2020, June). These choices were supported by Bacon age-depth model in the Appendix 3 where these dates were excluded automatically through the simulations. Based on the age-depth model run in Clam, the bottom of the core (110 cm) was dated ca. 6200 cal years BP (Figure 5.3). The modelled accumulation rate varied from ca. 33 to 99 yrs.cm^{-1} during this period, which was distributed in four successive phases from the bottom to the top of the core. An accumulation rate of 33 yrs.cm^{-1} was recorded from ca. 6200 to 5500 cal years BP (110-88 cm). From ca. 5500 to 2600 cal years BP (87-36 cm), a slight decrease in the accumulation rate (ca. 55 yrs.cm^{-1}) was observed, and then, the slowest sedimentation accumulation rate (99 yrs.cm^{-1}) was recorded between ca. 2600 to 1200 cal years BP (36-21 cm). The last phase, from 1200 cal years BP (20 cm to the top) indicated a slight increase in the accumulation rate, of ca. 60 yrs.cm^{-1}.

*Table 5.2: Lake Dangovavy uncalibrated and calibrated radiocarbon dates based on bulk sediment samples. Upper and lower calibrated ages are provided in cal years BP . * indicates dates that are excluded from age-detph model and considered as outliers.*

Depth (cm)	Sample label	Laboratory ID	C14 age (yr BP)	1 sigma error	95% calibrated age range (yr BP)	Probability (%)
04	DAN3–5	IT–C–1591	820*	50	669-785	90.6
21	DAN20–22	Beta–554608	1310	30	1242-1293	47.2
36.5	DAN36–37	Beta–525649	2620	30	2723-2772	95
56	DAN55–57	IT–C–1710	5050*	41	5711-5906	90.8
68	DAN67–69	Beta–554609	1820*	30	1695-1793	68.6
88	DAN87–89	IT–C–1589	4870	47	5567-5719	76.9
106.5	DAN106–107	Beta–525650	5400	30	6178-6288	83.8

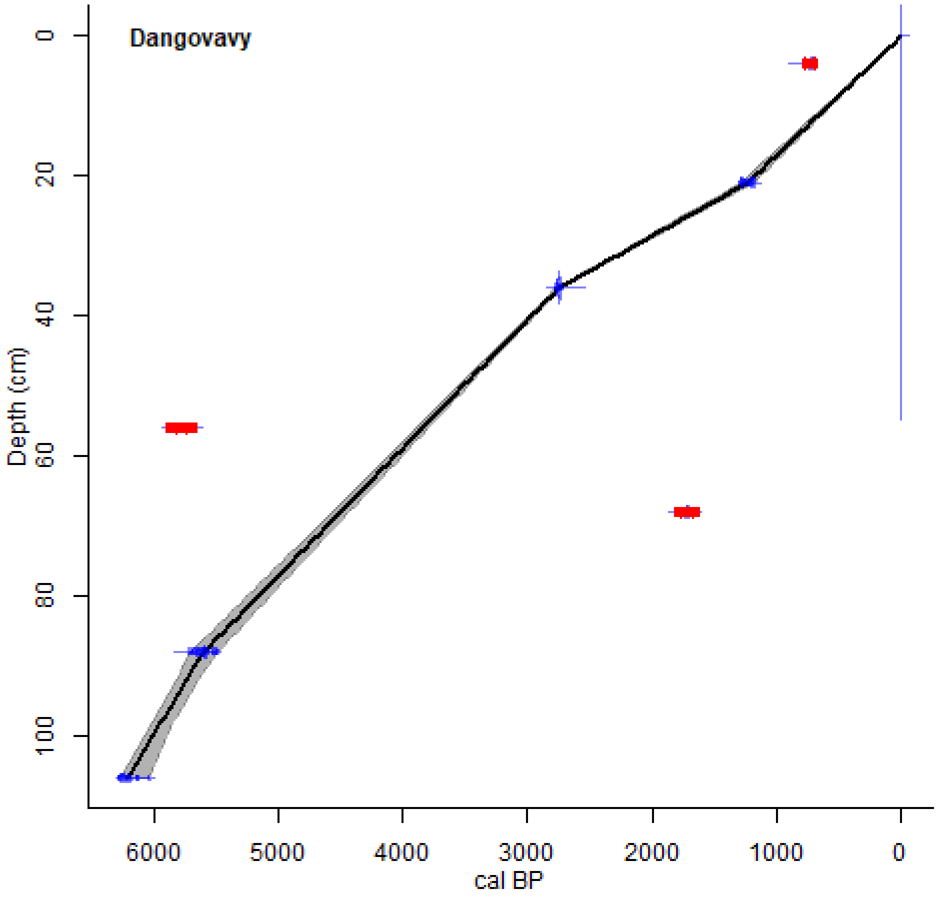


Figure 5.3: Lake Dangovavy age-depth model. Blue represents measured AMS radiocarbon ages, grey indicates the calibration range and red represents the outliers, which were subsequently excluded from the analysis.

5.4 DAN pollen and stable isotope (carbon δ^{13}C and C-N ratio) results

The DAN sediment core was analysed at intervals of 4 cm throughout the core at equivalent intervals of ca. 250 years, based on the accumulation rate described in section 5.3. The total pollen sum (TPS) in the DAN sediment core was 8642, which is equivalent to a mean±SD of 309±2 pollen per level. Aquatic plants (Cyperaceae and Polygonaceae) were excluded from the TPS and discussed separately, as their abundance does not reflect changes in terrestrial vegetation, which was the focus of this thesis. Stable carbon isotopes (δ^{13}C) and the C-N ratio were analysed in the same levels as the pollen and have a mean±SD of -23.6±1.8‰ and mean±SD of 19.3±1.7, respectively.

5.4.1 DAN pollen zones

Five statistically significant cluster zones, denoted DAN-01 to DAN-05, were identified in the pollen assemblage of Lake *Dangovavy* (Figure 5.4). Based on the ecological affiliation and abundance of taxa recorded in the sediment, these zones represented the major groupings or vegetation assemblages in the landscape over the last ca. 6200 cal years BP. From the bottom to the top of the core, the first pollen zone (DAN-01) represented an age interval from ca. 6200 to 5400, DAN-02 from ca. 5400 to 4300, DAN-03 between ca. 4300 and 3000, and DAN-04 spanned from ca. 3000 to 1000 cal years BP. The last zone was recorded from ca. 1000 cal years BP to the present period.

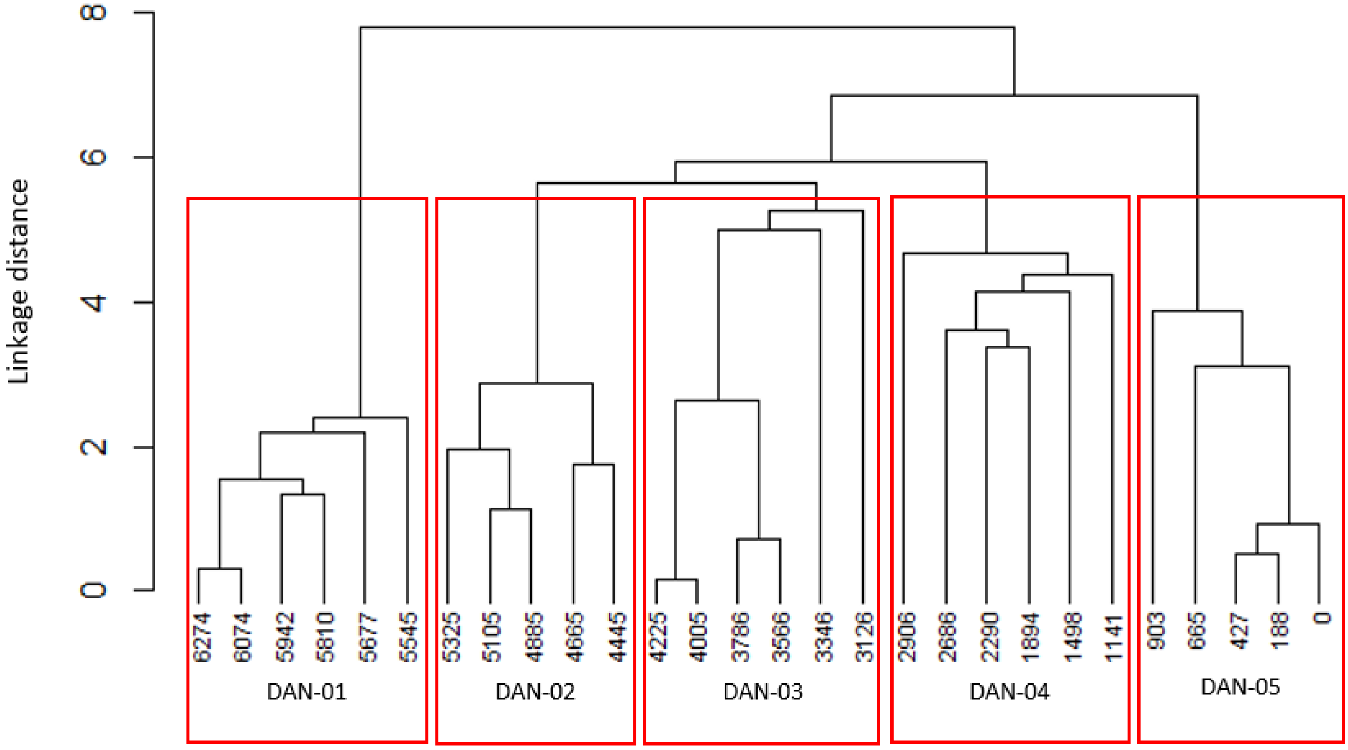


Figure 5.4: Hierarchical cluster analysis based on Euclidean distance and the coniss method, of the pollen taxa assemblages sampled from the Lake Dangovavy sediment core. The red rectangles indicate the boundaries between each cluster, or pollen zone.

5.4.2 DAN pollen diagram: pollen abundance and stable isotopes (carbon δ ^{13}C and C-N ratio)

This section describes the vegetation dynamics of Lake Dangovavy and its surroundings, according to the pollen and stable carbon isotopes results over the last ca. 6200 cal years BP. Based on the pollen zones, five statistically significant shifts in vegetation occurred in the area during this period (section 5.4.1). Figure 5.5 represented the pollen diagram of abundant terrestrial pollen taxa (greater than 2%), alongside the stable carbon isotopes and the stable C/N ratio results.

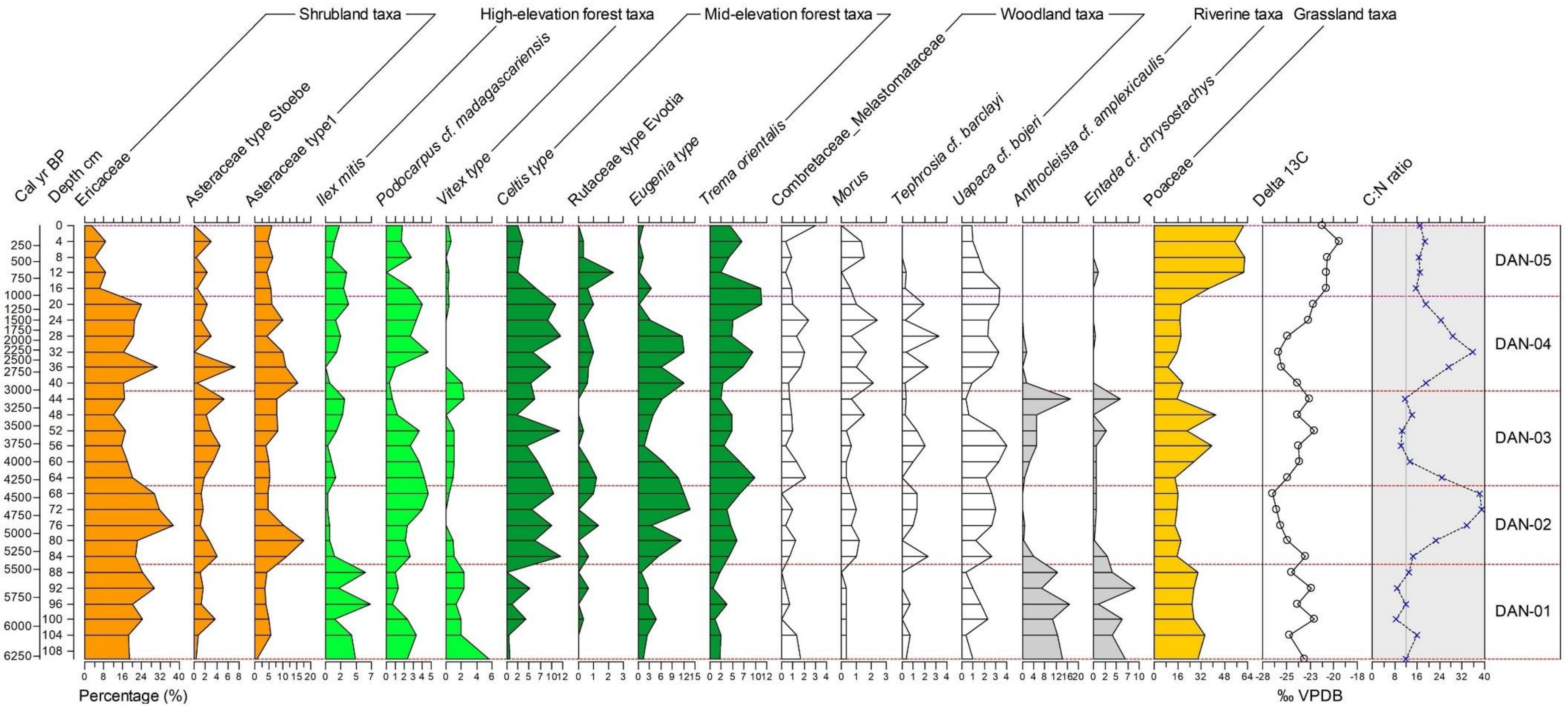


Figure 5.5: Lake Dangovavy pollen diagram with pollen taxa ≥2% grouped in their ecological affiliations. Shrubland taxa in orange, High-elevation forest taxa in lawn green, Mid-elevation forest taxa dark green, Wooded grassland in white, Riparian taxa in grey and Grassland in yellow. The δ^{13}C stable isotope results are represented by the line graph with circle symbol, while the C/N ratio is displayed in the grey box.

- **DAN-01 zone: ca. 6200 to 5400 cal years BP**

This first period was mostly marked by an abundance of ericoid shrubland and grassland taxa (characterised by an abundance of Poaceae pollen) with a mean±SD relative abundance of 22.7±1.8% and 29.2±1.4%, respectively. An abundance of riverine forest taxa and high-elevation arboreal forest taxa were also recorded with a TPS of 17.3% and 8.7%, respectively. The riverine forest taxa were represented by *Anthocleista* cf. *amplexicaulis* (mean±SD; 12.7±1.4%) and *Entada* cf. *chrysostachys* (mean±SD; 5.1±1.1%). The high-elevation forest taxa, which were found at an elevation greater than 2000 m on the island (Madagascar Catalogue, 2021), are represented by *Podocarpus* cf. *madagascariensis* (1.8±0.4%), *Ilex mitis* (4.2±0.9%) and *Vitex* type (2.6±0.6%). The mid-elevation arboreal forest and woodland taxa were less abundant compared to the previous taxa and had a TPS of 6.3% and 2.3%, respectively. On the other hand, the stable carbon isotope (δ^{13}C) results showed a mean±SD value of -23.7±0.4‰ during this period. The C/N ratio value was low with a mean±SD of 11.7±1.1.

- **DAN-02 zone: ca. 5400 to 4300 cal years BP**

The following period between ca. 5400 to 4300 cal years BP was characterised by an abundance of shrubland and mid-elevation forest taxa. Shrubland was characterised by a high increase in the mean±SD relative abundance of Ericaceae pollen (28.6±3%), showing a peak (37.7%) at ca. 4800 cal years BP. Asteraceae pollen also increased during this period with total mean±SD value of 11.9±2.9%. The arboreal taxa were characterised by a greater abundance of mid-elevation taxa, compared to high-elevation taxa with a TPS of 23% and 4%, respectively during this period. The mid-elevation taxa were represented by *Celtis* type (8.5±1.2), *Trema orientalis* (4.8±0.5) and *Eugenia* type (9.1±2%). This was accompanied by a slight increase in woodland taxa (TPS= 5.2%) particularly *Uapaca* cf. *bojeri* (2.4±0.3%). However, both riverine forest taxa and grassland taxa, represented by Poaceae pollen, decreased to 2% and 15%, respectively. The δ^{13}C isotope values were slightly heavier (-25.4±0.6‰) during this period, with a peak observed at ca. 4400 cal years BP (-26.6‰). The increase in the measurement of stable carbon isotope value during this period was accompanied by high stable C/N ratio with mean±SD value of 29.5±4.8.

- **DAN-03 zone: ca. 4300 to 3000 cal years BP**

Between ca. 4300 and 3000 cal years BP, a decrease in shrubland and forest taxa, with a likewise sudden increase in grass taxa, was recorded at Lake Dangovavy and its surrounds. Regarding the shrubland taxa, the mean±SD of Ericaceae and Asteraceae pollen decreased to 16.7±1.1% and 9.8±1.3%, respectively. The arboreal taxa also decreased, with a TPS of 17.2% and 5.4% for the mid- and high-elevation forest taxa, respectively. However, persistence of *Celtis* type (6.5±1.3%), *Trema orientalis* (5±1%) and *Uapaca* cf. *bojeri* (2±0.6%) were recorded during this period. On the other hand, grassland taxa, characterised by an abundance of Poaceae pollen, increased during this period with a mean value of (26.9±4.8 %). Peaks of grass pollen were recorded at ca. 3800 and 3400 cal years BP with a mean value of 39.3% and 42.4%, respectively. Nonetheless, the δ^{13}C isotope values presented a mean±SD value of -23.7±0.4‰ with low C/N ratio (mean±SD, 14.1±2.2) indicating more stable carbon isotopes from aquatic plants.

- **DAN-04 zone: ca. 3000 to 1000 cal years BP**

This period was marked by the return abundance of shrubland and mid-elevation forest taxa, with a TPS of 33.4% and 23.3%, respectively. Regarding the shrubland taxa, Ericaceae and Asteraceae pollen remained abundant, as in the previous pollen zone, with a mean value of 21.5±2.2% and 11.9±2.7%, respectively. Concerning the arboreal taxa, a slight increase in mid-elevation forest taxa was recorded: *Celtis* type (8.5±1%), *Trema orientalis* (6.5±1.2%) and *Syzygium* type (7.5±2.1%) with a TPS of 23.3%. The high-elevation component was low, as shown in the previous period, with a TPS of 4.7%. Woodland taxa continued to increase in abundance (TPS = 6.9%), represented by *Uapaca* cf. *bojeri*, *Morus* sp. and *Tephrosia* cf. *barclayi*, during this period. However, riverine forest taxa decreased with a TPS of 0.6%. In contrast to the two previous pollen zones, Poaceae pollen was low during this period with a mean value of 16.7±1.5%. The abundance of wooland and forest taxa is in accordance with a more negative value of δ^{13}C in the sediment (mean±SD -24.4±0.6‰). The C/N ratio value increased during this period with a mean±SD of 25.7±2.6.

- **DAN-05 zone: 1000 cal years BP to the present period**

The last period was characterised by the abundance of grassland, forest and woodland taxa. The relative abundance of grass was almost double the abundance observed during the first period (DAN-01), with a peak of 61.8% recorded at ca. 500–400 cal years BP. The shrubland, especially the ericoid shrubland, decreased to a mean±SD relative abundance of 6.2±1.2%. Arboreal forest taxa (i.e., high- and mid-elevation forest taxa, riverine forest and the woodland taxa), gradually decreased to the present period with a TPS of 4.2%, 11%, 0.2% and 3.7%, respectively. The non-arboreal forest taxa were very rare with a TPS of 0.8%. The δ^{13}C values tended to a more positive value (mean±SD, -20.89±0.29‰) during this last period. This period was also characterised by high C/N ratio value with a mean±SD value of 16.9±0.5.

5.4.3 DAN aquatic, rare terrestrial pollen and exotic taxa

The relative abundance of aquatic, rare terrestrial pollen, and exotic taxa from Lake Dangovavy were represented in Figure 5.6. Aquatic pollen was represented by an abundance of Cyperaceae (cf. *Cyperus*) and *Polygonum* type during the last 6200 cal years BP. Cyperaceae (*Cyperus* type) was consistently abundant over time, with a mean±SD value of 20.8±2.8% and was characterised by an increase at ca. 4300 and from ca. 1000 cal years BP with peak at 200 cal years BP. *Polygonum* pollen was less abundant compared to Cyperaceae and presented a mean±SD value of 3.8±0.6% over time. An increase in the relative abundance of *Polygonum* was noted from 1000 cal years BP to the present period (DAN-05) with a peak at ca. 400 cal years BP.

Rare terrestrial pollen was composed of some characteristic taxa present in the landscape (Kull, 2002a; Rakotondrasoa et al., 2012) but present a relative abundance less than 2% in the pollen diagram. On the other hand, exotic taxa were represented by abundance of *Eucalyptus* and *Pinus.* From 6200 to 5400 cal years BP (DAN-01), only a few rare arboreal taxa were noted, including Proteaceae *Faurea* type and *Dombeya* cf. *lucida*. Between DAN-02 and DAN-04 (5400–1000 cal years BP), some shrubs increased, such as *Euphorbia* cf. *hirta*, *Psorospermum* cf. *ferrovestitum* and *Weinmannia* cf. *humbertiana*. From 1000 cal years BP to the present period (DAN-05), there was a slight decrease in rare shrub and arboreal taxa, except the exotic pollen taxa.

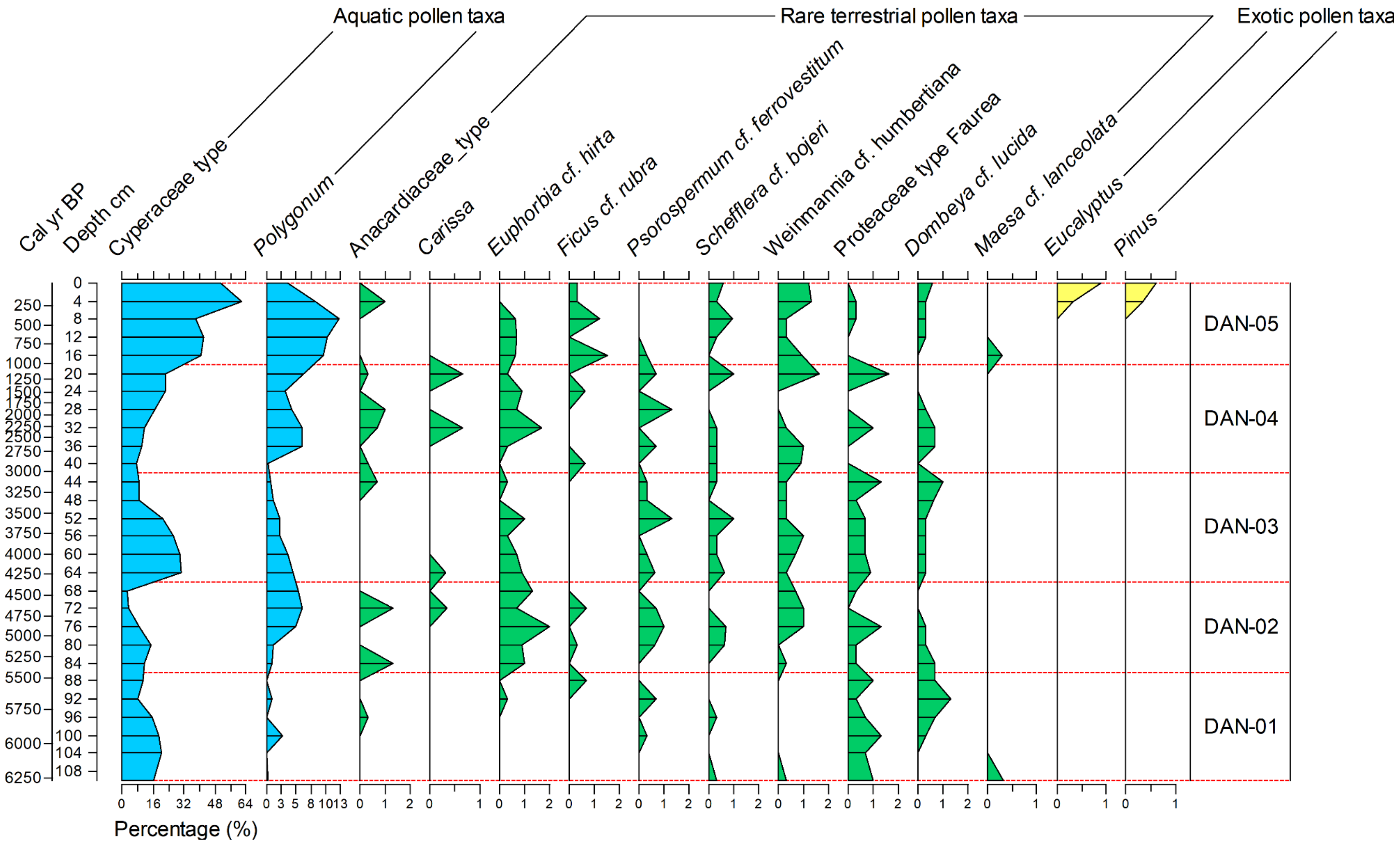


Figure 5.6: Lake Dangovavy aquatic, rare terrestrial and exotic pollen relative abundance (%) over the last 6200 cal years BP. Aquatic pollen is represented in blue, rare terrestrial pollen in green and exotic pollen in yellow

5.4.4 DAN pollen richness, evenness and diversity

Rarefied species richness, based on palynological richness from Lake Dangovavy, varied between 24 (ca. 5900 cal years BP) and 41 (ca. 2900 and 900 cal years BP) pollen taxa, with a mean±SD of 33±2 pollen taxa over time, see Figure 5.7. Between ca. 6200–4300 cal years BP (DAN-01 and DAN-02 pollen zone), pollen richness showed a mean±SD of 29±2 pollen taxa. From ca. 4300–1000 cal years BP (DAN-03 and DAN-04), pollen richness increased, with a mean±SD value of 36±1. Pollen taxa reached a peak of 40 and 41 pollen taxa at ca. 4200 and 2900 cal years BP, respectively. From ca. 1000 cal years BP to the present period (DAN-05), a slight decrease in pollen taxa was recorded with a mean±SD value of 34±2. Pollen evenness was stable from ca. 6000 to 1000 cal years BP but decreased during the last ca 900 years BP.

The greatest compositional changes (Beta diversity) occurred at four points over time (Figure 5.7). First with a value of 1.9 SD at ca. 5600 cal years BP, which corresponded to the transition between the DAN-01 and DAN-02 pollen zones. The second and third changes occurred at ca. 4200 and 3700 cal years BP, with a value of 2.6 SD and 2.3 SD, respectively, which corresponded with an increase in Poaceae pollen (see section 5.4.2). The last compositional change in the DAN core was recorded during the present period, with a value of 2.7 SD. It was also the highest, with a value of 2.7 SD. This corresponded with the highest abundance of grassland over time which was previously described in the pollen analysis.

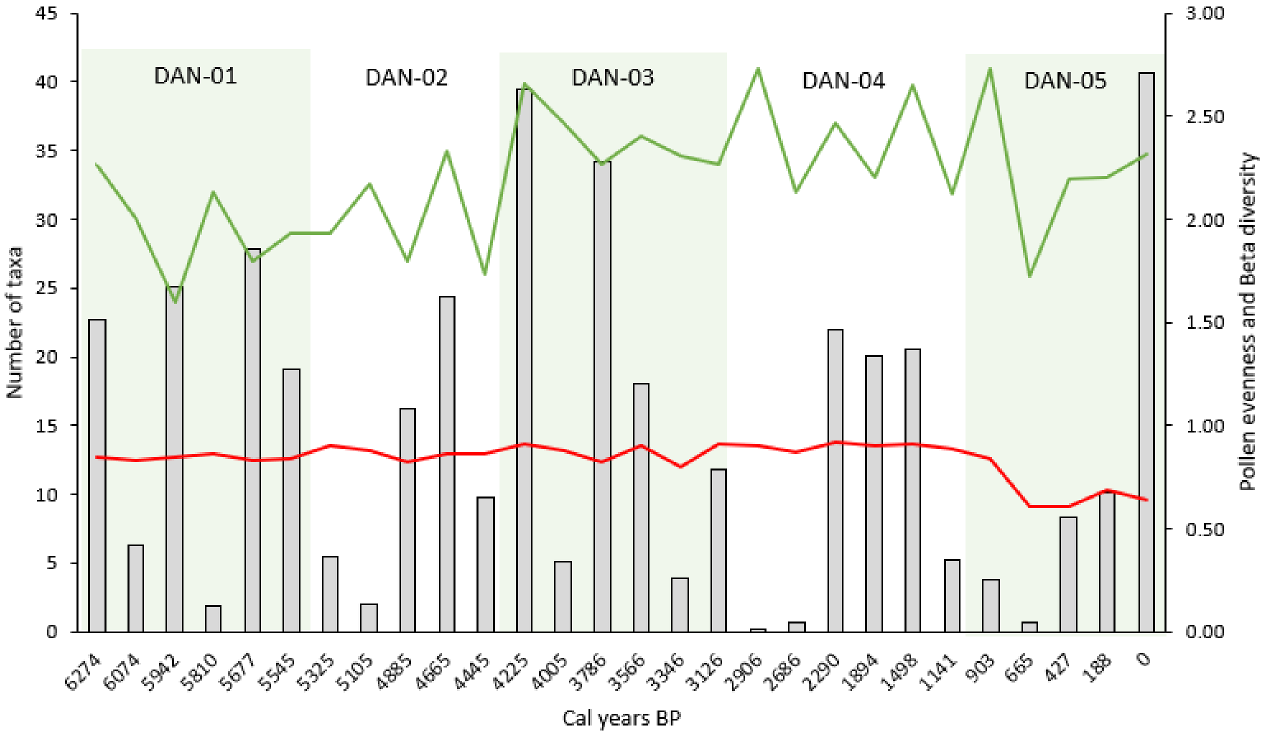


Figure 5.7: Lake Dangovavy pollen richness, evenness and compositional change (Beta diversity) over the last 6000 years. The green line represents pollen richness, red line pollen evenness and grey bars are Beta species diversity .

5.5 DAN Charcoal and coprophilous spores results

This section presents the charcoal (macro- and microcharcoal) and coprophilous spores results in Lake Dangovavy over the last 6200 cal years BP. Charcoal and coprophilous spores were analysed at the same temporal resolution as pollen (every 4 cm) and were used to understand fire history and herbivory activities, respectively.

5.5.1 DAN Charcoal results

Macro- and microcharcoal analysis in Lake Dangovavy showed that charcoal concentration varied during the Mid-Holocene in the lake and its surroundings (Figure 5.8), but only increased in the last millennium. A total of 9064 macrocharcoal particles, equivalent to a mean±SD of 342 charcoal particles.cm^{-3}, were counted. Microcharcoal had a mean±SD value of 428.2±73.5 cm^{-2}.cm^{-3} with a total area of 2140.8 cm^{2}.cm^{-3} of charcoal counted. Before ca. 5400 cal years BP (DAN-01), fire was present, but the concentration was relatively low for both macro- and microcharcoal, with a mean±SD of 15±1 particles.cm^{-3} and 43.8±1.6 cm^{2}.cm^{-3}, respectively. Between ca. 5400 and 4300 cal years BP (DAN-02), a moderate increase of macrocharcoal was recorded, with a mean±SD of 298±108 particles.cm^{-3}.

However, a high increase of microcharcoal was recorded during this period (mean±SD, 647±22.3 $cm^2.cm^{-3}$) with a peak recorded at ca. 5000 cal years BP (880.8 $cm^2.cm^{-3}$). A decrease in the presence of macro- and microcharcoal, and therefore fire occurrence, was noted between ca. 4300 and 3000 cal years BP (DAN-03). Macro- and microcharcoal had a mean±SD value of 200±115 $particles.cm^{-3}$ and 255.2±72.6 $cm^2.cm^{-3}$, respectively during this period. Following that, between ca. 3000 and 1000 cal years BP (DAN-04), macrocharcoal (mean±SD, 311±115 $particles.cm^{-3}$) and microcharcoal (mean±SD, 298.5±74.8 $cm^2.cm^{-3}$) concentrations increased, showing a re-occurrence of fire concentration in the area. Slight peaks of charcoal were recorded at ca. 1500 cal years BP with value of 800 $particles.cm^{-3}$ and 549.1 $cm^2.cm^{-3}$ for macro- and microcharcoal, respectively. The last pollen zone (DAN-05), from ca. 1000 cal years BP to the present, had very high concentrations in both macro- and microcharcoal, with a mean±SD value of 883±165 particles.cm-3 and 896.3±115.5. cm^2cm^{-3}, respectively, demonstrating the highest concentration of fire in the area compared to previous periods. The greatest peaks were recorded at ca. 700 cal years BP for macrocharcoal with a value of 1356 charcoal $particles.cm^{-3}$, and at ca. 200 cal years BP for microcharcoal (1320.7 $cm^2.cm^{-3}$ charcoal area).

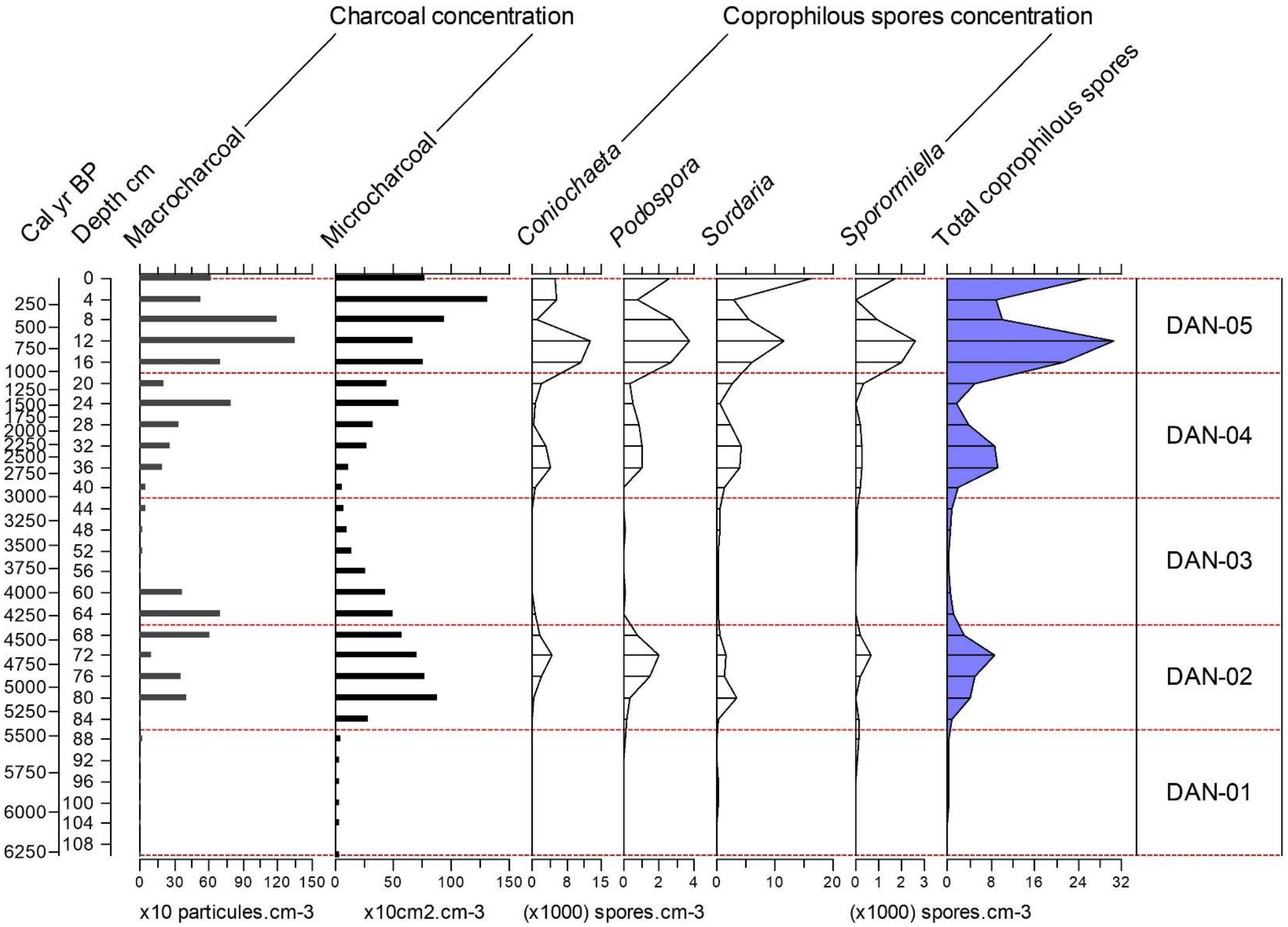


Figure 5.8: Lake Dangovavy *charcoal and coprophilous spores concentration. Macro- and microcharcoal concentration are represented in grey and black, respectively. Coprophilous spores are represented in white and violet*

5.5.2 DAN Coprophilous spores

Coprophilous spore concentration, a proxy for herbivory activities in the area, varied over time with a sharp increase noted during the last ca. 1000 cal years BP (Figure 5.8). A total of 740 coprophilous spores were counted, with a mean±SD value of $5.5 \pm 1.5 \times 10^3$ spores.cm^{-3}. The concentration of coprophilous spores was very low between ca. 6200 and 5400 cal years BP (DAN-01) with a mean±SD value of $0.2 \pm 0.1 \times 10^3$ spores.cm^{-3}. A slight increase in the concentration of coprophilous spores was recorded in DAN-02 (ca. 5400-4300 cal years BP), with a mean±SD value of $4.3 \pm 1.3 \times 10^3$ spores.cm^{-3}. The concentration of coprophilous spores decreased again to a mean±SD of $0.6 \pm 0.1 \times 10^3$ spores.cm^{-3} between ca. 4300 and 3000 cal years BP (DAN-03). The following period between 3000 to 1000 cal years BP (DAN-04), was characterised by a slight increase in the concentration of coprophilous spores, with a mean±SD value of $5 \pm 1.3 \times 10^3$ spores.cm^{-3}. From 1000 cal years BP to the present period (DAN-05), there was a massive increase of coprophilous spores concentration with a mean±SD of $19.3 \pm 4.2 \times 10^3$ spores cm^{-3}, indicating an high increase in herbivory activities in the area. The greatest peaks in concentration of coprophilous spores were recorded at 700 cal years BP and at the present period, with a concentration of 30.5×10^3 spores cm^{-3} and 25.8×10^3, respectively coinciding with the previous peak of macrocharcoal (see section 5.5.1 and Figure 5.8).

5.6 DAN Diatom results

Diatom preservation at Lake Dangovavy was very low in the lower part of the core, and therefore, the minimum count of diatoms (see Chapter 3) were not reached for samples between ca. 6200 and 2000 cal years BP in the sediment core. Diatoms were only countable in the lake from 30 cm to the top of the core, which corresponds to the last ca. 2000 cal years BP (DAN-04 and DAN-05 pollen zones). A total of 4800 diatoms were counted during this period. Twenty-five abundant habitat indicator diatom species were recorded during this period and their dynamism were represented in the Figure 5.9. Overall, during the last ca. 2000 cal years BP, Lake Dangovavy was characterised by a higher abundance of benthic taxa (71.81±2.4%), represented by the sub-groups of periphytic and aerophilic taxa, compared to a lower abundance of planktonic taxa (24.1±2.6%).

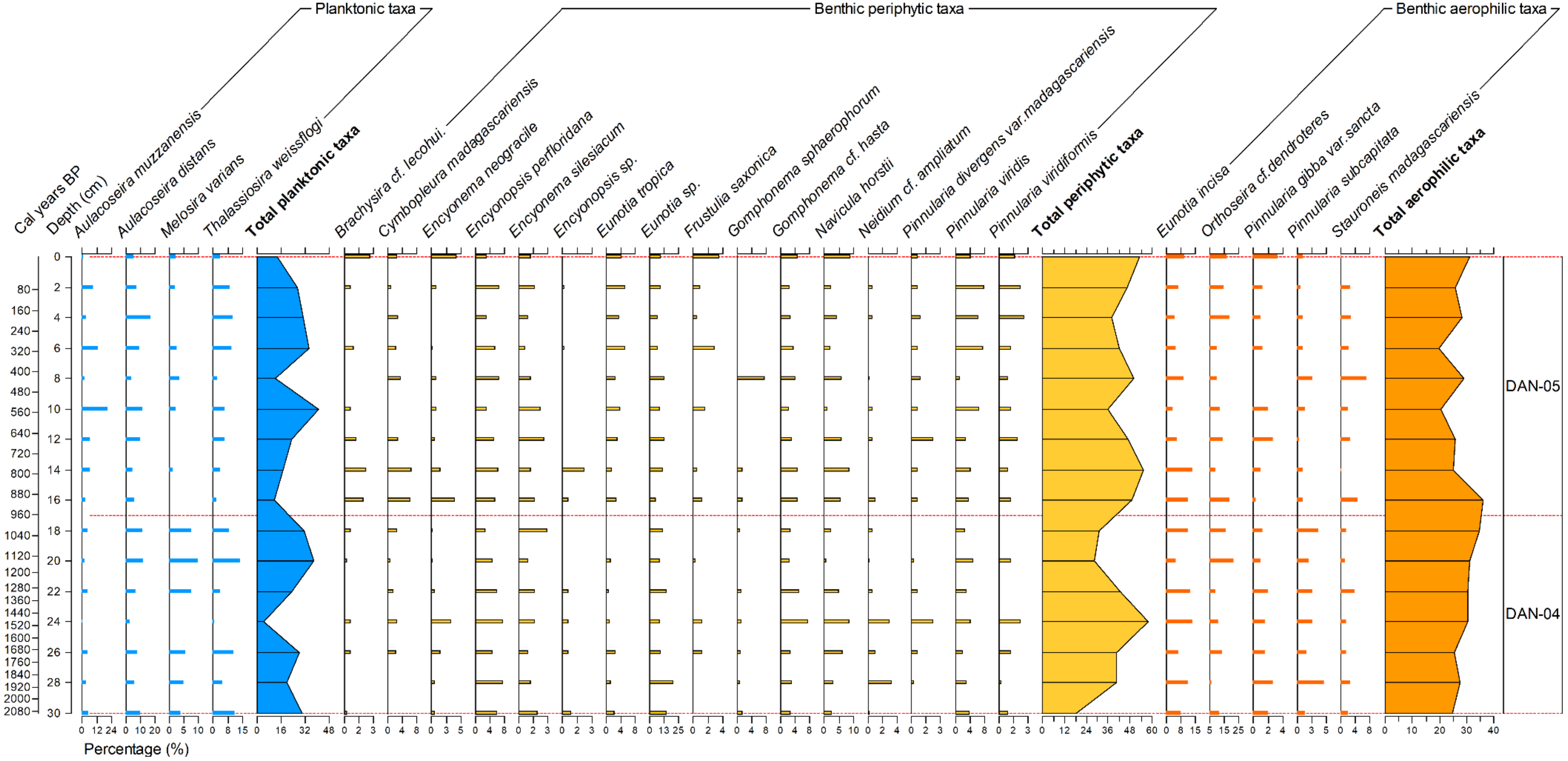


Figure 5.9: Relative abundance (≥2%) of diatom taxa recorded during the last 2000 cal years BP at Lake Dangovavy. Diatoms are grouped according to habitat preference where planktonic taxa are represented in blue, periphytic taxa in yellow and aerophilic benthic taxa in orange.

Between ca. 2000 and 1000 cal years BP (DAN-04), planktonic taxa had a mean±SD value of 25.1±4% with a minimum (4.6%) and maximum (38%) value at ca. 1500 and 1100 cal years BP, respectively. Benthic taxa were abundant with mean±SD value of 41±3.8% and 29.1±1.3% for periphytic and aerophilic taxa during the entire period. A peak of periphytic taxa (58%) occurred at ca. 1500 cal years and this corresponded negatively to the lowest value of planktonic taxa (Figure 5.9). However, a short period of abundance of planktonic taxa coupled with a decrease of benthic taxa was recorded at ca. 1100 cal years BP. During the last ca. 1000 cal years BP (DAN-05), planktonic diatom taxa remained low compared to benthic diatom taxa. Planktonic taxa had a mean±SD value of 23.8±3.6%, but with an important peak recorded at ca. 550 cal years BP with a relative abundance of 41%. Benthic taxa had a mean±SD total value of 70.2±5% where the non- and aerophilous diatom taxa showed a mean±SD value of 46.3±2.2% and 26.8±1.7%, respectively. Synchronised peaks in abundance of benthic taxa, both periphytic and aerophilic, coupled with low occurrence of planktonic taxa were identified on three occasions (Figure 5.10). The first was at ca. 900 cal years BP, with a notable peak of aerophilous taxa with a value of 36%, then at ca. 400 cal years BP with slight peaks of periphytic (50%) and aerophilic (29%) taxa. The last one was recorded at the present period with moderate peaks in periphytic and aerophilic taxa with values of 53.3% and 31%, respectively.

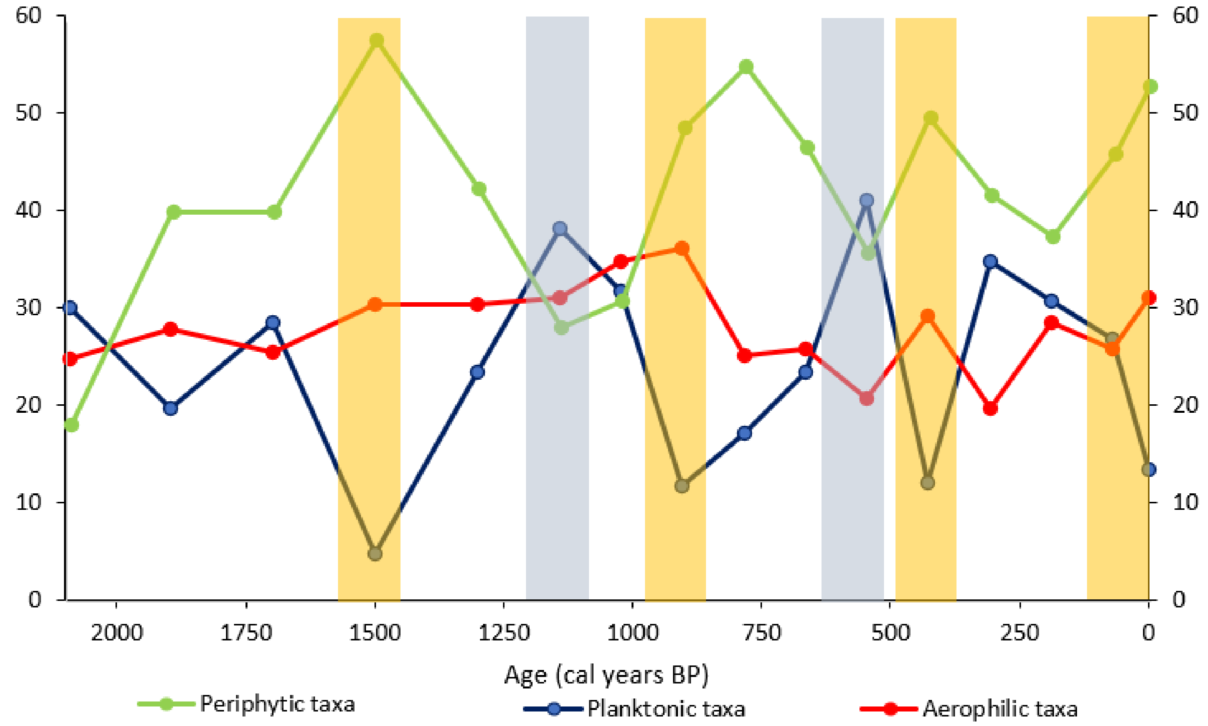


Figure 5.10: Changes in the relative abundance (%) of diatom taxa in Lake Dangovavy during the last ca. 2000 cal years BP. Diatoms are grouped according to habitat preference (planktonic, periphytic and aerophylic taxa). The yellow bars represent low lake levels, while blue bars deeper levels.

5.7 DAN multivariate analyses

The Detrended Correspondence Analysis (DCA) of pollen taxa showed that the gradient length of the first axis was 1.3 SD justifying the use of linear-based methods in Lake Dangovavy dataset.

5.7.1 Distribution of pollen in the DAN sediment core

The Principal Component Analysis (PCA) showed the distribution of abundant and characteristic pollen taxa in the DAN sediment core during the last ca. 6200 cal years BP (Figure 5.11). Five distinct vegetation types were recorded over time which were the grassland, ericoid shrubland, riverine and forest taxa including high- and mid-elevation taxa. The first two principal components, noted as PC1 and PC2, explained 57.8% of the variance in DAN sediment data, with a high contribution of riverine, ericoid shrubland and grassland i.e. greater than 15%.

The PC1 component showed positive loadings for riverine taxa (*Anthocleista* and *Entada*) and grassland taxa represented by Poaceae but a negative loading for upland taxa represented by *Celtis*, Ericaceae and *Syzygium*. This component possibly explained the distribution of taxa in relation to water availability in the area over time. In addition, by focusing on the forest taxa, PC1 showed positive a loading for some high-elevation forest taxa such as *Faurea*, *Ilex* and *Vitex*, while a negative loading for mid-elevation taxa was found for species such as *Celtis*, *Syzygium* and *Trema orientalis*. This might suggest that the PC1 component represented an elevation range in the area. The PC2 component showed positive loadings for *Anthocleista*, *Entada*, Ericaceae type, *Psorospermum*, *Syzygium* and *Vitex* but a high negative loading for Poaceae with Amaranthaceae type, *Eucalyptus*, *Ficus*, *Trema orientalis* and *Weinmannia*. Therefore, PC2 seemed to represent the openness of the vegetation, from a more or less closed canopy to a more open vegetation, containing an abundance of Poaceae pollen.

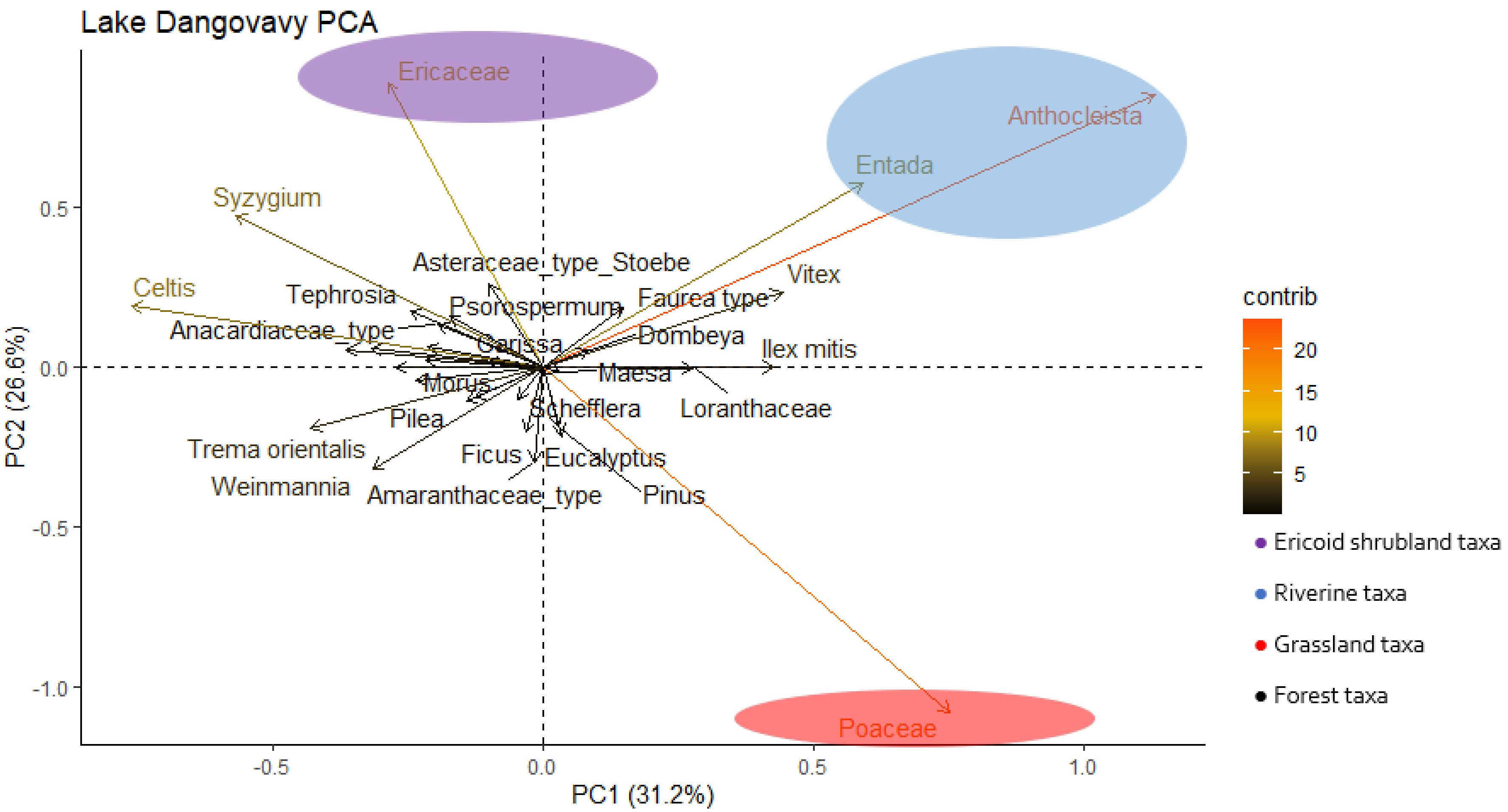


Figure 5.11: A Principal Component Analysis (PCA) determining the distribution of abundant and characteristic pollen taxa in a sediment core sampled from Lake Dangovavy. The colour gradient represents the contribution of each taxa to the axis components (lowest contribution = black to highest contribution = orange).

5.7.2 Relationship between pollen, charcoal, coprophilous spores and diatoms

5.7.2.1 Relationship between macrocharcoal, and microcharcoal

There was a highly significant positive relationship between the macrocharcoal and microcharcoal particles concentration in the DAN sediment core (n = 28; r = 0.7; R^2 = 0.5; p < 0.001; Figure 5.12). Also, there are increasing linear relationships between macro- and microcharcoal i.e., for every additional one macrocharcoal particles.cm^{-3} there was an increase of 0.3 $cm^2.cm^{-3}$ of microcharcoal.

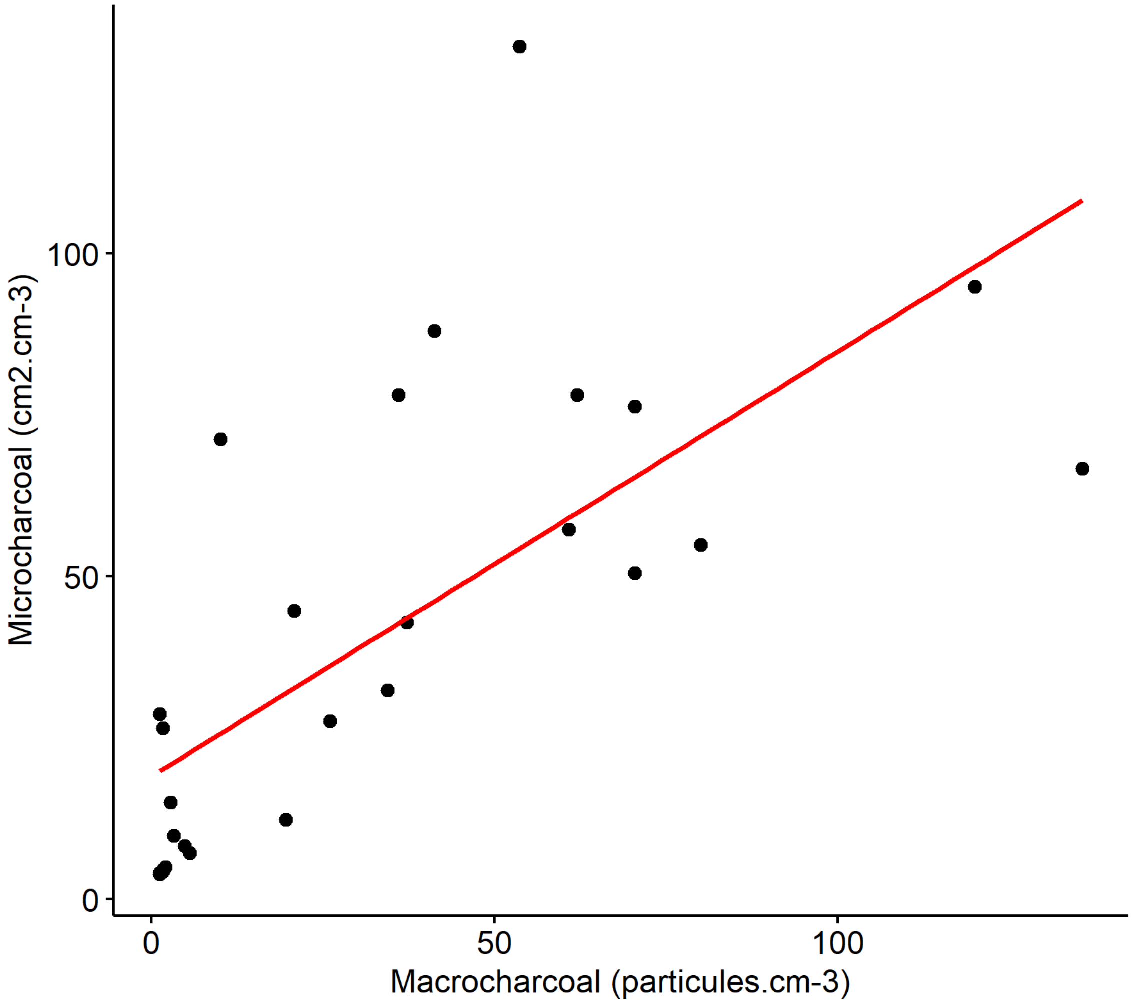


Figure 5.12: Pearson correlation and linear regression between macrocharcoal and microcharcoal particles in Lake Dangovavy *spanning from ca. 6200 cal years BP to the present period.*

5.7.2.2 Relationship between charcoal data and coprophilous spore

There was a moderate significant positive correlation (n = 28; r=0.6; R^2 = 0.5; p<0.001) between the coprophilous spores and macrocharcoal in the DAN sediment core (Figure 5.13).

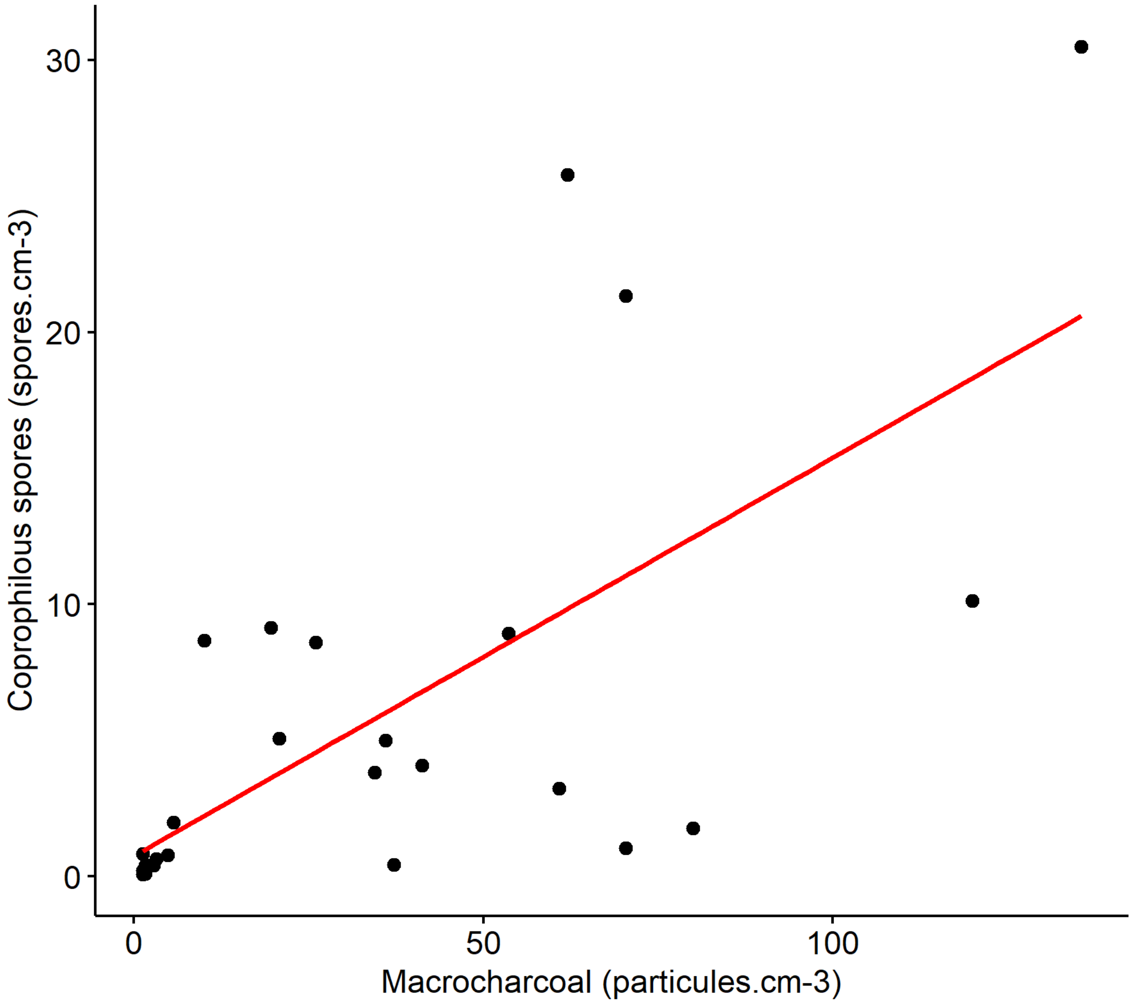


Figure 5.13: Pearson correlation and linear regression between macrocharcoal particles and coprophilous spores in Lake Dangovavy spanning from ca. 6200 cal years BP to the present period (n=28).

There was a low positive correlation between microcharcoal particles and coprophilous spore concentration in DAN sediment core (n = 28; r=0.5; R^2 = 0.3; p<0.05; Figure 5.14). Only ca. 40% of the observed variation was explained by the model's inputs.

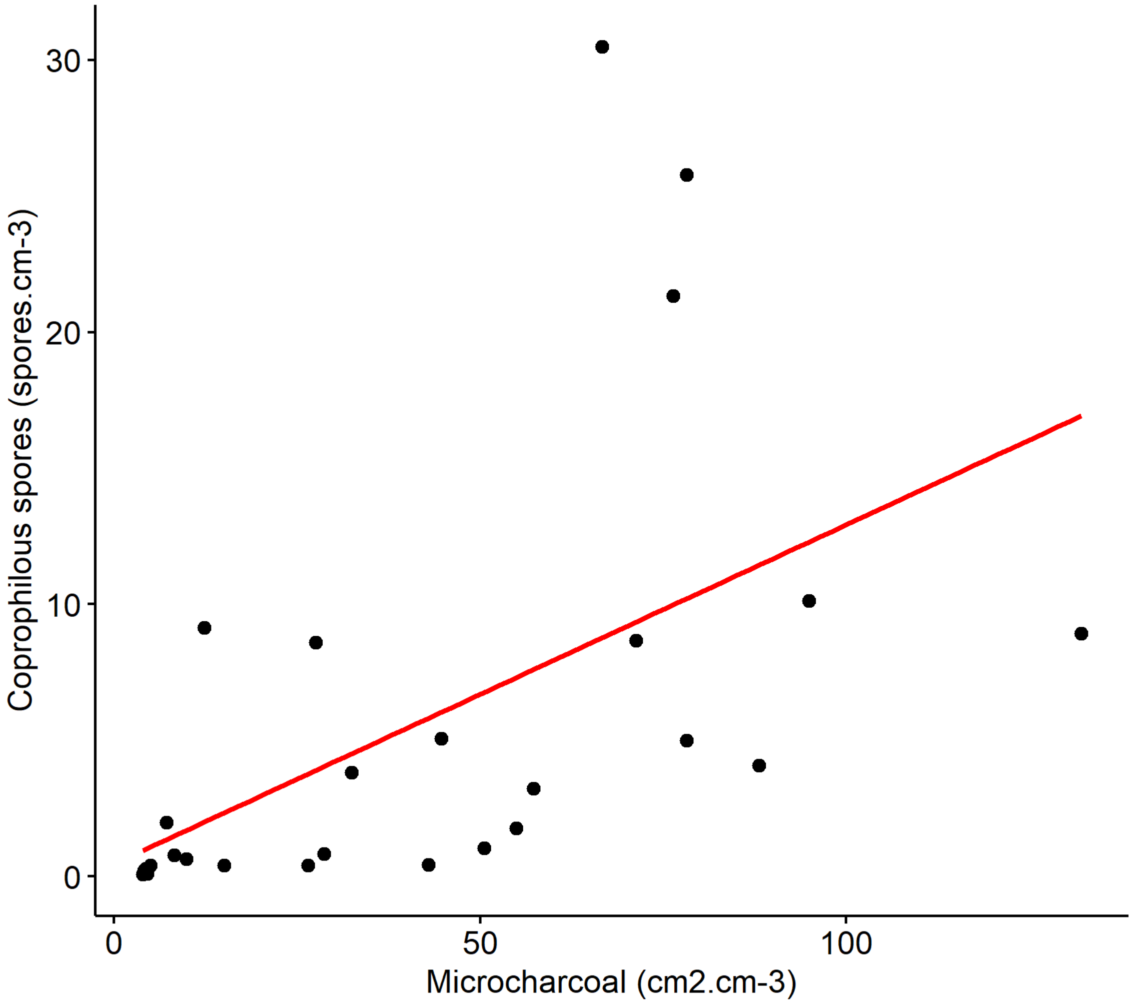


Figure 5.14: Pearson correlation and linear regression between microcharcoal particles and coprophilous spores in Lake Dangovavy spanning from ca. 6200 cal years BP to the present period (n=28).

5.7.2.3 Relationship between pollen and predictor variables

The Redundancy Analysis (RDA) showed the impact of predictor variables (charcoal, coprophilous spores and diatoms) on the variation of the response variable (pollen) in Lake Dangovavy over time.

a) Relationship between macro- microcharcoal and coprophilous spores on pollen variation during the entire Mid-Holocene

The three variables, i.e., macro-, microcharcoal and coprophilous spores, explained 27.9% of the variation in pollen taxa composition (Table 5.3). The first constrained axis (RDA1) explained 22.6% (3.314/14.6866=22.6%) of the variance while RDA2 and RDA3 explained only 3%, and 2.3%, respectively.

Table 5.3: The Redundancy Analysis (RDA) output for the variation of pollen explained by charcoal (macro- and microcharcoal) and coprophilous spores in Lake Dangovavy

	Inertia	Proportion
Total	14.6866	1
Constrained	4.0913	0.2786
Unconstrained	10.5953	0.7214

Eigenvalues for constrained axes

RDA1	RDA2	RDA3
3.314	0.443	0.335

The distribution of pollen variance in function of the predictor variables in Lake Dangovavy throughout the different pollen zone was shown in Figure 5.15. The variance of pollen from DAN-01 to DAN-04 (ca. 6200-1000 cal years BP) was not correlated with the predictor variables (Figure 5.15). During the last ca. 1000 cal years BP (DAN-05), there was a stronger correlation of macrocharcoal and coprophilous spores.

Therefore, other environmental variables different than fire (macro- and microcharcoal) and herbivory (coprophilous spores) possibly also occurred to explain the variation of the pollen dataset from Lake Dangovavy during the last ca. 6200 cal years BP.

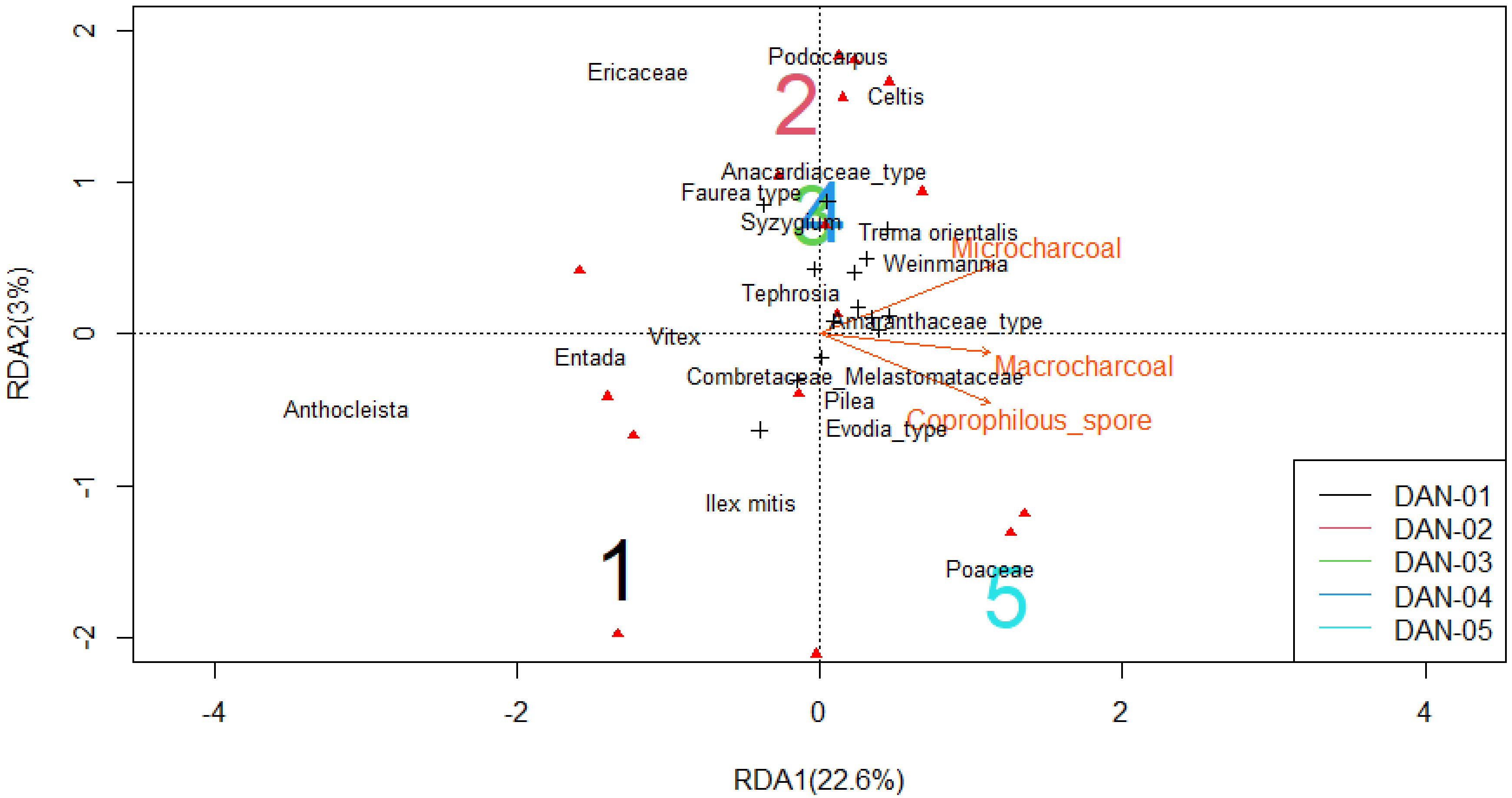


Figure 5.15: Redundancy Analysis (RDA) of abundant and selected rare pollen recorded in Lake Dangovavy during the last ca. 6200 years within the different pollen zones. Pollen taxa are represented in black, sites in red and predictors variables in orange

b) Relationship between indicator diatom groups and pollen during the last ca. 2000 years BP

The repartition of indicator diatom group according to their habitat preferences, i.e., planktonic and benthic taxa explained 35.1% of pollen variation in Lake Dangovavy during the last ca. 2000 cal years BP. The first constrained axis (RDA1) explained 24.9% of the variance while RDA2 explained 10.2% (Table 5.4).

Table 5.4: The Redundancy Analysis (RDA) output for the variation of pollen explained by diatom indicators taxa (benthic and planktonic) in Lake Dangovavy

	Inertia	Proportion
Total	13.881	1
Constrained	4.872	0.351
Unconstrained	9.008	0.649

Eigenvalues for constrained axes

	RDA1	RDA2
	3.463	1.410

By projecting the constrained axes onto the pollen zones, the results indicated that before ca. 1000 cal years BP (pollen zone, DAN-04) pollen had a greater association to planktonic diatom taxa; and a greater association to benthic diatom within the pollen zone, DAN-05 (Figure 5.16).

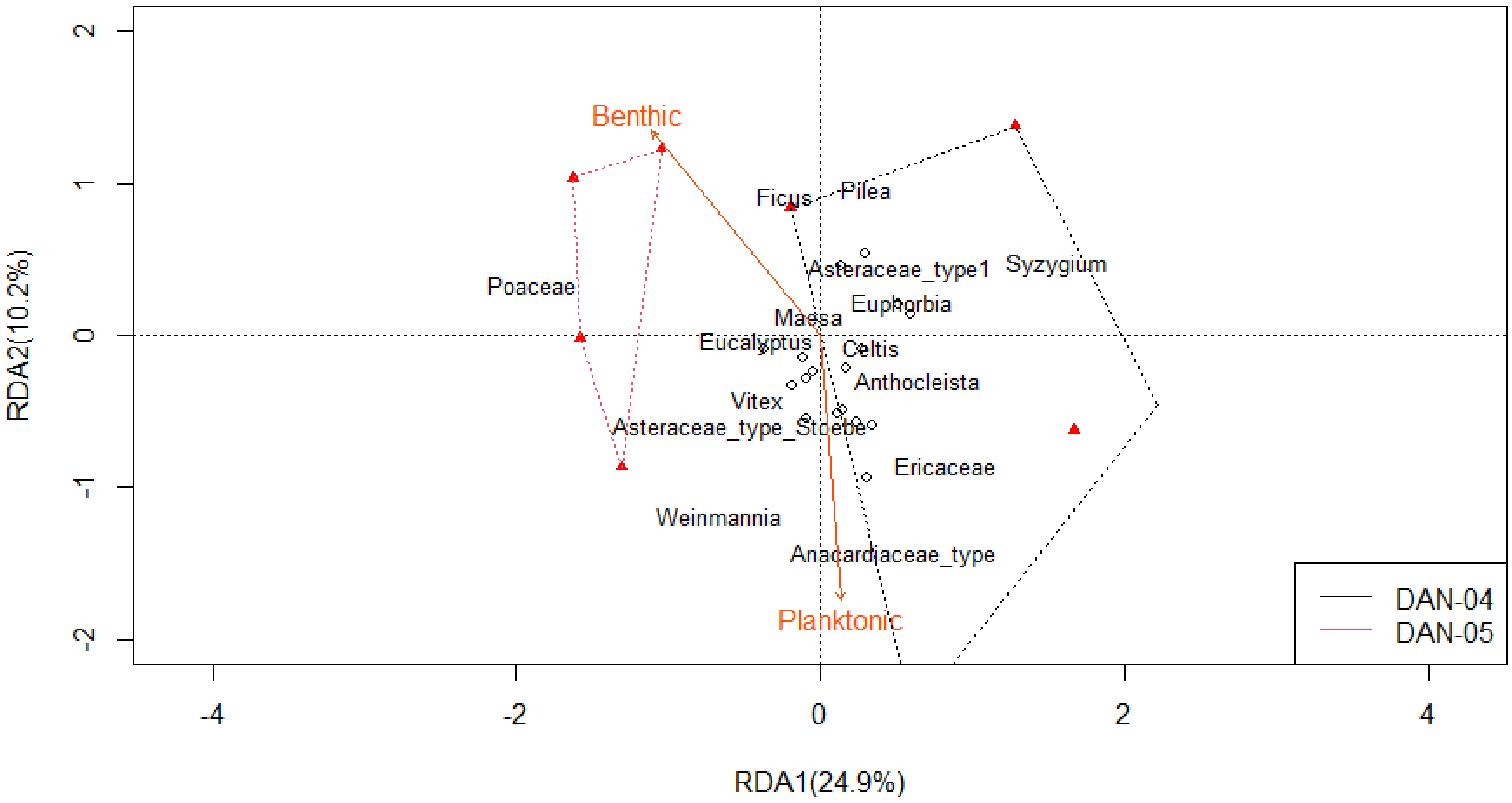


Figure 5.16: Redundancy Analysis (RDA) of abundant and selected rare pollen taxa recorded in Lake Dangovavy during the last ca. 2000 years with predictor variables charcoal and coprophilous spores

In summary, 27.9% of the pollen variation in Lake Dangovavy was associated with charcoal and coprophilous spores concentration during the last ca. 2000 cal years BP with the majority of change occurring during the last ca. 1000 cal years BP. Other environmental factors possibly had strongly influenced the pollen variation before the last millennium. In addition, during the last ca. 2000 years, 35.1% of the variation in the abundance of pollen taxa was associated with indicator diatom groups. Between ca. 2000 and 1000 cal years BP, pollen distribution in Lake Dangovavy was associated with an abundance of planktonic taxa, and thereafter became more strongly associated with benthic taxa during the last ca. 1000 cal years BP.

5.8 DAN overall synthesis of pollen, stable carbon isotopes, charcoal and coprophilous spores results

From ca. 6000 to 1000 cal years BP in Lake Dangovavy, there was a dominance of grass and Ericaceae pollen in the area. Mid-elevation forest, woodland taxa and Asteraceae taxa were more or less stable while riverine forest and high elevation forest taxa decreased toward the present period. From ca. 1000 cal years BP grass pollen increased enormously, while all other taxa declined. This latter was correlated to a decrease in pollen richness and evenness, and a more positive value of the $\delta^{13}C$ values. Charcoal (macro- and microcharcoal) was present and abundant in the area but was extremely high from ca. 1000 cal years BP and this latter correlated with a high coprophilous spore concentration.

Chapter 6 DISCUSSION

6.1 Introduction

This chapter aims to understand the landscape history and environmental changes of the forest-grassland mosaic ecosystems in the Central Highlands of Madagascar through palaeoecological investigation and review of published literature. It discusses and interprets results from two sites, the Tampoketsa-Ankazobe wetland and Lake Dangovavy located in the eastern and western slopes of the highlands, respectively. It starts by looking at the vegetation and environmental changes that occurred at Tampoketsa-Ankazobe wetland from ca. 11 200 cal years BP to present, and then at Lake Dangovavy from 6200 cal years BP to present. The pollen and stable carbon isotope records in the sediment cores that reflect the vegetation changes (structure and diversity) are assessed for both sites, alongside the palaeorecord data of fire, herbivory and climate inferred from charcoal, coprophilous spores and diatoms (see Chapter 4 and 5). The interaction of these environmental parameters during the period of human settlement and expansion in the region from ca. 200 cal years BP-until the present time (Burney et al., 2004; Douglass et al., 2019) are also explored and interpreted with available literature. These data allow us to investigate the role of the various drivers of vegetation change including climate, fire, herbivory, and human activity in the region. Comparison of the two sites with previous work helps to reconstruct the spatial changes in the region and contribute to the debates over the antiquity of open and mosaic ecosystems and the roles of anthropogenic and climatic drivers of change in Central Highlands Madagascar during the last millennium. These data provide an important contribution to biodiversity conservation and fire management in Madagascar.

6.2 Vegetation history and environmental change in *Tampoketsa-Ankazobe* wetland and its surrounds during the last ca. 11 200 years

The pollen results in the $TAMB_2$ sediment core suggested that the local vegetation in Tampoketsa-Ankazobe wetland and its surrounds were dynamic during the last ca. 11 200 cal years BP (see Chapter 4). Across the four (4) main zones identified in the pollen records (see Chapter 4 and Figure 6.1), the vegetation changed from a mosaic of ericoid shrubland and mid-elevation forest during the Early Holocene characterised by taxa such as Ericaceae, *Uapaca* cf. *densifolia* and *Celtis*, to an ericoid shrubland/ high-elevation forest mosaic vegetation represented by Ericaceae, *Ilex mitis* and *Podocarpus madagascariensis* dominating between Mid-Holocene and the Late Holocene, to finally becoming a grass-dominated landscape as seen today in the Central Highlands of Madagascar (Bond et al., 2008; Vorontsova et al., 2016). These changes in the vegetation during the Holocene occurred during variable climate conditions and increasing occurrence of fire, which likely occurred throughout the area.

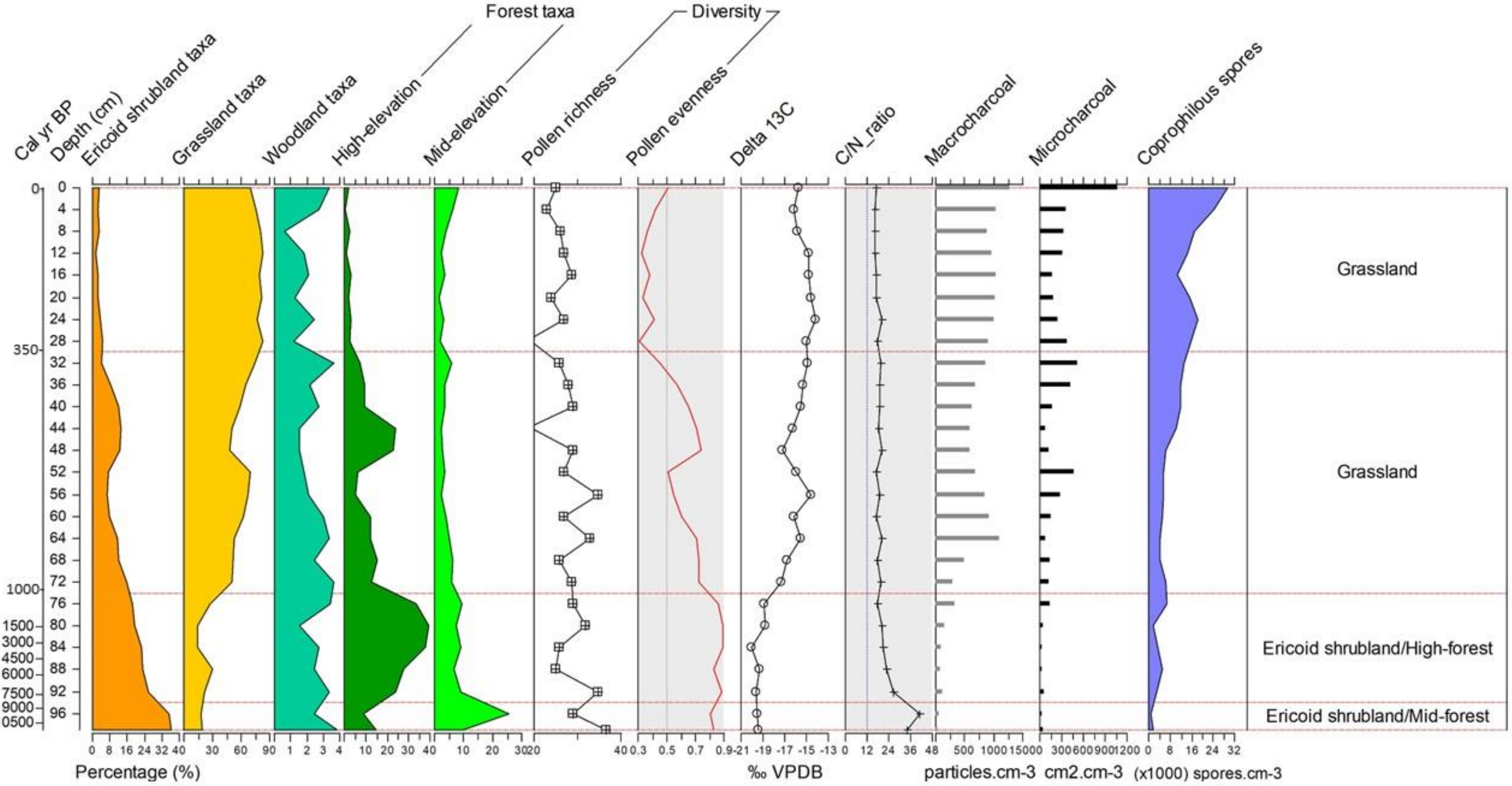


Figure 6.1: Diagram summarising the relative abundance and diversity of pollen record with stable carbon isotopes, charcoal and coprophilous spores in Tampoketsa-Ankazobe wetland during the last ca. 11 200 cal years BP. Attributed vegetation are provided on the right side and detailed taxa belonging in each vegetation type is provided in section 4.4.2 and Figure 4.5.

6.2.1 Mosaic of ericoid shrubland and mid-elevation forest taxa dominated vegetation from ca. 11 200 and 8300 cal years BP

During the Early Holocene, pollen assemblages in Tampoketsa-Ankazobe wetland were dominated by Ericaceae shrub pollen with some arboreal taxa (see chapter 4 and Figure 6.1). The ericoid shrubland is currently found at higher elevations i.e., greater than 2000 m (Burney, 1996; Burgess et al., 2004; Goodman, Raherilalao & Wohlhauser, 2018) down to 1500 m, in areas where fires are less common (Radimbison, 1990; Bond, personal communication 2021, June). Arboreal taxa in the record during this period was marked the abundance of taxa such as *Polyscias* sp. with some Combretaceae type, *Diospyros* and *Schefflera* pollen. These arboreal taxa are commonly located at mid-elevation (800-1600m) in Madagascar, today particularly around ravines due to higher humidity within these areas (Madagascar Catalogue, 2021). The presence of both ericoid and arboreal taxa suggested a mosaic landscape during this period, in which forest elements occurred only in restricted patches within an ericoid matrix. Grass pollen was relatively low (< 20%) during this period, compared to their abundance in modern pollen samples (ca. 27 to 90%) from grassland in Madagascar (Burney, 1988; Straka, 1991; Razafimanantsoa, 2015). Despite the low abundance of grass pollen, stable carbon isotopic (δ^{13}C) analysis of the sediment samples reflected a mixed C_3-C_4 plant assemblage with a slight trend towards C_3 plants (Vågen, Walsh & Shepherd, 2006; Crowley et al., 2011). Aquatic and marginal plants dominated by *Cyperus* (Muasya et al., 2011) were rare (see Figure 4.6, findings section), and the C/N ratio was high, greater than 12, indicating that δ^{13}C originated on land (Bonn & Rounds, 2010).

The abundant mosaic of ericoid shrubland and mid-elevation forest taxa in Tampoketsa-Ankazobe between 11 200 and 8300 cal years BP coincided with succession of warm/wetter condition followed by a cold period. The warm and wetter period between 11 200 and 10 000 cal years BP promoted the establishment of mid-elevation forest elements in the region (Burney, 1996; Gasse & Van Campo, 1998). This condition was generally synchronous with the regional AHP (African Humid Period), due to an increase in summer precipitation induced by the African monsoonal climatic, oceanic and terrestrial feedbacks (Claussen & Gayler, 1997; Tierney & DeMenocal, 2013). However, the cold period in the region from 10 000–8000 cal years BP corresponded to the cooling event in the northern hemisphere (Alley et al., 1997) which maintained the ericoid shrublands (Burney, 1996; Straka, 1996). The abundance of ericoid shrubland in our record on the eastern slopes coincided with the occurrence of montane bushland from the Lake Tritrivakely and Lake Itasy pollen record located in Vakinankaratra and Itasy regions, respectively along the western slopes of the highlands around the same period, i.e. ca. 10 000 cal years BP (Burney, 1987a; Straka, 1996). These results might suggest that ericoid shrubland regionally dominated the Central Highlands during the Early Holocene. However, the lower relative abundance of grassland recorded in Tampoketsa-Ankazobe wetland during this period contrasted to the western slopes records represented by the Lake Tritrivakely and Itasy during the same period with moderate to high grass abundance (Burney, 1987a; Straka, 1996; Gasse & Van Campo, 1998). The latter might indicate the importance of factors other than climate driving vegetation change in the region between ca. 11 200 and 8300 cal years BP.

As inferred from charcoal concentration, there was a low fire occurrence in Tampoketsa-Ankazobe landscape during this period with a difference of about 200 particle.cm^{-3} compared to the maximum concentration for the whole core investigated here. This finding contrasted with the record from Lake Tritrivakely at the same period, which showed a high fire frequency through charcoal concentration and influx (Burney, 1987a). This high fire frequency around Lake Tritrivakely was associated with an abundance of grass leading to an increase in biomass and the presence of a volcanic crater in the vicinity of the high massif mountain of Vakinankaratra, which is thought to lead to higher fire ignition sources (Burney, 1987a, 1996). Two phreatomagmatic deposits from volcanic activities were dated to have occurred ca. 32 000 and 19 000 cal years BP near Lake Tritrivakely (Rufer et al., 2014) earlier than the period covered in the present study. The Tampoketsa-Ankazobe wetland site, on the other hand, is located within a non-volcanic area (Balasubramanian et al., 1995), which might explain the low to no charcoal in the record during this period. Very low coprophilous spores concentration indicating low herbivory activities were also recorded at this time, similar to other findings from the region before human arrival (Burney, Robinson & Burney, 2003). Thus, the low occurrence of fire, herbivory activities and very low sediment accumulation rate recorded in the Tampoketsa-Ankazobe during the Early Holocene suggested an unlikely early human activities and land-use in the area. This low sediment accumulation rate was also recorded in some sites within the Central Highlands such as at Alaotra region during the last ca. 10 000 years (Mietton et al., 2018; Brosens et al., 2021). This might indicate a low to no human population in the highlands during that period compared to a suggested early human presence and activities in the Southwestern region (Hansford et al., 2018).

These findings could suggest that the warm and wet climate followed by cool period during the Early Holocene accompanied by low occurrence of fire and herbivory activities, might have favoured the establishment of ericoid shrubland taxa with forest elements probably restricted to mid-elevation during the period. Also, no early presence of human activities was recorded during the period. However, further ecological investigation of the responses of mid-elevation taxa and treelines to climatic factors should be conducted to investigate this further. More precisely on how past climate variability and the increasing temperature associated with climate change might affects these ecosystems.

6.2.2 Ericoid shrubland and high-elevation forest mosaic dominated vegetation between ca. 8300–1000 cal years BP

Between ca. 8300 and 1000 cal years BP, the landscape surrounding the Tampoketsa-Ankazobe wetland was characterised by ericoid shrubland with an increased abundance of high-elevation forest taxa. Compared to the previous period, there was a decline of Ericaceae shrub pollen (from ~36% to 20%), while arboreal forest taxa such as *Ilex mitis, Faurea* sp., *Podocarpus* cf. *madagascariensis* and *Vitex* sp. increased to ca. 33% throughout the period. These forest taxa are currently abundant in high-elevation montane sites (Burgess et al., 2004; Madagascar Catalogue, 2021). Based on our data, this period showed an expansion of wooded and forest elements into areas formerly occupied by ericoid shrubland. Grass pollen remained low as with the previous period but was characterised by a slight increase at ca. 4000 cal years BP. The abundance of shrubland and forest with some slight increase of grassland at certain periods coincided with the mixed C_3-C_4 plant assemblage in the stable carbon isotope results during the period with more terrestrial pollen source (high C/N ratio). Our findings corresponded to the pollen record at Lake Itasy from ca. 9000 cal years BP to 950 cal years BP (ca. 1000 AD), which was characterised by an expansion of forest/woodland at high-elevation (Straka, 1996). These changes of vegetation after the Early Holocene might have occurred at a more regional scale but more vegetation reconstructions are still needed to verify this.

The occurrence of both ericoid and high-elevation arboreal taxa in Tampoketsa-Ankazobe wetland between ca. 8000 and 1000 cal years BP suggested the presence of a mosaic landscape in the area and this occurred within variable climatic periods which tend to be warm and dry (Gasse & Van Campo, 1998) including the end of the AHP and the widespread dry climate (4.2ka drought event) around ca. 5000 and 4000 cal years BP , respectively due to decreasing amount of summer monsoon rainfall in Africa suggesting a possible migration of the ITCZ (Gasse, 2000; Mayewski et al., 2004; Tierney & DeMenocal, 2013; Scroxton et al., 2020). Climate also became warm compared to the previous period and ericoid shrubland might have occupied the high-elevation areas where cooler conditions exist (Burgess et al., 2004).

Low local fire occurrence and herbivory activities were recorded in the Tampoketsa-Ankazobe wetland data between ca. 8300 and 1000 cal years BP. The low occurrence of fire during the period may explain the persistence of ericoid shrubland in the area, although the rising temperatures (Gasse & Van Campo, 1998) and associated forest expansion may have resulted in a modest decrease (from ~36% to 20%) in ericoid shrubland in comparison to the cold period in the Early Holocene. Palaeorecords (fire and herbivory activities) from the region particularly in the western slopes of the highlands such as those from Lake Kavitaha and Tritrivakely demonstrated sudden peaks of charcoal and increase of coprophilous spores from ca. 1400 and 1200 years BP, respectively and were interpreted as a source from anthropogenic fire (Burney, 1987a,b; Burney et al., 2004). This might suggest that less significant trace of human occupation was recorded in Tampoketsa-Ankazobe and its surroundings before ca. 1000 cal years BP despite evidence of human settlement in the Central Highlands at ca. 2000 cal years BP (Burney et al., 2004). The combined evidence suggests that even if there was a human presence and signs of pastoralism activities at other archaeological and palaeoecological sites in the Central Highlands (Burney, Robinson & Burney, 2003; Burney et al., 2004; Samonds et al., 2019; Crowley et al., 2021), the area around Tampoketsa-Ankazobe might have been settled later. This is still reflected in the presence of a forest, ericoid shrubland and grasslands mosaic in the area that is currently close to (ca. 10 km) Ambohitantely protected area.

To summarise, the mosaic of ericoid shrubland and high-elevation forest taxa present in Tampoketsa-Ankazobe between ca. 8000 and 1000 cal years BP were conditioned by the variability of climate during a possible migration of the ITCZ and the low occurrence of fire during the period. Less human activities was recorded in the area and its surrounds between ca. 2000 and 1000 cal years BP compared to palaeoecological records from the western slopes, which demonstrated the beginning of pastoralism (Burney, 1987b).

6.2.3 Increasing grassland dominated vegetation between ca. 1000 and 350 cal years BP

Between ca. 1000 and 350 cal years BP, the pollen record in Tampoketsa-Ankazobe wetland experienced a massive decrease of Ericaceae shrubland and arboreal forest taxa (from ~36 to ~10% and 30 to 17%, respectively), but a high increase abundance of grass pollen ("from ~20 to 60%"). This shift of vegetation corresponds with the highest value of compositional change with the lowest pollen richness and evenness recorded in the area over time (see chapter 4, Figure 4.7). High-elevation tree taxa, represented by *Podocarpus madagascariensis*, *Ilex mitis*, *Vitex* sp. and *Faurea* sp. decreased but remained present in the area (Figure 6.1), suggesting a contraction of the forest patches mostly found in the higher elevations and a corresponding expansion of grasslands at the expense of shrublands and forest. The abundance of Poaceae pollen during this period is within the range of Poaceae pollen in surface samples from areas predominantly covered with grasslands on the island (Burney, 1988; Straka, 1991; Razafimanantsoa, 2015). This was also reflected in the stable carbon isotope analysis of the sediments, which showed a very high increase of C_4 plants. It corresponded to the high C/N ratio reflecting the terrestrial pollen source of the $\delta^{13}C$ value.

This increasing abundance of grassland in Tampoketsa-Ankazobe wetland corresponded to the opening of vegetation in the Central Highlands, and elsewhere on the island, based on pollen analysis (Burney, 1987a,b; Matsumoto & Burney, 1994; Virah-Sawmy, Willis & Gillson, 2009; Wirah-Sawmy, Gillson & Willis, 2009; Razanatsoa, 2019; Samonds et al., 2019). During the last ca. 1000 cal years BP, the Central Highlands region experienced a drier and warmer climate interpreted as a short drought period recorded at ca. 950 cal years BP from diatom and pollen analysis which corresponded with the MWP (Medieval Warm Period) recorded mostly in the Northern hemisphere but was marked by warm period recorded in Africa due to solar activity and the influence of multidecadal oscillation of the Atlantic (Gasse & Van Campo, 1998; Virah-Sawmy, Willis & Gillson, 2010; Lüning, Gałka & Vahrenholt, 2017). Dry conditions were also recorded in much of tropical Africa during the last millennia (Mayewski et al., 2004). The shift of dominance of grass pollen in our record corresponded to the drought period in the region, suggesting the possible importance of climate as a driver (or at least an initiator) of grassland expansion at this time.

The charcoal concentration in Tampoketsa-Ankazobe wetland also increased (from ~34 to 234 particles.cm^{-3}) during this period, suggesting an increase in fire associated with the increase of grass and likewise a decrease of shrubs and trees in the area. The increase of fire occurrence during the period might also be the source of increasing grass cover and decreasing ericoid shrubland and trees i.e., consistent with a shift in vegetation possibly initiated by drought but then maintained by vegetation/fire feedbacks. Our records also showed peaks of fire occurrence accompanied by increased herbivory activities at ca. 500 and 380 cal years BP, respectively that occurred during the regional cool period LIA (Little Ice Age) (Tyson et al., 2000). Those peaks of fire and herbivory activities in the area occurred after the known extinction of megafauna on the island at ca. 1000 cal years BP, although a very low indication of megafauna activities was recorded in the Central Highlands prior to this period (Burney et al., 2004; Crowley, 2010; Godfrey et al., 2019a). The results suggest the presence of humans and their activities associated with fire and pastoralism during this period. This human influence in the area corresponded to the sudden sharp increase of sediment accumulation rates in $TAMB_2$ core (see Figure 4.3) which is often associated with an increase in population and cropland density impacting land-use and erosion (Baud et al., 2021). Based on the sharp increase of fire occurrence and herbivory activities in the area, human influence mostly occurred from ca. 500–400 cal years BP possibly adapting to the cold climate conditions during this period. These traces of human influence occurred a few centuries later than the previous published palaeofire records, which were recorded by Burney (1987b) in the region at ca. 1000 cal years BP, again suggesting a later settlement in the area surrounding the site.

In summary, the data suggested an increasing openness of vegetation surrounding Tampoketsa-Ankazobe wetland between ca. 1000 and 350 cal years BP. The vegetation was characterised by a massive decrease in ericoid shrubland, a loss or contraction of high-elevation forest patches and expansion of grassland. These changes occurred during a warm and dry period and coincided with the beginning of a human signal in the records indicating increasing anthropogenic influence on the landscape reflected by sharp increase of sediment accumulation rate during the period.

6.2.4 Open grassland ecosystem during the last ca. 350 cal years BP

For the last ca. 350 cal years BP to the present period, the pollen assemblages in Tampoketsa-Ankazobe wetland were characterised by a low pollen richness (Figure 4.7) along with a very high abundance of Poaceae pollen (ca. 80%) compared to ericoid shrubland and arboreal tree taxa, including both mid- and high-elevation taxa, which appeared as traces (ca. 2%). This was reflected in the stable carbon isotope results indicating an abundance of C_4 plants despite an increase in aquatic plants during this period (see section 4.4.3). This dominance of C_4 plants corresponds to the high C/N ratio confirming a terrestrial pollen source of the stable carbon isotope results. Grass pollen attained its maximum value of ca. 80% during this period, corresponding to the characterisation in surface sample analysis as an open grassland ecosystem (Burney, 1988; Straka, 1991; Razafimanantsoa, 2015). The climate in the region was dry as based on diatom records from the region (Gasse et al., 1994; Gasse & Van Campo, 1998), and this was confirmed with the high-resolution data in Lake Dangovavy during the period with an increased abundance of benthic compared to planktonic, taxa (see section 5.10). The dry climate likely contributed to the increase of grassland during this period, as recorded in the area during the previous period and also in other regions in Madagascar such as the southeast (Virah-Sawmy, Willis & Gillson, 2010).

In parallel, Tampoketsa-Ankazobe wetland showed a high abundance in charcoal and coprophilous spores, indicating a higher fire occurrence and herbivory activities during the last ca. 350 cal years BP. The increase of fire regime and herbivory activities during this period, likely linked to pastoralism activities in the area. Currently fire remains high in Ankazobe region which is often associated with high deforestation rate where people cleared forest for agriculture (e.g. Gade 1995; Rajemison 2010). Deforestation fires are common in tropical ecosystems and they are exacerbated by the increased length and intensity of the dry season (Van Der Werf et al., 2008). In the Tampoketsa-Ankazobe wetland record, occurrence of fire continued to increase during the last ca. 300 cal years BP (1600 AD) in contrast to the palaeofire record in other regions, for instance at Lake Kavitaha in Itasy region which experienced a decrease of fire within the same period (Burney, 1987b). This contrast might be linked to local land-use, as people in Ankazobe district are more pastoralist (Kull, 2000; Ratsirarson & Goodman, 2000; Pareliussen, 2004), which requires recurrent fire use and explains the continuing high deposition rate of charcoal in the region while in Itasy, livelihood is focused on agriculture (Andrianampiarivo, 2017). This might also explain the decline of woody taxa in Tampoketsa-Ankazobe wetland with the need to expand pasture land (Kull, 2000). The results contrast with Burney (1987a) in Lake Kavitaha where arboreal taxa supposedly “regenerated” from 300 BP to the present period.

To summarise, since ca. 350 cal years BP, vegetation in the landscape surrounding the Tampoketsa-Ankazobe wetland was dominated by an open grassland ecosystem with a reduction in the mosaic woody taxa. These changes were most likely due to anthropogenic fire linked to pastoralism, but also influenced by the dry climate.

6.3 Vegetation history and environmental change at Lake Dangovavy during the last 6200 BP years

Reconstruction of vegetation from the pollen results in the Dangovavy (DAN) sediment core showed that past vegetation at Lake Dangovavy and its surrounds was dynamic during the last 6200 cal years BP (see Chapter 5; Figure 6.2). From the five (5) main vegetation zones identified through pollen assemblage in DAN sediment core, vegetation in the area successively changed from a mosaic of grassland-ericoid and high-elevation forest dominated during the Mid-Holocene to an ericoid-mid-elevation forest mosaic dominated until ca. 4200 cal years BP, and then forest-savanna mosaic dominated until ca. 3000 cal years BP. Between ca. 3000 and 1000 cal years BP, the vegetation was dominated by ericoid shrubland and mid-elevation forest to finally become a more open grassy ecosystem during the last ca. 1000 cal years BP. These changes in the vegetation during the last ca. 6200 cal years BP took place during a variable climate condition and fire frequency as inferred from published reviews and our diatom and charcoal data. The latter indicates that local and regional fire patterns are similar due to a significant positive correlation between macrocharcoal and microcharcoal (see section 5.5.1).

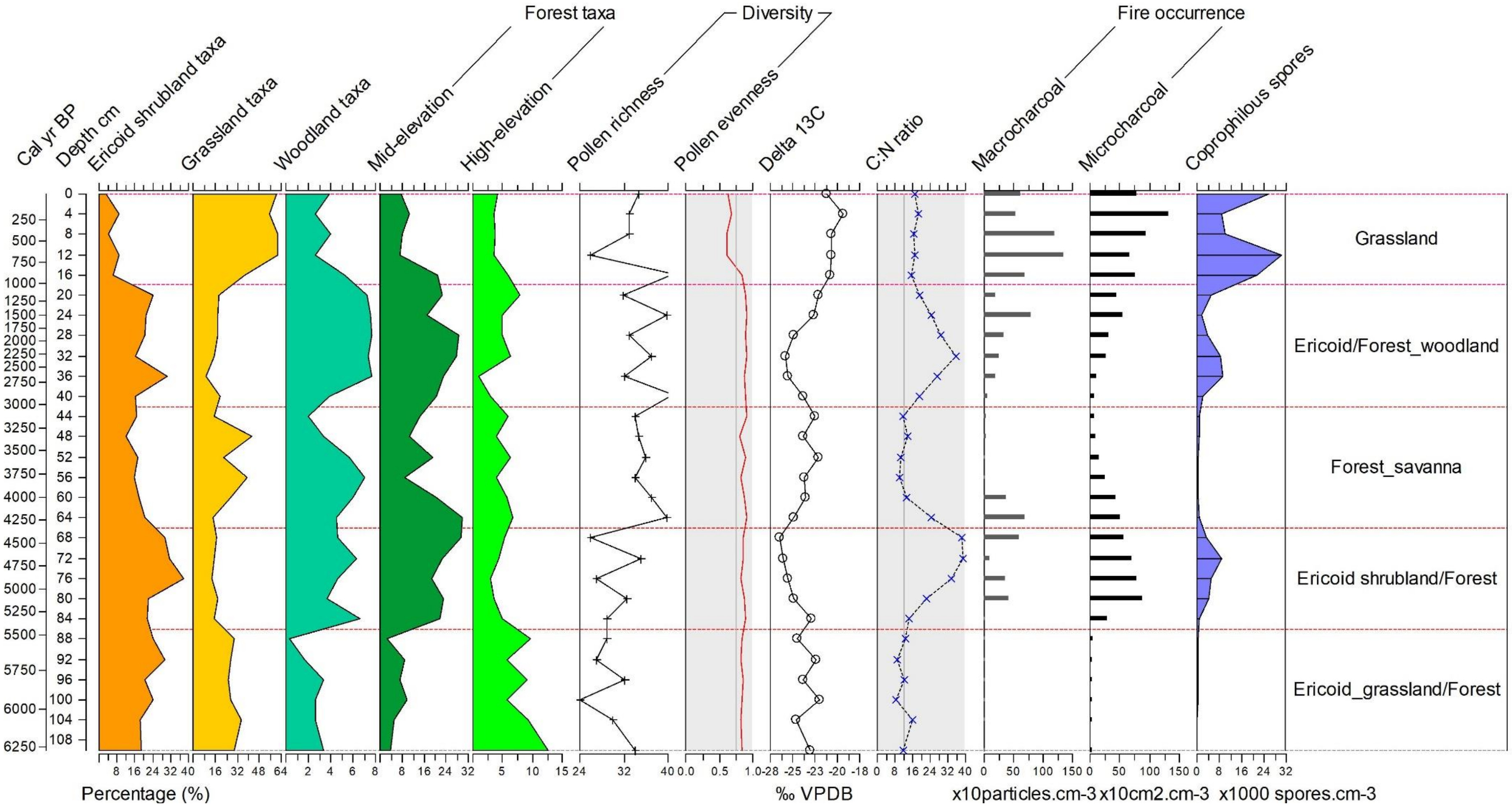


Figure 6.2: Diagram summarising the relative abundance and diversity of pollen record with stable carbon isotopes with charcoal and coprophilous spores in Lake Dangovavy during the last ca. 6 200 cal years BP. Attributed vegetation are provided on the right and detailed taxa belonging in each vegetation type is provided in section 5.4.2 and Figure 5.5 .

6.3.1 A mosaic ecosystem dominated by grassland-ericoid shrubland and high-elevation forest between ca. 6200 and 5400 cal years BP

Between ca. 6200 and 5400 cal years BP, the pollen assemblage at Lake Dangovavy and its surrounds was dominated by Poaceae, Ericaceae and some arboreal taxa. Co-existence of grass (ca. 30%) and ericoid pollen is currently characteristic of surface samples analysed from the montane grassland ecosystems in Madagascar (Burney, 1988). The arboreal forest taxa were characterised by the occurrence of high-elevation tree taxa including *Podocarpus* cf. *madagascariensis*, *Ilex mitis* and *Faurea* sp; as well as riverine tree taxa (*Anthocleista* cf. *amplexicaulis* and *Entada* cf. *chrysostachys*). The presence of both montane grass-ericoid and arboreal taxa suggested a mosaic landscape during this period, but one in which forest taxa were restricted in high-elevation and alongside ravines. The abundance of shrubs and arboreal taxa during the period were confirmed by the stable carbon isotopes with more C_3 plants dominating. Also, at Lake Dangovavy, C_3 montane grasses were supposedly abundant during this period according to the δ^{13}C low C/N ratio value which is characteristic of C_3 grasses (Archibald, Hempson & Lehmann, 2019), and the general switch to C_3 grass species at higher elevations (e.g., Cabido et al., 1997). C_3 grasses are currently found under some forest patches of the Central Highlands, which are dominated by the genus *Oplismenus* (Solofondranohatra et al., 2018). However, more research is needed to confirm the type of dominant grass from the sediment in the region during this period using proxies such as phytoliths, which unlike pollen can distinguish Poaceae beyond the family level.

The abundance of mosaic montane grassland and ericoid shrubland with forest patches at Lake Dangovavy during the Mid-Holocene corresponded with the previously published pollen record from Lake Tritrivakely by Burney (1987c), where grass and ericoid pollen supposedly co-existed in the region between ca. 9000 to 5500 cal years BP. Both records are from the western slopes of the highlands and presented similar patterns with a particular presence of montane grassland during the Mid-Holocene. The abundance of these taxa during this period coincided with generally lower temperatures in the Southern Hemisphere with particularly cool periods in the eastern parts of Africa (Mayewski et al., 2004). In addition, gradual decrease in the strength of the Indian summer monsoon and Asian summer monsoon rainfall have been recorded in the Indian Oceans from ca. 6000 cal years BP (Gupta, Das & Anderson, 2005; Wang et al., 2005) which promoted the decrease of humidity in the region during this period (De Boer et al., 2014). It coincided with the presence of dry conditions in the Central Highlands of Madagascar, as demonstrated through pollen, diatom and speleothem analyses (Burney, 1987a; Gasse & Van Campo, 1998; Wang et al., 2019). The cool and dry conditions might explain the abundance of grass, particularly C_3 grasses, in the area and the forest taxa along the river and upper montane sites with higher local moisture availability (Goodman, Raherilalao & Wohlhauser, 2018).

A low abundance of charcoal and coprophilous spores indicated low fire occurrence and herbivory activities at Lake Dangovavy and its surrounds during this period. The dry conditions experienced in the area during the Mid-Holocene could mean that there were fewer lightning events that would have ignited fires during this period. This low fire occurrence could also have favoured and maintained the mosaic landscape of supposed C_3 dominated grassland, ericoid shrubland and forest taxa during the period which are known to be fire intolerant (Vieilledent et al., 2018; Archibald, Hempson & Lehmann, 2019). In addition, the low abundance of herbivory activities in the area indicate low grazing and therefore low density of megafauna during the period, where expansion of megafauna above 1300 m a.s.l in the region is supposedly very limited (Burney, Robinson & Burney, 2003; Crowley et al., 2021). Consequently, the latter might also promote increasing in shrubs and trees during the period, as seen in the African savanna (Roques, O'Connor & Watkinson, 2001).

To summarise, a mosaic of grassland, ericoid shrubland and high-elevation forest taxa occurred in Lake Dangovavy between ca. 6200 and 5400 cal years BP. There was climate-fire controlled vegetation during this period where the cold/dry climate and the low fire occurrence were hostile for an abundance of montane C_3 grass and ericoid shrubland but also maintained an abundance of trees located within areas of higher moisture, such as higher elevations and/or alongside the river.

6.3.2 Mosaic of ericoid shrubland and mid-elevation forest taxa between ca. 5400 and 4300 cal years BP

This period was characterised by the increasing abundance of Ericaceae, Asteraceae pollen and some arboreal taxa such as *Celtis* sp., *Eugenia* sp., *Trema orientalis* and *Uapaca* cf. *bojeri*. Ericoid shrubland and Compositae are currently abundant in the major massif montane regions on the island, in vegetation type classified as Madagascar ericoid thickets, that occur at elevations greater than 2000 m a.s.l. under a much colder climate (Burgess et al., 2004; Goodman, Raherilalao & Wohlhauser, 2018). However, as seen in the $TAMB_2$ site, the ericoid shrubland is also found down to 1500 m in locations where wildfires are uncommon and suppressed in the region (Radimbison, 1990; Bond, personal communication 2021, June). The arboreal taxa during this period were more dominated by mid-elevation tree taxa, which is similar to their current status on the island (Goodman, Raherilalao & Wohlhauser, 2018; Madagascar Catalogue, 2021). The abundance of shrubland and arboreal taxa during this period correlated with the results of the stable carbon isotopes ($\delta^{13}C$) analysis of the sediments, which showed an abundance of C_3 terrestrial plants reflected by the high C/N ratio value and the low abundance of *Cyperus* aquatic pollen. This also corresponds with the decreased abundance of grass pollen during the period. These changes in the vegetation from ca. 5400 to 4300 cal years BP in Lake Dangovavy corresponded to the wettest period in the Late Quaternary of Madagascar as described by Burney in (1996) which showed an identical pattern to southern Africa (Wang et al., 2019) and was also influenced by southern African rainfall (Brook, Cowart & Brandt, 1998). In addition to the higher effective moisture, cool conditions were recorded in the Central Highlands during this period (Goodman & Jungers, 2014). These climatic conditions might have helped to maintain the mosaic ecosystem during this period, where the mid-elevation forest taxa were promoted by the humid period while the ericoid shrubland, expanded in the mid-elevation, was supported by cold periods.

The increase of charcoal concentration particularly the microcharcoal (from ~44 to 650 $cm^2.cm^{-3}$) indicated increase occurrence of fire at Lake Dangovavy and its surrounds between ca. 5400 and 4300 cal years BP. Fire increase during this period could be related to the wet period, higher biomass and with more lightning events that would have ignited fires in the area. In fact, lightning is recorded as source of fire in the highlands (Kull, 2002b) and no evidence of human settlement has been yet found in the highlands before ca. 2000 cal years BP (Douglass et al., 2019). In addition, volcanic activity reportedly occurred in the Vakinankaratra region during this period (Burney, 1987a) and might also promote fire in the area. Likewise, the slight increased of coprophilous spores (from ~0.2 to $4.3.10^3$ $spores.cm^{-3}$) could indicate a slight increase of megafauna density in the area during the period. However, this change in the abundance of coprophilous spores might be related to the wetter period which probably increase the size of the lakes and thus the taphonomy of the spores (Raper & Bush, 2009). This is in contrast with results from the Tampoketsa-Ankazobe wetland (Chapter 4) and Lake Tritrivakely where herbivory remained low during this period (Burney, Robinson & Burney, 2003). More data will clarify the abundance of megafauna in the region, but our palaeoecological proxies suggest a difference in the local distribution of megafauna during the period.

In addition, considering that montane grasslands have been dominated by C_3 grass traits as speculated in the previous period, they are less tolerant to fire and are preferred by grazers (Archibald, Hempson & Lehmann, 2019). This could mean that the remaining grasses after fire passage were grazed by herbivores, which could explain the decrease of grassland during this period. This assumption is supported by the analysis of carbon isotope data of extinct hippos in the region which reflect pure C_3 diets in the high-elevation sites of the Central Highlands (Crowley et al., 2021). The ericoid shrubland persisted, despite the moderate increase of fire and this could be explained by the forest acting as a fire break that prevented the spread of fire throughout the landscape. The interaction between topography, and vegetation fire feedbacks, helps to create fire refugia for the ericoid shrubland (Krawchuk et al., 2016; Meddens et al., 2018).

In summary, the data suggest a shift in dominance of ericoid shrubland and mid-elevation forest taxa between ca. 5400 and 4300 cal years BP. There was climate, fire refugia and herbivory feedbacks controlling the vegetation during this period. The humid period promoted more lightning-sourced fire and the development of the mid-elevation forest taxa which act as fire refugia for the ericoid shrubland. Grazing activities impacted the slight decrease of montane grass in the area in addition to the fire. This narrative is speculative, however, and more data is needed to differentiate the type of grass existing in the region with a particular focus on records during the Mid-Holocene and the impact of megafauna on the vegetation dynamics.

6.3.3 Forest-Savanna mosaic between ca. 4300 and 3000 cal years BP

This period was characterised by a shift in compositional change as reflected in the Beta diversity analysis from the pollen data (Figure 5.7) and marked by an abundance of Poaceae pollen, as well as a slight and significant decrease of arboreal and ericoid shrubland taxa. Grassland increased compared to the previous period and peaked both at ca. 3800 and 3400 cal years BP. Those peaks are recorded around the maximum representation of Poaceae (at ca. 4000 cal years BP) in the region, supposedly the driest and warmest period in the highlands, and interpreted as the most severe drought period in the Central Highland’s region during the entire Holocene (Gasse & Van Campo, 1998; Virah-Sawmy, Willis & Gillson, 2010; Wang et al., 2019) that corresponded to the 4.2 ka event in the African continent (e.g., Scroxton et al., 2020). This drought may have resulted in a significant decrease of ericoid shrubland in Lake Dangovavy compared to the two previous periods. Arboreal taxa also decreased but some mid-elevation and woodland tree taxa, such as *Celtis* cf. *gomphophylla, Trema orientalis* and *Uapaca* cf. *bojeri*, persisted. In fact, in the highlands, the *Celtis* cf. *gomphophylla* and *Trema orientalis* are margin forest taxa (Burney, 1988) that are classed as deciduous taxa (Leroy, 1952) and pioneer taxa (Koechlin, 1972). *Uapaca* cf. *bojeri*, the only species of *Uapaca* found in Vakinankaratra region, where Lake Dangovavy is located, (Kull, Ratsirarson & Randriamboavonjy, 2005; Rakotondrasoa et al., 2012; McPherson, 2011), is a light-demanding and fire-resistant tree characteristic of the savanna ecosystem (Rakotondrasoa et al., 2012; Razafimanantsoa et al., 2013). The combined evidence of abundant grassland and trees characteristic of savanna or forest margins within a drought period suggest a presence of forest-savanna mosaic ecosystem surrounding Lake Dangovavy between ca. 4300 and 3000 cal years BP. Pollen records from Lake Tritrivakely showed similar trends to our results and the vegetation was characterised by a "savanna-like assemblage ecosystem" (Burney, 1987a). These open savanna ecosystems would have covered a more regional distribution in the highlands with closed forests confined to patches alongside water sources. Despite the increase of grassland during this period, the stable carbon isotopes in Lake Dangovavy remained dominated by C_3 plants. This could be explained by the reflection of aquatic plants in the $\delta^{13}C$ results confirmed by the low C/N ratio (see Figure 5.5), and also the abundance of *Cyperus* plants during the period (see Figure 5.6) which support the dry event during the period.

There was a peak in macrocharcoal indicating high local fire occurrence at the beginning of the period (ca. 4200 cal years BP) in Lake Dangovavy but charcoal later decreased and was generally low during the entire period. The high fire occurrence at the beginning of the period might have promoted the abundance of grassland and pyrogenic tree such as *Uapaca* cf. *bojeri* and *Trema orientalis* compared to the ericoid shrubland and other trees, which are fire intolerant and started to decrease when the fire was combined with drought periods. A threshold might have been reached when the combination of fire with drought lead to an ecosystem shift to a more open savanna dominated system. On the other hand, a low abundance of coprophilous spores, suggesting low herbivory activities and thus low megafauna biomass, was recorded in the area during the same period. This low herbivore activities might be linked to reduced local animal density and functional species extinction in the landscape (Gill et al., 2009) possibly due to the drought event that occurred during this period (Gasse & Van Campo, 2001). It was also reflected in Tampoketsa-Ankazobe wetland (see section 4.5.2) and Lake Tritrivakely (Burney, Robinson & Burney, 2003), and therefore suggesting a regional pattern.

To summarise, vegetation in Lake Dangovavy changed to a forest-savanna mosaic with an abundance of grassland between ca. 4300 and 3000 cal years BP. This corresponds with the presence of a drought period occurring during the 4.2ka event and the possible beginning of an increasing fire in the area during the same period. These conditions led to the reduction of herbivory activities during the period.

6.3.4 Forest/Woodland and ericoid shrubland mosaic between ca. 3000 and 1000 cal years BP

Between ca. 3000 and 1000 cal years BP, vegetation at Lake Dangovavy and its surrounds was characterised by an increased abundance of Ericaceae and Asteraceae pollen with the mid-elevation arboreal taxa. The co-existence of ericoid shrubland and Asteraceae, was not as high as it had been during the Mid-Holocene. Mid-elevation tree taxa were represented by marginal forest and woodland taxa, such as *Celtis* cf. *gomphophylla*, Combretaceae type, *Morus* sp. *Trema orientalis, Tephrosia* cf. *barclayi* and *Uapaca* cf. *bojeri* (Figure 5.5). In addition, there was a low presence of Poaceae pollen during this period, as reflected by more C_3 plant signatures in the stable carbon isotopes ($\delta^{13}C$) results. The C/N ratio was also high during this period reinforcing the abundance of C_3 plants from the terrestrial environment, in addition to the low abundance of aquatic *Cyperus* plants.

The abundance of the mosaic of ericoid shrubland and margin forest/woodland taxa during this period particularly from ca. 3000 to 2000 cal years BP corresponded to the return of a cool and wet period in the Central Highlands of Madagascar as suggested by the analyses of mineral-magnetic proxies (Williamson et al., 1998). The cool period likely persisted in the region until ca. 1000 cal years BP (Gasse & Van Campo, 1998). From ca. 2000 to 1000 cal years BP, the hydrological regimes in the area, as analysed through diatom abundance, showed that Lake Dangovavy was shallow in general as indicated by the high abundance of benthic diatom taxa (see Figure 5.9). A peak of the benthic diatom taxa coupled with the lower representation of planktonic diatom taxa was recorded at ca. 1500 cal years BP suggesting that Lake Dangovavy levels declined further and may have even shifted to moist/water-saturated ground. This coincided with the start in the disappearance of riverine taxa (*Anthocleista* cf. *amplexicaulis* and *Entada* cf. *chrysostachys*) and sudden massive decreases in water-dependent tree taxa (e.g., *Eugenia* sp.) in the vegetation. In addition, a short humid period was recorded at ca. 1100 cal years BP in the area through a peak and abundance of planktonic diatom taxa compared to the benthic taxa (see Figure 5.10), but the change was not recorded in the vegetation. The abundance of these planktonic taxa might indicate flash floods, short-lived high-intensity events in which diatoms respond to due to their short generation time (Wolin & Stone, 2010). However, this general trend to more shallow lake i.e., dry environment in Lake Dangovavy between ca. 2000 and 1000 cal years BP contrasted with the diatom record in Lake Tritrivakely, which suggested a relatively humid period in the highlands during this time (Gasse & Van Campo, 1998; Wang et al., 2019). This indicates that the site around the Lake Dangovavy possibly experienced different local conditions (microclimate) from ca. 2000 to 1000 cal years BP, but more data from various other sites from the Central Highlands are needed.

As inferred from charcoal concentration, there was an increase in fire occurrence (from ~200 to 310 particules.cm^{-3}) during the period. The peak of charcoal abundance was recorded at ca. 1500 cal years BP and this coincided with the period where the lake was shallow as characterised by the peak of benthic taxa. The presence of fire combined with moderate dry climate might have favoured woodland taxa but was not enough to promote the spread of grass. Herbivory activities also moderately increased during the period but with more abundance from ca. 3000 to 2000 cal years BP compared to ca. 2000-1000 cal years BP. Therefore, the increase of herbivory activities in the area from ca. 3000 to 2000 cal years might be explained by a slight return in abundance megafauna in the area during the short return of humid period, which started to decrease between ca. 2000-1000 cal years BP due to a shifting dry period accentuated by an increase of fire in the area. Our findings suggest that the increase of fire at Lake Dangovavy during this period might be associated to early human settlement which was accentuated by dry climate particularly around 1500 cal years BP.

To summarise, between ca. 3000 and 1000 cal years BP, the vegetation at Lake Dangovavy and its surrounds was characterised by a mosaic of ericoid shrubland, and mid-elevation forest-woodland within cool/humid period from ca. 3000 and 2000 cal years BP promoting an abundance of megafauna and cool/dry period from ca. 2000 to 1000 cal years BP with a presence of natural lightning fire events.

6.3.5 Grassland dominance from ca. 1000 cal years BP to the present

During the last ca. 1000 cal years BP, pollen assemblages were characterised by very high abundances of grassland represented by Poaceae pollen compared to shrubland and forest pollen taxa. This was reflected in decreasing pollen richness and evenness in the area reflecting trends to more homogenous species. The high relative abundance of Poaceae is characteristic of sediments taken from areas predominantly within grasslands on the island (Burney, 1988; Straka, 1991; Razafimanantsoa, 2015). These changes were supported by C_4 plant dominance, as shown in the stable carbon isotopes ($\delta^{13}C$) results Grassland started to increase since ca. 900 cal years BP in Lake Dangovavy and its surrounds and reached its maximum from ca. 600 cal years BP to the present period. The abundance of ericoid shrubland and forest/woodland taxa, experienced a massive decrease during this period in relation to previous periods.

The abundance of grassland during this last period was associated with a regional dry period with supposed severe drought recorded at ca. 950 cal years BP as prescribed by pollen and diatom record in the region (Gasse & Van Campo, 1998; Virah-Sawmy, Willis & Gillson, 2010). It was also reflected at a local scale through diatom results in Lake Dangovavy, which showed a peak of aerophilous diatom taxa at ca. 900 cal years BP suggesting potentially a shallow lake during the period. In addition, at Lake Dangovavy and its surrounds, additional dry periods likely occurred at ca. 400 cal years BP and at the present period through peaks of benthic diatom taxa. These findings reinforced the impact of the importance of drought periods on the vegetation change during the last millennium in additional to anthropogenic events (e.g., Godfrey et al., 2019a; Railsback et al., 2020).

Very high increase in charcoal and coprophilous spore concentrations indicating high fire occurrence and herbivory activities were recorded in Lake Dangovavy during the last ca. 1000 cal years BP. During this last millennium, the increase of herbivory activities on the island was supposedly linked to the introduction of cattle as the megafauna were already extinct during the period (Burney, Robinson & Burney, 2003). For the Central Highlands region, the introduction of pastoralism was a few centuries later compared to other regions (Burney et al., 2004; Stachurski et al., 2013). During this period (DAN-05), at Lake Dangovavy, charcoal and coprophilous spores were correlated (see Figure 5.15) and showed coincident peaks at ca. 700 cal years BP, with subsequent peaks at ca. 200 cal years BP and the present period. The first peak at ca. 700 cal years BP was similar, but differed in terms of the onset of activities a few centuries later, to Burney (1987) at Tritrivakely where *Sporormiella* spore started to increase at ca. 960 ± 90 years BP. Human activities have spread in the region since that time, and are not only limited to pastoralism but also fire for swidden agriculture (Gade, 1996; Kull, 2000), which might be the source of high fire occurrence at Lake Dangovavy and its surrounds at ca. 200 cal years BP and at the present period.

The vegetation at lake Dangovavy and its surrounds shifted to its current state with open grassland ecosystem dominated from ca. 900 cal years BP. This change of vegetation was associated with a severe regional drought event at ca. 900 cal years BP and then followed by increasing human activities by fire use from 700 cal years BP as well as some sequences of short dry periods at ca. 400 cal years and during the dry period.

6.4 Contribution to the vegetation cover debates and conservation implications in the Central Highlands of Madagascar

6.4.1 Origin of open and mosaic ecosystems in the Central Highlands

Madagascar was initially posited as a whole island forested, and based on this, the open and mosaic ecosystems such as grasslands, ericoid shrubland (heathland) and woodlands are often interpreted as secondary vegetation, symptomatic of forest clearance and burning of vegetation (e.g., Perrier de la Bathie, 1928; Gade, 1996; Grinand et al., 2013b). This view has been challenged by palaeoecological and evolutionary evidence suggesting an ancient origin for at least some of the grasslands of the Central Highlands (Burney, 1987a; Bond et al., 2008; Vorontsova et al., 2016; Solofondranohatra et al., 2018, 2020). This new hypothesis was then recently challenged again by Joseph & Seymour (2020, 2021) who suggest an anthropogenic grassland due to the lack of diversity of grazers and endemic grassland dwelling vertebrates.

Based on Tampoketsa-Anakazobe wetland and Lake Dangovavy palaeoecological data, the mosaic landscape in the Central Highlands of Madagascar is ancient. It has been present in the region at least since the Early to Mid-Holocene (ca. 11 000–5000 years ago), with variable extent forest patches in a matrix of heathland and grassland-heathland vegetation for Tampoketsa-Ankazobe and Lake Dangovavy, respectively (Figure 6.3). These results support previous findings in the region at Lake Tritrivakely by Burney (1987c) and at Lake Itasy by Straka (1996). The presence and abundance of the ericoid shrubland in the highlands pre-human settlement at ca. 2000 cal years BP was highlighted during this research. Ericoid shrublands decreased over time in both sites, Tampoketsa-Ankazobe wetland and Lake Dangovavy. Their changing extent was associated with the frequency of fire and climate variability over time. Our results suggest that Ericoid shrublands were abundant at mid elevation during cooler climate when fire was low, but restricted to high elevation during warmer periods with high fire regime particularly from ca. 1000 cal years BP. Similar trends have been observed in the current Miombo woodland in Mozambique where ericoid shrublands were replaced by grasslands once the climate became warmer and drier (McWeth et al., 2016). This indicates that the distribution of these ecosystems is primarily driven by changes in climate associated with wetter and cooler conditions. In Mountain regions, their retraction to higher elevation is an indication of a warming climate. But in addition, the maintenance of their abundance is affected by the frequency of fire regimes which would be critical for management purposes. Also, in later periods people might favour grassy rather than ericaceous vegetation as better for grazing hence the conversion of some ancient shrublands to grasslands.

In addition, there was a difference in the vegetation composition and dynamism of the landscape in both sites. Compared to Tampoketsa-Ankazobe wetland, the vegetation surrounding Lake Dangovavy contained more abundant grass around the Mid- Holocene, which is long before the suggested human settlements on the island was supposed to occur at ca. 2000-1350 cal years BP (Burney et al., 2004; Crowley, 2010; Anderson et al., 2018; Douglass et al., 2019). This natural expansion of grassland was also observed in the pollen records from Lake Tritrivakely by Burney (1987c) and Lake Itasy by Straka (1996). These sites, together with Lake Dangovavy, are located on the western slopes of the Central Highlands of Madagascar. These might be explained by the fact that different patterns of grassland abundance were and are found in the Central Highlands of Madagascar with more natural grassland found in the western slopes compared to the eastern slopes at least around Tampoketsa-Ankazobe wetland.

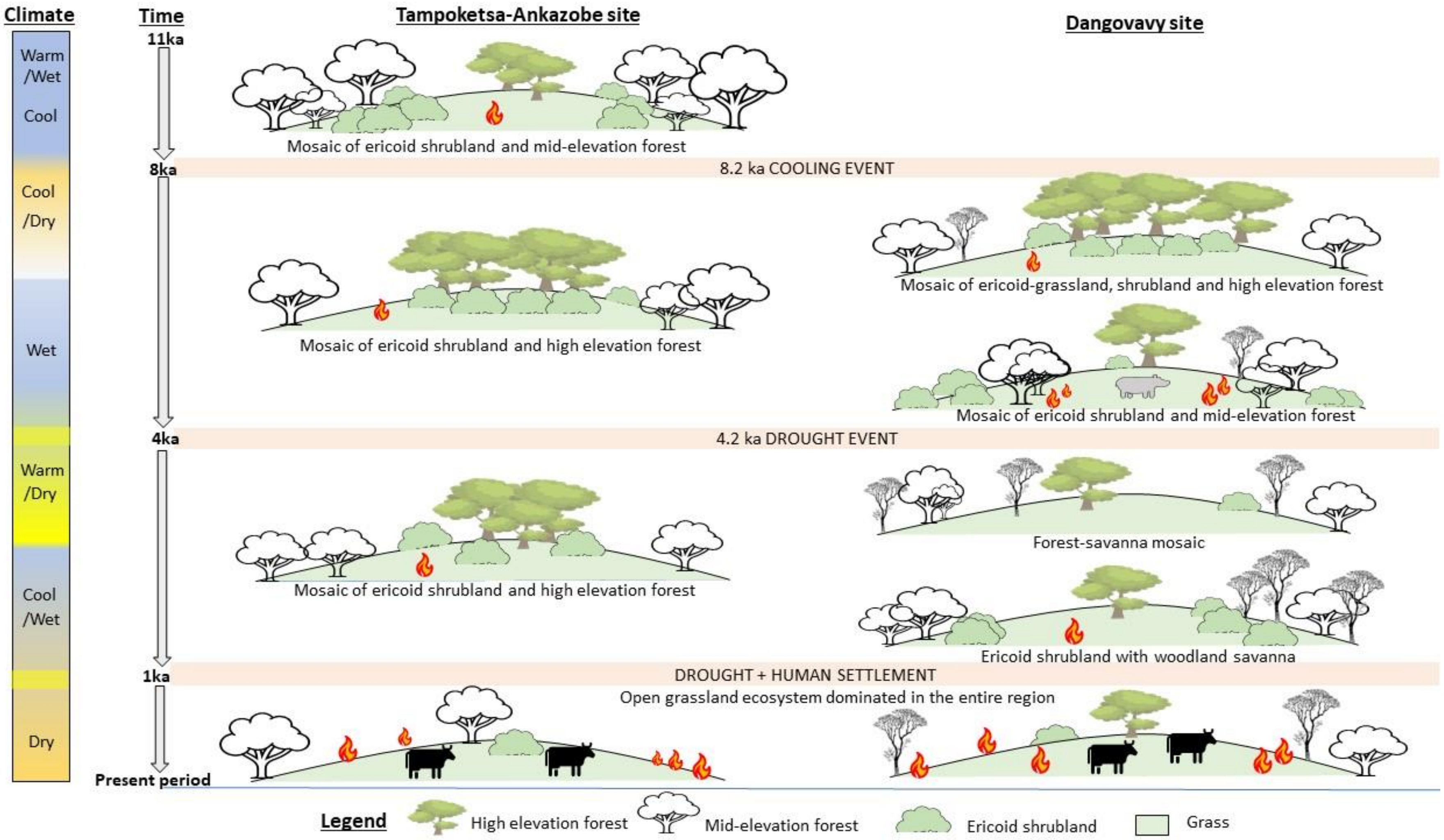


Figure 6.3: Holocene vegetation history and environmental change in the Central Highlands of Madagascar using multiproxy analyses of two sediment cores from Tampoketsa-Ankazobe wetland and Lake Dangovavy. Climatic events were based on previously published research (e.g. Alley et al., 1997, Wang et al., 2019 for the 8.2k events; Scroxton et al., 2020; Carolin et al., 2019 for the 4.2k events and Malika et al (2009) for 950 cal years BP in addition to diatom results in Lake Dangovavy.

Despite these differences in the vegetation composition in the mosaic landscape of the region, the modern grass expansion at both sites and slopes began from ca. 1000 cal years BP (Figure 6.3). The increase in grassland in both sites during this last millennium exceeded its abundance in any previous period. This suggests a similar environmental history around this period which affected the regional changes of vegetation. In fact, between ca. 1500 and 950 cal years BP, pollen records from various sediment cores taken across the island showed opening vegetation with loss of woody cover (Burney, 1987a; Matsumoto & Burney, 1994; Virah-Sawmy, Willis & Gillson, 2009; Wirah-Sawmy, Gillson & Willis, 2009; Razanatsoa, 2019). According to the Lake Dangovavy diatom record, during the last millennium this shift in abundance of grassland was associated with a peak of aerophilous diatom taxa indicating an intense dry period (Gaiser & Rühland, 2010). This intense dry period in the area corresponded with a drought period recorded elsewhere on the island during the same period (Gasse & Van Campo, 1998; Virah-Sawmy, Willis & Gillson, 2010; Wang et al., 2019). In addition, at Lake Dangovavy, some additional short dry periods were recorded respectively at ca. 400 cal years BP and the present period. These might be interpreted as the fact that the regional expansion of grassland during the last ca. 1000 cal years BP in the Central Highlands might be due to the drought period but followed and intensified by short sequences of dry periods in addition to the human activities through anthropogenic fire.

6.4.2 Conservation implications and management of the open and mosaic ecosystems in the Central Highlands of Madagascar

6.4.2.1 Importance of open and mosaic ecosystems

Mosaic ecosystems are the norm in the Central Highlands of Madagascar, with woodland/forest patches in a matrix of more open vegetation based on the palaeoecological records covering the last ca. 11 200 cal years BP in this research. The extent of wooded elements and the nature of open vegetation have varied over time and space. Heathland was abundant in the eastern slopes while combined grassland-heathland was found abundant in the western slopes of the Central Highlands. Not only in the Central Highlands, mosaic landscapes were also found to be natural in the southeastern part of the Malagasy littoral forest with a dominance of ericoid grassland vegetation pre-human arrival (Virah-Sawmy, Willis & Gillson, 2009; Wirah-Sawmy, Gillson & Willis, 2009). More widely, for instance, open and mosaic ecosystems have been proven to exist without human intervention in tropical areas, such as the pollen record from southern Mozambique (Ekblom, 2008) and southern tropical Brazil (Behling & Pillar, 2008). The importance of fire in maintaining open and mosaic ecosystems in areas where rainfall is high enough to support forests is well established (Bond, 2019).

Focusing on the Central Highlands of Madagascar, the mosaic ecosystems are proven to provide services for the local population. For instance, the so-called "*Tapia* forest" in the open savanna woodland of Central Highlands shelters the endemic silk moths (*Lepidoptera*: Lasiocampidae) which have been collected and exploited by local people for food and textiles sources for centuries (Razafimanantsoa et al., 2013). Farmers benefit also from the region's availability of open grassland for grazing their cattle, which present a special place in Malagasy culture and tradition (Klein, Réau & Edwards, 2008). As noted in the fieldwork, particularly next to Tampoketsa-Ankazobe where heathland remained present, local people made brooms from *Erica* plants. In addition, these open mosaic ecosystems are known to support high endemicity and diversity of species compared to closed forests. For instance, a high abundance of endemic ant species (Fisher & Robertson, 2002) and high diversity of birds (Martin et al., 2012) were found in the open habitat dominated by grasslands than in the closed forest area in some parts of the Central Highlands. The importance of endemic orchids in the Central Highlands is also recorded (Yokoya et al., 2015).

6.4.2.2 Conservation and management implication

According to their antiquity and importance as shown in this study as well as previous work (e.g., Burney, 1987c; Solofondranohatra et al., 2020, Samonds et al., 2019), the mosaic landscapes of the Central Highlands i.e., both ancient heathland and grassland elements, are worthy of conservation. These ecosystems should not be reforested as targeted by the government afforestation project, which are largely focussed on the open landscapes of the Central Highlands (see Chapter 1). However, particularly for the grassland ecosystem, not every grassland area in the region is ancient, but some are derived from anthropogenic clearance as proposed by Irwin et al. (2010). Therefore, more understanding of landscape history, like the one conducted in this research, is needed to decide which areas of grasslands and heathlands are ancient and should be conserved, and which areas are the result of forest loss before. This will enable better targeting and implementation of implementing reforestation and long-term conservation projects, which should be focussed on restoration of formerly forested areas with species that are indigenous to the region.

As seen through our palaeoecological data, the landscape surrounding the Tampoketsa-Ankazobe wetland, was not forested before human arrival but was a mosaic of woodland in a matrix of heathland. The decision to afforest, particularly by monoculture plantations of exotic trees such as *Pinus* spp., *Eucalyptus* spp. and *Acacia* sp., in the area and Ankazobe district should then be re-analysed. As well as damage to indigenous biodiversity, exotic species would increase biomass fuel, which increases the intensity of the fire and possibly endangering the remaining forest patches in the area, by decreasing regeneration of native species (Baohanta et al., 2012). On the other hand, grassland and fire became prevalent in the area during the last 1000 years. Therefore, careful fire management that will bring burning back to its historical range of variability is needed in the area to promote the re-establishment of ericoid shrubland in its natural habitat and to protect remaining forest. This was already started by the park manager in the protected area of Ambohitantely, close to our study site, where areas with suppressed fire present an abundance of ericoid shrubland over grassland compared to areas frequently burned (Radimbison, 1990). This approach and effort should then be intensified.

At Lake Dangovavy, the vegetation was dominated by variable extent forest patches in a matrix of grassland-heathland vegetation since ca. 6000 years. Therefore, grassland and heathland in the area are ancient and need to be conserved. Grassland was abundant and very dynamic with the fire regime compared to the previous site until 1000 years ago. Grassland and fire are integral parts of the ecosystem at Lake Dangovavy during the period up until 1000 years ago but intensified since then. Conservation in the landscape should challenge the deforestation narrative, and consider the open vegetation i.e., grassland and heathland as ancient vegetation as worthy of conservation. Fire should not be seen as a threat in the landscape but part of the ecosystem as it maintained the presence of fire-resistant species (*Uapaca* cf. *bojeri*) in the pollen record since the Mid-Holocene. Reforestation projects in the area should then be focused and based on those fire-resistant native excluding exotic species (Bertrand, 1999; Razakamanarivo et al., 2012). However, fire management is also needed around Lake Dangovavy as prescribed in the previous site because woodland/forest and shrubland decreased exponentially during the last 1000 years. The fire should not be banned as natural fire has been demonstrated in the area (Kull, 2002b), but new strategies should be elaborated on how to not exceed the threshold in order toavoid the disappearance of the remaining fire-adapted trees such as the *Upaca* cf. *bojeri*.

This will involve a nuanced approach that considers the vegetation and fire history of individual sites and considers the current vegetation and fire regimes in the context of the historical range of variability and likely future climate change.

6.5 Summary

This research highlighted some of the most debated topics on the island, particularly focusing on the Holocene and the past 1000 years. It points out that the Central Highlands of Madagascar included open and mosaic ecosystems long before human arrival. An abundance of natural grassland was recorded in the vegetation mosaic of the western slopes compared to the eastern slopes of the highlands, at least in the vegetation surrounding the Tampoketsa-Ankazobe wetland near Ankazobe district. Expansion of grassland was recorded during the last 1000 cal years BP for both slopes in the Central Highlands Madagascar, which may have been caused by a severe drought at ca. 900 cal years BP followed by human practices of fire within some sequences of short intense dry periods, that increase in duration and intensity towards the present period. Critical thresholds might have been reached during this last millennium with a combination of dry and increasing fire leading to the current state of the vegetation in the Central Highlands region.

Conservation of the open and mosaic ecosystems of the Central Highlands are not only indispensable because of their antiquity, but also because of the ecosystem services that they provide. In addition, it has been demonstrated through this research that there were differences in the vegetation composition in the mosaic landscape of the region over time. This implies that biodiversity conservation in the Central Highlands of Madagascar should then be conducted locally (*in-situ*), or at least separately, for the two highland slopes but not generalised for the entire region as currently conducted. Finally, for both highland slopes, either the eastern or western slopes, reforestation if it has to be conducted should promote the use of native trees rather than exotic trees and be confined to areas that were formerly forested before 1000 years ago.

Chapter 7 SYNTHESIS AND CONCLUSION

7.1 Introduction

Mosaics of forests and grasslands in subhumid zones that can climatically support forests are frequently assumed to be the results of human activities (Willis, Gillson & Virah-Sawmy, 2008; Bond, 2019). This is the case in the tropical island of Madagascar, which is classified as one of the world's greatest biodiversity hotspots (Ganzhorn et al., 2001). On the island, forest-grassland mosaic landscapes are most common in the Central Highlands region, where high deforestation rates due to swidden agriculture and increasing grassland area have been recorded, particularly in the last 50 years (Vieilledent et al., 2018). The Central Highlands is one of the regions targeted by a national reforestation program, which aims to restore 4 million hectares of assumed to be degraded forest (but are potentially natural open ecosystems) by 2030 (Lacroix et al., 2016; Ranjatson et al., 2019). Understanding legacies of past human activities in these open ecosystems would allow to further elucidate their ecology (e.g. McMichael, 2021), considering the lack of long-term cultural, environmental and palaeoecological data in this region (Douglass et al., 2019). The history and drivers of change in these mosaic forest-grassland landscapes are currently debated and it is not clear if the grasslands are the result of anthropogenic activities or if they are an ancient vegetation type. Debates are based on the reviews and interpretation of taxonomic, ecological and evolutionary evidence of the current landscape (Joseph & Seymour, 2020; Solofondranohatra et al., 2020).

Understanding landscape history has implications for restoration and reforestation projects within these areas. Yet, few long-term records have investigated the state and origin of the landscape prior to human arrival and settlement (e.g., Burney, 1987c; Straka, 1996). Moreover, the changes in fire activities that occurred within the area alongside climate variability are not fully understood (Burney, 1996; Gasse & Van Campo, 2001; Burney et al., 2004). Such a lack of data could potentially lead to inappropriate decision-making in conservation and restoration projects, such as afforestation of ancient grasslands, which is particularly damaging to biodiversity when exotic species are used.

This research aimed to contribute to understanding the origin and history of the forest-grassland mosaic ecosystems in the Central Highlands of Madagascar and their dynamism during the Holocene, and to analyse the drivers of change within the period, by investigating two study sites, named Tampoketsa-Ankazobe wetland and Lake Dangovavy in the eastern and western slopes of the highlands, respectively. Appropriate conservation and management strategies of the landscape in the Central Highlands was also targeted.

New records of past vegetation, fire, herbivory activities and hydrological changes were generated within these two sites using a palaeoecological approach. Past vegetation was inferred from pollen and stable carbon isotope analyses, while charcoal, coprophilous spores and diatoms were used to reflect past fire occurrence, herbivore activities and hydrological changes. Results were analysed and interpreted in terms of the environmental change and the interacting effects of climate, fire occurrence and herbivory activities. These newly generated records add to the few existing palaeoecological records in the area and provide an understanding of Holocene climate variability, vegetation change and human arrival and settlement in the Central Highlands of Madagascar. Finally, the implications of the findings for conservation, restoration and management strategies were explored.

Three main hypotheses investigated in the present study are stipulated below:

Hypothesis 1: The Central Highlands of Madagascar was a mosaic ecosystem at least since the Early Holocene comprising a high abundance of grassland before human settlement in the region (ca. 2000–750 cal years BP).

Hypothesis 2: Climate was variable in the region over time, but dry periods have increased over the last 2000 years BP and have exacerbated the effects of human activities on the vegetation.

Hypothesis 3: Fire and herbivory activities in the Central Highlands of Madagascar have shaped the ecosystems throughout the Holocene but have accelerated in the last two millennia due to human increased settlement and activities.

7.2 The Central Highlands of Madagascar were dominated by mosaic vegetation with open ecosystems since at least the Early and Mid-Holocene, with variations in forest extent

Findings from the pollen and stable carbon isotopes in the sediments analysed in this research suggest that the Central Highlands of Madagascar were dominated by open ecosystems at least from the Early and Mid-Holocene. Forest patches co-existed alongside open heathlands and grasslands in mosaic landscapes. Forest extent varied mainly in response to changes in climate, with some evidence of climate-fire-interactions until ca. 1000 years ago, when aridification and human impact increased leading to a decrease in forest extent and increase in the prevalence of open ecosystems dominated by grassland.

This shows that:

i) The Central Highlands of Madagascar was composed of mosaic ecosystems with a mixture of open and closed vegetation since the Early Holocene, in other words, prior to human settlement around ca. 2000 cal years BP.

This heterogeneity of the vegetation is probably linked to topography, as suggested by the current ecology of the remaining large patches of forest in the highlands, for example in the Ambohitantely protected area, where the distribution of vegetation is distributed according to slope and hydrology, with forest areas largely confined to ravines and riverine areas (Radimbison, 1990; Langrand & Wilme, 1997; Ratsirarson & Goodman, 2000). The varied topography provides a range of microenvironmental conditions, enhancing the resilience of past vegetation to climate change and disturbance, for example, through fire-climate refugia and stabilising feedbacks. For example, in forest patches, understory vegetation is more sparse and this helps to prevent fire penetrating the forest (Figure 6.3). The varied topography also provides refugia for certain species that maintain the diversity and structure over time. This was confirmed in the Tampoketsa-Ankazobe wetland between ca. 8000-1000 cal years BP where tree forest taxa retreated to higher elevations with more moisture during more prominent dry periods. In addition, fire occurrence also played an important role in maintaining the heterogeneity of the mosaic ecosystems in the region. Lake Dangovavy, for example, had a higher occurrence of fire in the mid-elevation area with an associated increase in fire-resistant species such as the *Uapaca* cf. *bojeri*, compared to the common species found within the Tampoketsa-Ankazobe wetland. Therefore, even though both sites were located within the same topographic feature, fire contributed to a variation in forest and open ecosystem components in both sites over time.

Together, these findings not only confirm the antiquity of the open and mosaic ecosystems in the Central Highlands of Madagascar but also demonstrates their resilience to climate change and existing fire before the last millennium BP. Further analysis, which is beyond the scope of the current thesis, should be able to help understand the resilience of the various ecosystems within the region to future trends of climate and anthropogenic fire regimes.

Specifically future research could focus on identifying critical thresholds where mosaic landscapes become unviable.

ii) Both sites investigated in the present study suggested the presence of open heathland and grassland-heathland matrix at the Tampoketsa-Ankazobe wetland (eastern slopes) and Lake Dangovavy (western slopes), respectively, prior to the last millennium. These findings highlight the importance of ericoid shrubland ecosystems in the region, whether in the eastern or western slopes of the highlands prior to human presence. Previous studies have also demonstrated the abundance of ericoid shrubland during the Early Holocene (Burney, 1987a; Straka, 1996) and even further back during the glacial periods in the region (Gasse & Van Campo, 1998, 2001). It has also been noted that Madagascar has higher diversity in Ericaceae species compared to Eastern Africa (Grubb, 2003). However, ericoid shrublands have received little attention in the research and conservation sectors in the region, and on the island as a whole, due to the lack of knowledge in the landscape history and their ecology, and also with the focus on a forest-grassland dichotomy on the island. This research showed that Ericaceae are relatively abundant in the eastern slopes where less fire occurred compared to the western slopes which will require different management and conservation strategies between both slopes in the Central Highlands of Madagascar. Additional research is needed, however, to understand the ecology, management and conservation of ericoid shrubland, particularly with their response to climate (temperature and rainfall), and various fire activities to ultimately inform their conservation and the ecosystem services they provide to the local inhabitants.

iii) Grassland was also abundant during early Holocene but with differences between the eastern and western sites. The pollen record from Lake Dangovavy, for example, had a higher prevalence of grass abundance compared to Tampoketsa-Ankazobe wetland. In addition, the grass in the western slopes is dominated by natural grazing grass (Burney, 1987c; Solofondranohatra et al., 2018). This shows that even though the landscape currently shows a common pattern of abundance in grassland at the present time, not all open grasslands in Madagascar are anthropogenic despite the possibility of early human presence during this period (Hansford et al., 2018). This finding contributes to the debate about the antiquity of grassland in the Central Highlands of Madagascar by considering the idea of the natural presence of grassland in the region (Bond et al., 2008; Vorontsova et al., 2016; Solofondranohatra et al., 2018). In addition, particular attention should be paid to local changes and history prior to any conservation implementation and restoration.

It would help to know on which sites or parts of the highlands had/have ancient or anthropogenic open landscapes and the nature of these landscapes in terms of the extent of the forest mosaic and the relative dominance of ericaceous versus grassy landscapes.

7.3 Climate was variable and tended to be dry over the last ca. 2000 cal years BP

Evaluation of the literature, combined with the newly generated records from this study, suggests that climate was variable in the Central Highlands of Madagascar during the Holocene.

i) During the Holocene up until ca. 2000 cal years BP, a succession of wet/dry, cold/warm periods and drought were recorded in the region (Gasse & Van Campo, 1998; Williamson et al., 1998; Virah-Sawmy, Willis & Gillson, 2010; Wang et al., 2019) and these are suggested to have shaped the landscape in the area as affirmed in Tampoketsa-Ankazobe wetland and Lake Dangovavy. The wet period promoted the extension of mid-elevation forest taxa, while the dry periods restricted forest to higher altitudes with an abundance of grassland during an intensification of drought.

ii) Between ca. 2000 and 1000 cal years BP, the Central Highlands experienced dry climate conditions based on the high-resolution reconstruction of past hydrological change in Lake Dangovavy, which was characterised by a shallow lake during this period. The hydrological reconstruction in the lake provides the first high-resolution climate reconstruction in the Central Highlands during the last ca. 2000 years BP. In addition, Lake Dangovavy and its surrounds showed that a short, but intense dry period took place at ca. 1500 cal years BP and this corresponded to the sudden increase of fire in the area.

iii) During the last ca. 1000 cal years BP, an island-wide drought occurred at ca. 950 cal years BP (Gasse & Van Campo, 1998; Virah-Sawmy, Willis & Gillson, 2010; Razanatsoa, 2019). This was associated with the peak of aerophilous diatom indicator taxa in Lake Dangovavy indicating a shallower lake to sub-aerial moist habitat. In addition to the regional trends of dry periods, a series of intense dry periods were recorded in the area particularly at ca. 400 cal years BP and at the present period. Our findings could be linked to and explain the extinction events and environmental change that occurred in Madagascar during the last millennium BP (Crowley et al., 2017; Godfrey et al., 2019; Hixon et al., 2021). This perspective helps to understand the patterns observed across the island reported in the literature with respect to the debate about climatic or anthropogenic causes of the extinction events.

7.4 Fire history differs on the eastern and western slopes in the Central Highlands of Madagascar before human settlement but high occurrence of fire was recorded for both slopes since ca. 1000 cal years BP

Fire in the tropics occurs in areas that are neither fuel limited (i.e. too dry) or ignition limited (too wet) (Murphey & Bowman, D.M., 2012). Within these bounds, fire regimes (intensity, area and frequency) are modified by a range of biotic and abiotic factors including fire-vegetation feedbacks, rainfall seasonality. Furthermore, human management and manipulation of fire can change the frequency and seasonality of ignitions, as well as enhancing or impeding the spread of fire through landscapes for example through fragmentation of the fuel load or introduction of highly flammable non-native species. Fire regimes thus have environmental, biological and cultural dimensions (e.g. Bowman et al., 2014). Deforestation fires are common in tropical ecosystems and they are proven due to the increase length and intensity of the dry season (Van Der Werf et al., 2008). For Madagascar, current fire is mostly classified as results of human activities with low natural fire (Bloesch, 1999; Frappier-Brinton & Lehman, 2022) and more common in the central plateau and western lowlands in the dry season (Kull, 2000).

Based on the palaeofire record in the Tampoketsa-Ankazobe wetland and Lake Dangovavy, there was a contrast of fire activities between the two highlands slopes from the Early Mid-Holocene to ca. 1000 cal years BP. The eastern slopes of the highlands were characterised by less occurrence of fire relative to the western slopes. During the last millennium, however, both slopes in the highlands have experienced a common and similar trend with a massive increase in fire corresponding to an increase in herbivory activities across the region. These findings could inform changes in the fire regime on a spatial scale within the Central Highlands and, in particular, inform management practices of the landscape at the landscape local scale.

i) In the eastern slopes, represented by Tampoketsa-Ankazobe wetland, there was evidence of low fire occurrence that coincided with low herbivory activities, compared to the entire Holocene period, allowing the establishment and dominance of heathlands and a variable extent patch of forest, which is still currently abundant nearby the study area, i.e. in Ambohitantely protected forest (Goodman, Raherilalao & Wohlhauser, 2018). This finding provides an understanding of past fire history in the region and indeed confirms the assumption that the current fire activity is mostly man-made, at least around the site investigated, in the present study from the eastern slope. This is particularly accentuated with the arrival and practice of pastoralism which is the main source of fire in the area (Pareliussen, Olsson & Armbruster, 2006). Extension of the sites in the present study to other sites withing the broader area is needed to confirm this finding. However, the implication is that research and management should focus on regulating fire use to maintain the mosaic landscape, specifically the fire-sensitive elements such as ericoid shrubland and forest patches facing the increase of human land-use through fire use.

ii) In the western slopes, confirming the previous palaeoecological investigations in the region such as Burney (1987) and Straka (1996), this study showed the presence of more fire than at the present day during the Mid-Holocene. This high fire activity was reflected from Lake Dangovavy vegetation, which presented an abundance in pioneer and fire-resistant taxa such as *Trema orientalis* and *Uapaca* cf. *bojeri* over time. These fire events were possibly associated with climate-vegetation-fire feedbacks allowing for the maintenance of the mosaic landscape in the region. Identifying those areas that are prone to natural fires is important as they provide a great way to reconcile biodiversity conservation and human livelihoods particularly associated to pastoralism activities.

7.5 Aridification and human impact over the past 1000 years has led to increase in fire and the dominance of open ecosystems

Tropical regions have demonstrated an insignificant change in their vegetation communities in response to past and episodic climate variability and wildfire during the Holocene. However, with increasing land-use and climate change recorded, there is a significant change in vegetation communities in these regions. This is particularly manifested by the rise of land-use through intensification of agricultural activities and fire use in the last millennium (e.g. Brugger et al., 2016). Burning and indicators of human disturbance during the last millennium have elevated beyond past levels, leading to a reduction in peat swamp forest pollen e.g., in Borneo (Cole et al. 2015), in Uganda (Russel et al 2017); in the Amazon, (Brugger et al., 2016). In some cases, these have been aggravated by records of aridification (e.g. Mexico; Davies et al. 2004).

In the last ca. 1000 cal years BP, vegetation in the Tampoketsa-Ankazobe wetland in the eastern slopes and Lake Dangovavy in the western slopes were characterised by an increased abundance of grassland-dominant vegetation. Ericoid shrubland, woodland and forest taxa including high-elevation, mid-elevation and riparian arboreal taxa experienced a massive decrease at both sites. These changes correlated with the regional drought period at ca. 950 years BP in the Central Highlands (Gasse & Van Campo, 1998; Virah-Sawmy, Willis & Gillson, 2010) corresponding to a more shallow water levels in the Lake Dangovavy. This period was followed a few centuries later by various local human interventions through fire and herbivory activities at ca. 500-400 cal years BP and 700 cal years BP for Tampoketsa-Ankazobe wetland and Lake Dangovavy, respectively.

The increased abundance of grassland in the open landscape mosaics of the Central Highlands, compared to heathland and forest patches, refines the narrative which proposed a shift from a woodland closed forest to an open grassland landscape (Perrier de la Bathie, 1928; Humbert, 1955b; Gade, 1996). In addition, this increase in abundance of grassland in the open mosaic ecosystems of the Central Highlands of Madagascar was correlated to a local short dry period and the aridification period on the island at ca. 950 cal years BP (Gasse & Van Campo, 1998; Virah-Sawmy, Willis & Gillson, 2010). This indicates that the vegetation change in the Central Highlands during the last millennium BP, possibly started as a result of the aridification but was accentuated by human activities through fire and pastoralism. This might be useful in clarifying the debate about the vegetation change and extinction of megafauna on the island, whether climatic (Virah-Sawmy, Willis & Gillson, 2010) or anthropogenic (Crowley et al., 2017, Railsback et al., 2020) or a synergy between the two (Godfrey et al., 2019; Razanatsoa et al., 2021). Critically, the interaction between aridification and increased anthropogenic activities, especially fire, has implications for resilience of mosaic ecosystems, with the possibility of meeting ecological thresholds of more water dependent and fire-sensitive elements in the future.

7.6 Implications of the research to biodiversity conservation, fire management and restoration

Major policies and strategies around biodiversity conservation in Madagascar are still based on the forested island narrative, which stipulates that this “green” forested island has been cleared since human arrival through swidden agriculture and pastoralism (e.g., Gade, 1996; Lowry, Schatz & Phillipson, 1997; Vieilledent et al., 2018). This narrative has, for example, been used to inform the recent AFR 100 (the African Forest Landscape Restoration Initiative) with a particular focus in the Central Highlands (Lacroix et al., 2016). However, our research suggests that the natural presence of open ecosystems in the Central Highlands has existed at least for the last ca. 11 000 cal years BP in the region which contradicts the current vegetation narrative in Madagascar. Instead, it identifies the long presence of mosaic ecosystems with grassland and heathland elements that are themselves worthy of conservation to maintain its intended states and ecosystem services (Jackson & Hobbs, 2009) and more importantly avoid afforestation using exotic species.

The sites studied here suggest differences in the landscape history between the eastern and western slopes. By individually examining each case study, for Tampoketsa-Ankazobe wetland and its surrounds, with a pre-dominance of mosaic of heathlands and forest extent taxa within a low fire regime, restoration projects should be conducted in the area to restore the patches of forest proven to be formerly present with the open ecosystem. When restoring the forest elements of the mosaic, care should be taken to use the native species found abundant throughout the pollen record, e.g., *Uapaca* cf. *densifolia, Ilex mitis* and *Faurea* sp., rather than using exotic trees which have begun to spread in the area (Pareliussen, 2004). For its surrounding, including the protected area of Ambohitantely, a need to maintain the remaining ancient open landscape through proper fire management is required. For this to happen, local topography should be used to guide the establishment and maintenance of fire refugia where fire-sensitive taxa can stabilise through fire-vegetation feedbacks (i.e. shading out of grassy understory that provides fuel for fire) (Beckett & Bond, 2019).

For the vegetation surrounding Lake Dangovavy, pre-dominantly characterised by open ecosystems dominated by grassland and heathland, and some patches of forest extent taxa within a more variable fire regime, conservation effort should be promoted. This should focus particularly on the natural presence of grassland and heathland elements in the landscape, which is often not considered during reforestation and restoration projects so as to avoid afforestation. In addition, the presence of natural fire ignited by volcanoes and lightning prior to human settlement should be considered as this possibly contributed to the persistent presence of fire-resistant taxa (e.g., *Uapaca* cf. *bojeri*) over time in the area. Therefore, conservation projects should focus on the restoration of such taxa as it was initiated by Baohanta et al., (2012) but not the use of exotic trees (e.g., *Eucalyptus camaldulensis* and *Pinus patula*) to avoid afforestation (Gade, 1996). In parallel, as local people in the area use fire for their livelihoods (Kull, 2000), fire management should focus on the regimes that are adequate to maintain the diversity of the landscape and in consultation with the population. Again, maintaining heterogeneity in accordance with local topography will provide the best chance of resilience to changing climate as well as providing a wide range of habitat for biodiversity and ecosystem services.

In parallel, as local communities depend on the open and mosaic ecosystems for their livelihoods and subsistence (see Chapter 2), our findings would imply more action from policymakers in conservation projects to avoid ecological conflict in the field. Integration of local communities in conservation should be promoted and improving their source of income is one of the key strategy to achieve this (Razanatsoa et al., 2021a). For instance promoting the textiles from endemic silk moths in the open *Tapia* woodland (Razafimanantsoa et al., 2013).

7.7 Significance of the study, and research opportunities

This thesis provided new high-resolution records for the Central Highlands of Madagascar and makes a significant contribution to the debate around vegetation cover and the drivers of change in Madagascar during the Holocene. New records of past environmental change were generated for the Central Highlands including past vegetation, fire history, herbivory activities and past climate. These are crucial for understanding continental-level historical data which are very limited for the island and, not to mention, are the only datasets available in the African Pollen Database (APD, https://africanpollendatabase.ipsl.fr/#/home), Neotoma (https://www.neotomadb.org/) and Global Paleofire Database (GPD, https://www.paleofire.org/index.php). The study contributes to our understanding of the past ecology of other open mosaic ecosystems around the world located in climates that are wet and warm enough to support forests and which are often classified as degraded forests (Willis, Gillson & Virah-Sawmy, 2008; Bond, 2019).

For Madagascar's interest, this research provides more clarity on past vegetation change and its main drivers during the Holocene, which is currently debated in the literature for the island, particularly in the Central Highlands' region (Bond et al., 2008; Vorontsova et al., 2016; Solofondranohatra et al., 2018, 2020; Joseph & Seymour, 2020). This research indicates that up until ca. 1000 cal years BP, the Central Highlands of Madagascar has been characterised by open mosaic ecosystems dominated by heathland and grassland vegetation with limited patches of forest. These open ecosystems have been maintained by interactions between climate and fire as the main drivers of vegetation change. These results not only help determine the origin and age of the vegetation, but also highlight the importance of those vegetation types for any biodiversity conservation or restoration project in the region.

Recent studies have demonstrated the importance and richness of the Malagasy grassland ecosystem and growing body of research focussing on grassland history, expansion and diversity within the biome in Madagascar (Bond et al., 2008; Vorontsova et al., 2016; Hackel et al., 2018; Solofondranohatra et al., 2018, 2020). However, there remain several questions regarding the spatial and temporal extent of these grasslands in the Central Highlands region. Although our results respond to this in part, additional reconstructions of past vegetation need to be performed in different areas across the region. This is particularly important for the eastern and western slopes of the highlands which lack published past environmental data to verify whether topography plays an important role in differentiating between vegetation communities. It is also important to conduct calibration studies within these sites by comparing modern pollen rain with current vegetation composition to validate the pollen results (e.g., Burney, 1988; Straka, 1991; Razafimanantsoa, 2015). The use of pollen records as a proxy was limited to the plant family level for some particular taxa such as the Poaceae. It would be particularly helpful to identify Poaceae pollen in these sediment records at least to the level of subgroups, i.e., short grass versus tall grass, using phytoliths as already conducted elsewhere (e.g., Dabengwa, Gillson & Bond, 2021). This would help understand the evolution and expansion of the grass family in the landscape. Working on a delimitation map of the presence of ancient and anthropogenic grassland in the region would also be indispensable for a successful afforestation program. Furthermore, it would be instructive to explore altitudinal switches from C_3 to C_4 grass dominance as a marker of temperature change in palaeorecords. This could potentially open opportunities for interdisciplinary approaches, for instance, between general vegetation surveys of the grassland and soil carbon isotopes analyses to distinguish the current division between C_3 and C_4 grass plants in the landscape.

In addition, our results suggested that ericoid shrubland were common in both records throughout the Holocene. However, there are very few up-to-date published ecological data about these ecosystems, except that they are currently very abundant in the high-elevation montane areas on the island (Burgess et al., 2004; Goodman, Raherilalao & Wohlhauser, 2018). It has also been suggested that Madagascar has one of the highest diversities in Ericaceae species (Grubb, 2003). Therefore, more research needs to be done on the ericoid shrubland, particularly regarding their response to climate (temperature and rainfall), to various fire regimes and also their importance to the surrounding communities to inform conservation. Furthermore, our analysis of hydrological change was limited to the last 2000 years BP due to the absence of diatoms in the deeper levels of the sediment cores. Establishing long-term data (extending back to the Early-Holocene) of climate or hydrological regimes within each area of investigation would support the comparison of responses at micro- to regional scales. The Central Highlands are lacking high-resolution past climate data, particularly during the Early and Mid-Holocene which could be particularly important for future projects.

Looking ahead, more comprehensive past environmental data in the Central Highlands might help in exploring future scenarios of landscape change under different combinations of climate change and land-use. It would be important to integrate conservation and livelihood considerations in the sustainable management of the Central Highlands, especially given current high levels of poverty and pressure to mitigate climate change.

In the broader context, the study demonstrates the utility of palaeoecology in restoration and management and in guiding tree-planting that is based on a sound understanding of landscape history. This is especially pertinent in light of the current UN decade of restoration and the Bonn challenge that aim to conduct reforestation in tropical Africa under the AFR 100.

7.8 Conclusion

This thesis provided new resolution palaeoecological records for the Central Highlands of Madagascar during the last ca. 11 200 cal years BP. It provided a better understanding of the origin of the forest-grassland and their dynamism over time in the region, but also identified the main drivers of change over time. Vegetation history and its dynamism over time were investigated using pollen and stable carbon isotope analyses. The role and impacts of the drivers of change over time were conducted using analyses of charcoal, coprophilous spores and diatoms as proxies for fire, herbivory and hydrology, respectively. The analyses conducted here showed that the Central Highlands of Madagascar were not forested during the Early and Mid-Holocene but were composed by a mosaic of forest patches of variable extent, in a matrix of ericoid shrubland and ericoid-grassland along the eastern and western slope sites, respectively. Our palaeorecords showed that the vegetation in each site was dynamic during those periods. Up until 1000 years ago, variation of climate, topography and occurrence of fire are suggested to be the dominant drivers of the mosaic and open ecosystems in the eastern and western slopes sites of the Central Highlands.

During the last millennium, both slopes experienced vegetation shifts towards open grassland ecosystems which coincided with a combination of regional drought recorded at ca. 950 cal years BP and human activities from the ca. 500-400 cal years BP and 700 cal years BP in the eastern and western slopes, respectively. Recommendations were provided to inform current and future local conservation strategies for each area, but also in the entire region, which might prove useful in the context of global and local debates around reforestation projects. This particularly concerns reforestation projects that should be kept to formerly forested areas, using indigenous species to conserve ancient grasslands and heathlands.

More generally, the project has proven the critical importance of long-term records obtained from palaeoecological research in informing the restoration and management of ecosystems, especially in this context of mosaic and open ecosystems that are often misunderstood (Bond, 2019). This mainstreaming of palaeoecology needs a better integration of ecological and evolutionary data with local stakeholder engagement, who may find the palaeoecological literature difficult to engage with. It, therefore, falls upon palaeoecologists to present the work in forms that are relevant and accessible.

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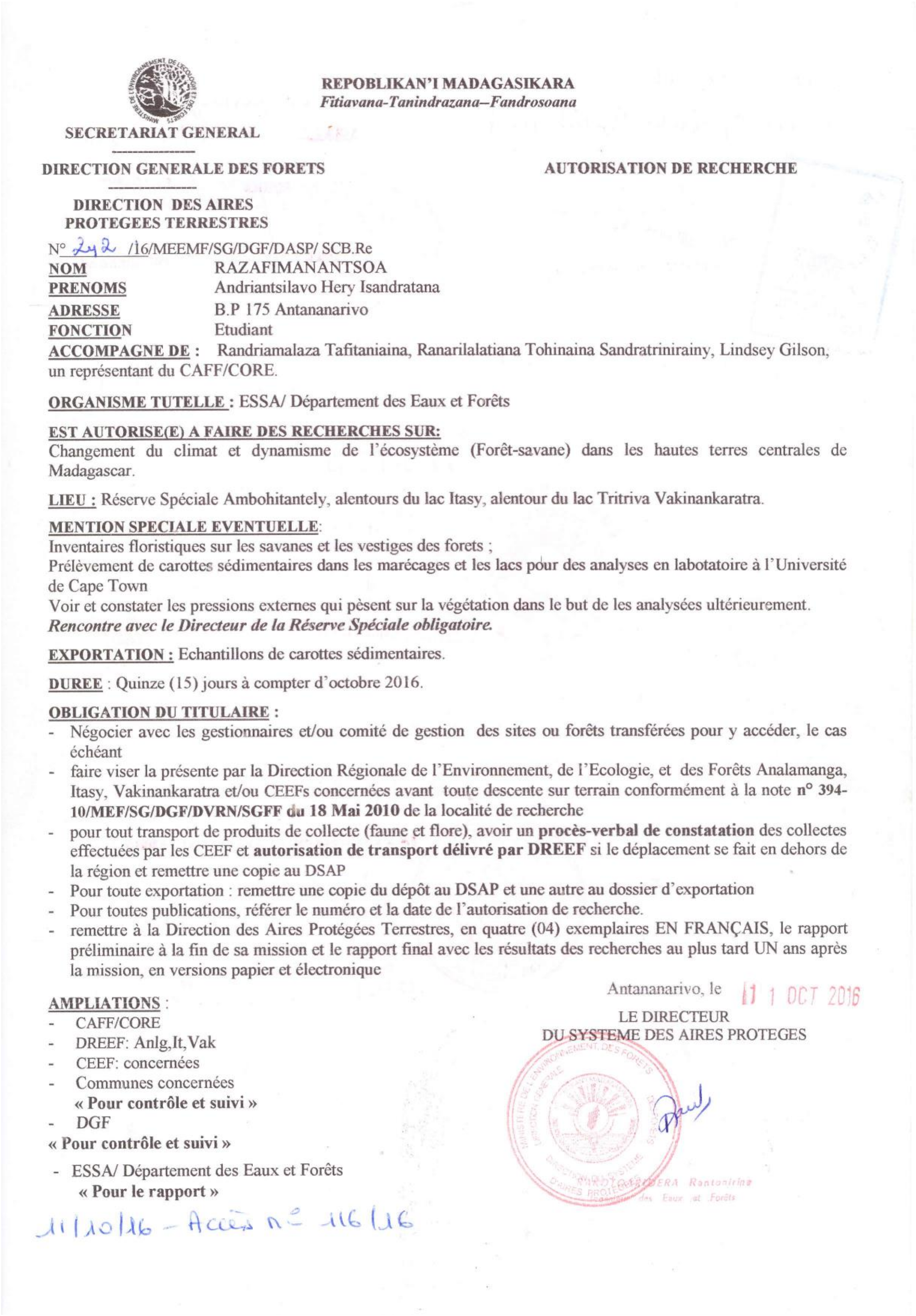
APPENDIX

Appendix 1: Research permit from the Ministry of Environment and Mines



REPOBLIKAN'I MADAGASIKARA
Fitiavana-Tanindrazana–Fandrosoana

SECRETARIAT GENERAL
DIRECTION GENERALE DES FORETS
DIRECTION DES AIRES PROTEGEES TERRESTRES

AUTORISATION DE RECHERCHE

N° 242 /16/MEEMF/SG/DGF/DASP/ SCB.Re

NOM	RAZAFIMANANTSOA
PRENOMS	Andriantsilavo Hery Isandratana
ADRESSE	B.P 175 Antananarivo
FONCTION	Etudiant

ACCOMPAGNE DE : Randriamalaza Tafitaniaina, Ranarilalatiana Tohinaina Sandratrinirainy, Lindsey Gilson, un représentant du CAFF/CORE.

ORGANISME TUTELLE : ESSA/ Département des Eaux et Forêts

EST AUTORISE(E) A FAIRE DES RECHERCHES SUR:
Changement du climat et dynamisme de l'écosystème (Forêt-savane) dans les hautes terres centrales de Madagascar.

LIEU : Réserve Spéciale Ambohitantely, alentours du lac Itasy, alentour du lac Tritriva Vakinankaratra.

MENTION SPECIALE EVENTUELLE:
Inventaires floristiques sur les savanes et les vestiges des forets ;
Prélèvement de carottes sédimentaires dans les marécages et les lacs pour des analyses en labotatoire à l'Université de Cape Town
Voir et constater les pressions externes qui pèsent sur la végétation dans le but de les analysées ultérieurement.
Rencontre avec le Directeur de la Réserve Spéciale obligatoire.

EXPORTATION : Echantillons de carottes sédimentaires.

DUREE : Quinze (15) jours à compter d'octobre 2016.

OBLIGATION DU TITULAIRE :

- Négocier avec les gestionnaires et/ou comité de gestion des sites ou forêts transférées pour y accéder, le cas échéant
- faire viser la présente par la Direction Régionale de l'Environnement, de l'Ecologie, et des Forêts Analamanga, Itasy, Vakinankaratra et/ou CEEFs concernées avant toute descente sur terrain conformément à la note **n° 394-10/MEF/SG/DGF/DVRN/SGFF du 18 Mai 2010** de la localité de recherche
- pour tout transport de produits de collecte (faune et flore), avoir un **procès-verbal de constatation** des collectes effectuées par les CEEF et **autorisation de transport délivré par DREEF** si le déplacement se fait en dehors de la région et remettre une copie au DSAP
- Pour toute exportation : remettre une copie du dépôt au DSAP et une autre au dossier d'exportation
- Pour toutes publications, référer le numéro et la date de l'autorisation de recherche.
- remettre à la Direction des Aires Protégées Terrestres, en quatre (04) exemplaires EN FRANÇAIS, le rapport préliminaire à la fin de sa mission et le rapport final avec les résultats des recherches au plus tard UN ans après la mission, en versions papier et électronique

Antananarivo, le 11 OCT 2016

LE DIRECTEUR
DU SYSTEME DES AIRES PROTEGES

[illegible]ERA Rantonirina
[illegible] des Eaux et Forêts

AMPLIATIONS :

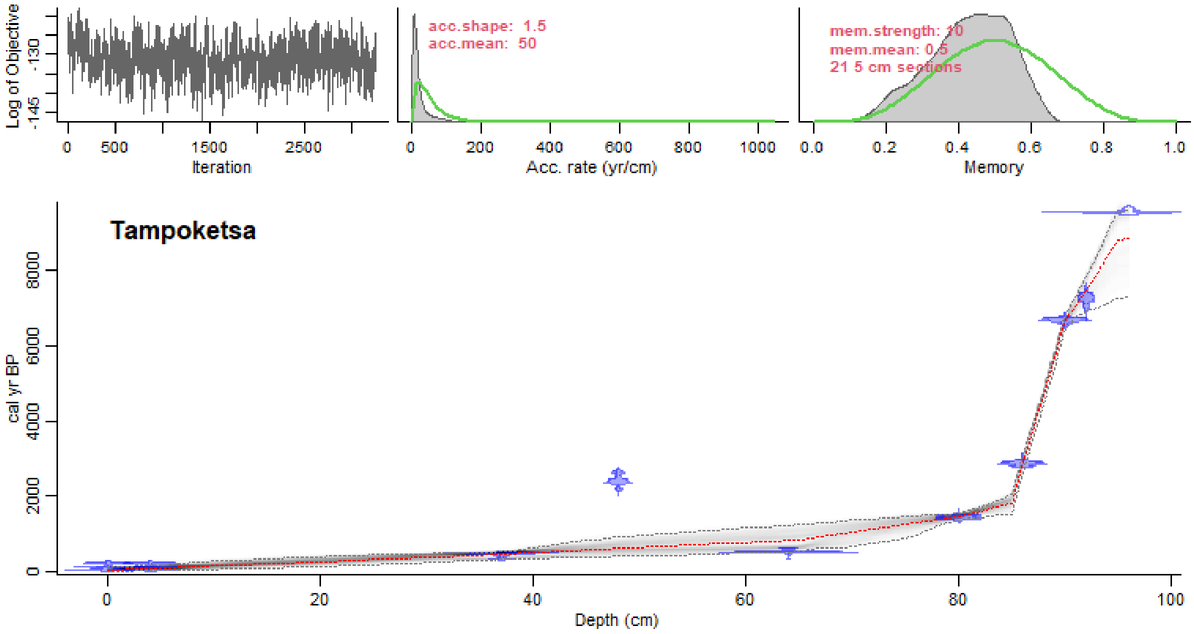
- CAFF/CORE
- DREEF: Anlg,It,Vak
- CEEF: concernées
- Communes concernées
  « Pour contrôle et suivi »
- DGF

« Pour contrôle et suivi »

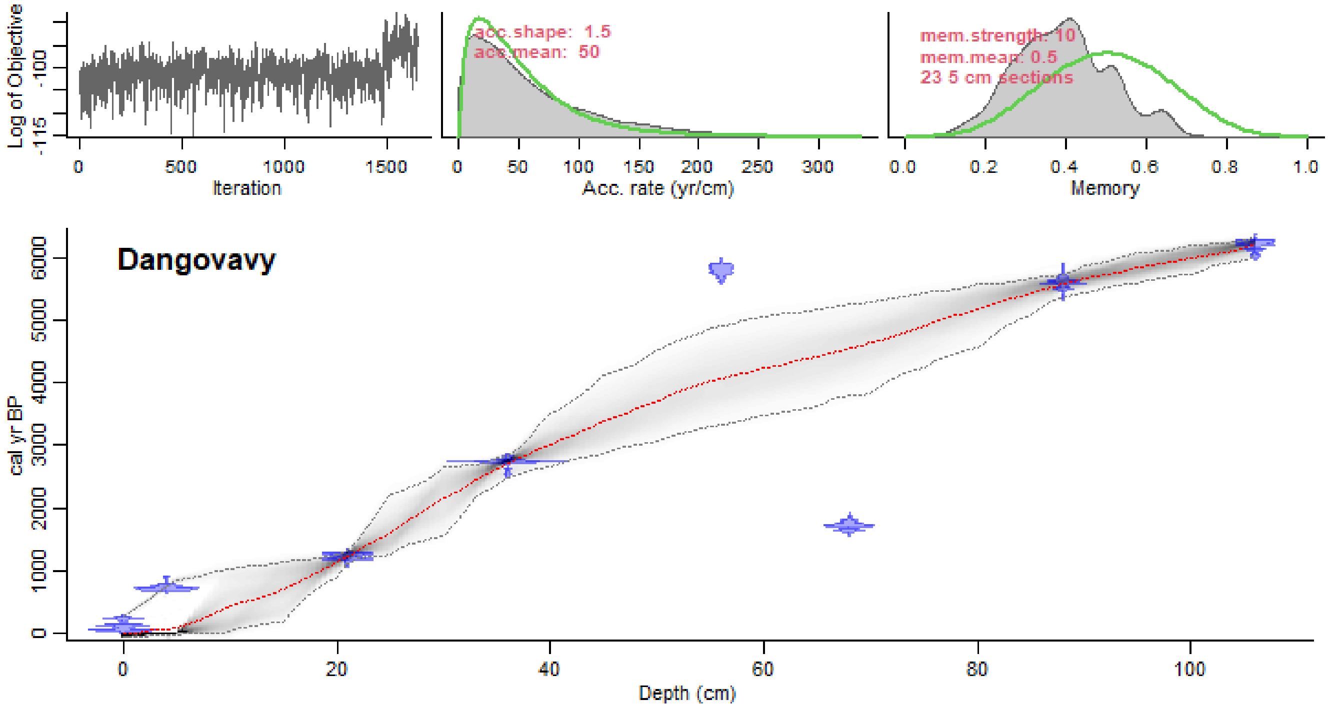
- ESSA/ Département des Eaux et Forêts
  « Pour le rapport »

11/10/16 - Accès n° 116/16

Appendix 2: Bacon Age-depth model of the sediment core collected in Tampoketsa-Ankazobe wetland



Appendix 3: Bacon Age-depth model of the sediment core collected in Lake Dangovavy



Appendix 4: Pearson correlation and linear regression between macrocharcoal and microcharcoal particles from the Tampoketsa-Ankazobe core (outlier 0cm removed)