

**Impact of human land-use and rainfall variability in
tropical dry forests of southwest Madagascar during the
late Holocene**



Estelle Razanatsoa

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Supervisors:

Lindsey Gillson, Stephan Woodborne (co), Malika Virah-Sawmy (co)

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ABSTRACT

Over the last 2000 years, climatic and anthropogenic factors have influenced vegetation in Madagascar, but the contribution of these two factors has been the subject of intense debate, a debate hampered by the scarcity of palaeoecological studies on the island. Southwest Madagascar is semi-arid and comprises fragmented tropical dry forests where human subsistence strategies are diverse. Therefore, it provides a perfect setting to generate new palaeoecological records and investigate vegetation response to changes in human land-use and rainfall variability. The aim of this thesis is to understand how and when land-use changed, and rainfall variability impacted the landscape in the southwest region, using dendroclimatological and palaeoecological approaches. Carbon isotopes in the rings of four baobab trees (*Adansonia* spp.), were compared with pre-existing palaeoclimate data to produce rainfall records for the past 1700 years. Pollen, carbon isotopes, and charcoal in sediment cores from two lakes namely Lake Longiza and Lake Tsizavatsy (located in the northern and southern sites respectively in southwest Madagascar) were analysed to produce vegetation and fire records during the late Holocene in the region.

Combination of the four baobab isotope records yields a new 700-year record for the southwest, which suggests an aridity trend over time, associated with a long-term reduction and increase in the duration of wet and dry periods respectively. Drying was more pronounced for the southern site than the northern site. A comparison with a high-resolution record from the northwest region allowed the rainfall of the southwest to be extended back to the last 1700 years as follows: from AD 300-500, the southwest region experienced a dry period which was followed by a wet period until AD 1000. Subsequently, there was a dry period from AD 1000-1250, followed by a wet period in the southwest. The period from AD 1300-1400 represented the wettest period in the record, followed by a decreasing wet period until AD 1600. The period between AD 1600 and 1800 represented the driest period, peaking around AD 1700. This was followed by a relatively wet period of about 50 years and another 100-year dry period. The last period assessed, from AD 1985 to 2000, was a relatively wet period. Such variability of the rainfall might have affected ecosystems and human land-use in the region.

The tropical dry forest biome of southwest Madagascar has taxa from the dry forest, riparian forest and savanna woodland in the pollen records of both sites. In the core from the northern site (Lake Longiza), the pollen record suggests a heterogeneous mosaic of dry forest and

riparian forest that was present over the last 2400 years. In the earliest part of the record, the community was dominated by trees from both the dry forest and riparian ecosystems. The onset of changes was recorded around AD 420, with a decrease in dry forest and riparian trees and an increase in grasses and xerophytes, possibly driven by dry conditions. This was followed by a short recovery of trees and C₃ plants around AD 870 punctuated by a decrease in dry forest taxa around AD 980, possibly associated with the suggested expansion of pastoralism. After this period, the landscape became more open and grassier, as indicated by the dominance of C₄ plants in the stable isotope record. Similar patterns of change in the pollen record, with a further increase in grasses and pioneer taxa, were recorded around AD 1900. Charcoal influx also started to increase drastically at this time, suggesting fire and forest clearance associated with a shift to agriculture. These large shifts in human land-use (probably a combination of both pastoralism and agriculture) coincided with the decline of floral diversity of the landscape, as indicated by pollen rarefaction. However, the diversity of the floral community gradually recovered, because of the persistent heterogeneity of the landscape.

The core from the southern site (Lake Tsizavatsy) had a basal date of approximately 700 years BP but presented a hiatus of about 500 years from AD 1420-1910. The preceding period of AD 1300-1420 was marked by a decrease in the abundance of trees during the wettest period in the region, which was most likely because of human activities (foraging and pastoralism), as inferred by the increase in charcoal influx and pioneer taxa. During the second period, from AD 1910-2010, there was an increase in xerophytic taxa, which suggests a long dry climate, recorded prior to this period. In addition, from AD 1950, trees decreased while pioneer taxa increased, despite the stable influx of charcoal recorded during this period. This possibly indicates the effect of human activities that did not involve the use of fire, probably conducted by ethnicities other than the forager communities, which are still present in the area today.

This thesis contributes significantly to the understanding of palaeoclimate, palaeoecology and the history of human subsistence in a biodiverse region of Madagascar, where no other record is currently available. Results from stable isotope analysis from baobabs showed a drying trend over the past 700 years, which has interacted with land-use to affect vegetation structure and composition over time. The pollen and charcoal results suggest the northern site, where vegetation was a mosaic of dry forest and riparian forest, experienced an impact of human activities through a shift to agriculture especially in the last 100 years. The savanna woodland of the southern site, however, was less affected by humans, probably as occupants were

subsistence foragers, but the vegetation had a higher response to aridity. The results show that two distinctive human subsistence (pastoralism and foraging) were present simultaneously in the region until modern times. The northern site has evolved possibly from foraging into extensive agriculture, probably related to the fertility of the alluvial soil in the area, while the southern community remained dominated by foragers, while adopting today a seasonal practice of agriculture.

From a conservation perspective, strategies of conservation for each ecosystem investigated here are proposed. In the northern site, monitoring and reducing fire-use within the dry forest ecosystem would allow tree recovery. In addition, restoring and establishing protected areas within the riparian forest would allow these ecosystems to act as refugia for regional biodiversity. Such measures will likely reduce the pressure on these ecosystems, where agriculture is a threat due to the availability of both water and fertile soil in their surroundings. Alternative livelihoods are required for the northern populace, for example through the exploitation of invasive aquatic plants such as *Typha*, which can be used in making of handcrafted artefacts, to reduce pressure on forest ecosystems through agricultural practices. For the southern site, maintaining the resilience of the savanna woodland through reforestation of functional species is also important to allow sustainability of services provided by these ecosystems. These strategies are applicable locally for Madagascar and for worldwide tropical dry forests, one of the globally most threatened vegetation types due to anthropogenic pressure and climate change.

Key words: Palaeoecology, tropical dry forests, human land-use, rainfall variability, southwest Madagascar

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1. CHAPTER ONE: INTRODUCTION

In the Anthropocene, climate change and human land-use are viewed as the critical drivers of environmental change and degradation of the earth's ecosystem (Whitlock *et al.*, 2018).

Climate variability operates at scales of seasons to millennia and has shaped ecosystems and associated human subsistence (Willis *et al.*, 2007; Virah-Sawmy *et al.*, 2010; Bellard *et al.*, 2012) especially in semi-arid and arid areas, where rainfall is scarce with a pronounced seasonality (Mooney *et al.*, 1995; Middleton and Thomas, 1997). Little research, however, has investigated the impact of climate variability on the vegetation of arid regions on long (decadal-millennial) timescales, and on the tropical dry forest ecosystems specifically. The tropical dry forests occupy more than 40% of tropical landmass and are among the most threatened global ecosystems (Figure 1.1; Miles *et al.*, 2006). The lack of long-term research is because of the paucity of high-resolution palaeoecological records available, due to poor preservation of pollen grains in sediment, which limits long-term analysis of vegetation patterns (see Chase and Meadows, 2007 for Southern Africa, Virah-Sawmy *et al.*, 2016 for arid Madagascar). With anthropogenic climate change, the Intergovernmental Panel on Climate Change (IPCC) predicts more severe and longer dry seasons combined with an increase in temperature in the tropics (IPCC, 2007). Such changes are expected to lead to higher tree mortality (IPCC, 2007). This prediction is made complicated by the interacting effects of CO₂ fertilisation, which favours tree recruitment, as well as changes in fire regimes. The high diversity of morphological and functional adaptations of species in the tropical dry forests has historically provided these ecosystems with a plasticity in response to heat and water stress, for example through water conservation (Alvarez Añorve *et al.*, 2012). This resilience might be eroded if ecosystems are degraded, however, and enhancing and restoring this plasticity could improve the adaptive capacity of these threatened ecosystems.

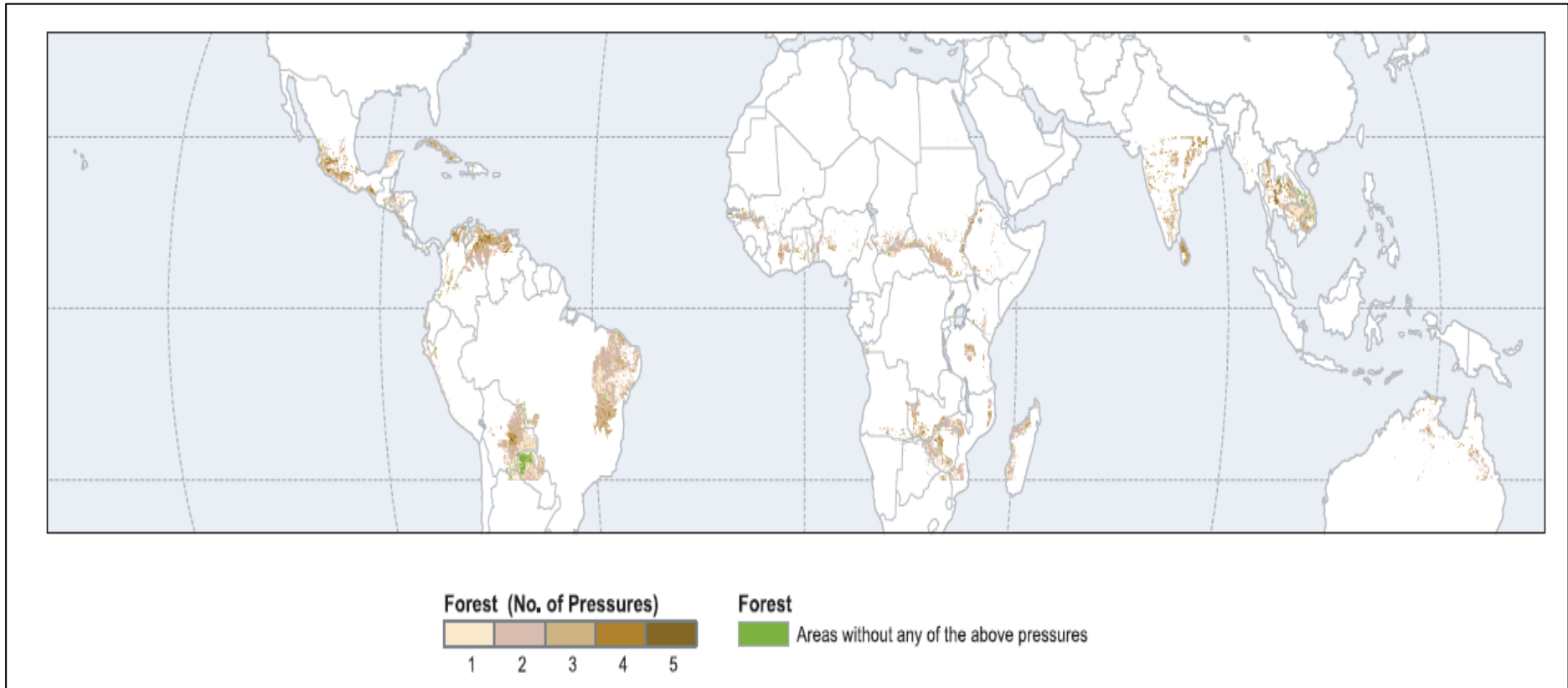


Figure 1.1: Global distribution of the tropical dry forests and its associated pressures including forest fragmentation, conversion to agriculture, human population, fire and climate change from Miles *et al.*, (2006).

Human induced fires, conversion of forest into agriculture, and livestock grazing are the major anthropogenic threats that lead to forest loss and fragmentation in most of the regions where tropical dry forests occur (Miles *et al.*, 2006.). Tropical dry forests are ecologically defined as areas containing different vegetation assemblages such as savanna, riparian forest, coastlines and mangroves and that include deciduous or evergreen taxa in either open or closed canopy structures (Sánchez-Azofeifa *et al.*, 2005; Pennington *et al.*, 2006; Portillo-Quintero *et al.*, 2015). These ecosystems provide various services for humans such as food, pasture, wood for construction and fuel (Fajardo *et al.*, 2005; Portillo-Quintero *et al.*, 2015). They are currently considered as one of the most heavily utilised and disturbed ecosystems worldwide (Hoekstra *et al.*, 2005; Gillespie *et al.*, 2012; Portillo-Quintero *et al.*, 2015). However, this biome is still understudied and the response of its various ecosystems to long-term climate change and continuous anthropogenic activities is not fully understood. Palaeoecological research is important in identifying the long-term trends and patterns of changes in response to these threats specifically in areas such as Madagascar.

The island of Madagascar is classified as among the biodiversity hotspots (Myers *et al.*, 2000; Mittermeier *et al.*, 2005) based on criteria related to its exceptional biota, and the degree of threats this biodiversity is facing (Myers *et al.*, 2000; Mittermeier *et al.*, 2005). The island contains around 12,364 vascular plant species (Callmander *et al.*, 2013) of which about 85% are endemic (Goodman and Benstead, 2005; Callmander *et al.*, 2013). The southwest contains some of the most unique plant communities on the island where 48% of the genera and 95% of the species are endemic (Elmqvist *et al.*, 2007; Phillipson, 1996). This region is marked by the abundance of life forms presenting adaptation to drought. For instance, six out of nine species of baobabs (genus *Adansonia*) are endemic across the region. This endemism is also high for fauna such as lemurs, frogs, and birds (Goodman and Benstead, 2005). However, this biodiversity is threatened by habitat loss through agriculture and mining (Laurance *et al.*, 2009), slash-and-burn agriculture, anthropogenic fires, overgrazing, invasive species and overharvesting (Myers *et al.* 2000; Harper *et al.* 2008, Mittermeier *et al.*, 2011). And degraded ecosystems in the island might not be resilient to climate change over the long-term with a predicted reduction in rainfall and increased drought under the tropics (IPCC 2007).

1.1.Hypothesis of environmental change in Madagascar

Environmental change in Madagascar during the late Holocene has been the subject of debate within palaeosciences, because the island has experienced changes in vegetation cover and faunal extinctions within the last 2000 years (Crowley, 2010; Crowley *et al.*, 2017; Godfrey *et al.*, 2019). During the past two thousand years, between AD 500 and 1500, Madagascar experienced a substantial reduction of its large animals associated with habitat change in various palaeosites across the island (Burney *et al.*, 2004, Crowley, 2010; Crowley *et al.*, 2017). This extinction occurred not only in very large species (>150 kg) but also in small species (<10 kg) as detailed in Burney *et al.* (2004), Crowley (2010) and Dewar (2014), with most extinctions occurring between 2500-500 cal years BP (Crowley 2010). Some of the extinct animals include taxa such as the giant tortoises, elephant birds, hippopotami, and lemurs. In terms of vegetation change, opening and/or loss of forest cover notably in the northwest, southwest and southeast were recorded between 1500 years ago up to 950 cal years BP (Matsumoto and Burney, 1994; Virah-Sawmy *et al.*, 2010; 2016; Voarintsoa *et al.*, 2017a). These changes coincided with dates of human presence across the island ranging from 10,000 cal years BP - 1350 cal years BP (Hansford *et al.*, 2018; Anderson *et al.*, 2018).

Debate focuses on whether the main causes of faunal extinction and vegetation change are anthropogenic or climatic. The synergy hypothesis (Burney, 2003; Burney *et al.*, 2004) suggests that a period of aridification led to the reduction of ecosystem's resilience which then amplified human impact and triggered extinctions and vegetation change (Humbert, 1927; MacPhee *et al.*, 1985; Burney, 1987a; MacPhee and Burney, 1991; Burney and Flannery, 2005; Muldoon, 2010; Crowley *et al.*, 2017). During the disappearance of these megafauna, there was an expansion of natural fires in grassy biomes leading to a decrease in forest extent. This led to a loss of habitat for forest dependent species resulting in their extinction, mostly during the first millennium CE/AD (Bond *et al.*, 2008; Willis *et al.*, 2008). In contrast, the aridification hypothesis (Virah-Sawmy *et al.*, 2010) suggests that there was a synchronous habitat change in Madagascar that started with an early period of aridification in the northwest, central highlands, southwest and southeast, culminating between 1000 and 900 cal years BP (AD 950 and AD 1050). This island wide aridification triggered megafaunal extinctions especially in the arid southwest (Mahé and Sourdats, 1972; Virah-Sawmy *et al.*, 2009b; 2010; Tovondrafale, 2014). However, evidence is now emerging that these habitat changes and extinction should be addressed locally within the region's climatic and

anthropogenic context (Burney, 1997; Dewar *et al.*, 2013; Dewar, 2014; Goodman and Jungers, 2014) which are vastly different across the island.

1.2. Tropical dry forests in Madagascar

The tropical dry forests of Madagascar occupy the western region from Cape d'Ambre in the north and limited by the River Mangoky in the south (Figure 1.2; Grubb, 2003) with variation in rainfall and human land use across the region. This region includes two bioclimatic zones and is characterised by the presence of a southward gradient of rainfall due to trade wind patterns including the Intertropical Convergence Zone (ITCZ), and tropical cyclone genesis (Donque, 1972; Chikoore *et al.*, 2015; Jury, 2016) (Figure 1.2). The northwest, classified as the dry bioclimatic zone, receives a mean annual rainfall of about 1160 mm (Voarintsoa *et al.*, 2017a) and contains exclusively tropical dry forests including, but not limited to, dry deciduous forests (hereafter dry forest), wooded savanna, and mangrove. The southwest region contains tropical dry forests with mosaics of riparian forest, wooded savanna and dry forest up to Mangoky River (Figure 1.2). As rainfall becomes scarce further south, xerophytics dominate corresponding to the spiny thicket forest. The southwest region is classified as sub-arid climate and receives less than 800 mm per year with irregular rainfall (eight to nine months of dry season between March to November) and cyclical drought (Cornet, 1974; Middleton and Beinart, 2005). These dry periods can extend for several years within the locality's microclimate and have become more prolonged and frequent in recent decades (Donque, 1972; Dewar and Wallis, 1999; Jury, 2003; Randriamahefasoa, 2013; Waeber *et al.*, 2015). This was confirmed by the increasing aridity recorded in pollen records from the southwest region in the last 1000 years (Virah-Sawmy *et al.*, 2016) and a decreasing trend of rainfall in instrumental records since the late 19th century (Elmqvist *et al.*, 2007). The rainfall gradient and drying trends might have impacted the different vegetation types within the tropical dry forests. For instance, dry-adapted taxa abundance has increased following the rainfall gradient (Rabesandratana, 1984; Phillipson, 1996). Considering the dominant vegetation types in the western region, a shift of the state of vegetation from dry forest to spiny thickets forest (Figure 1.2) is evident as already recorded in the southermost area of the southwest region where annual rainfall is less than 500 mm.

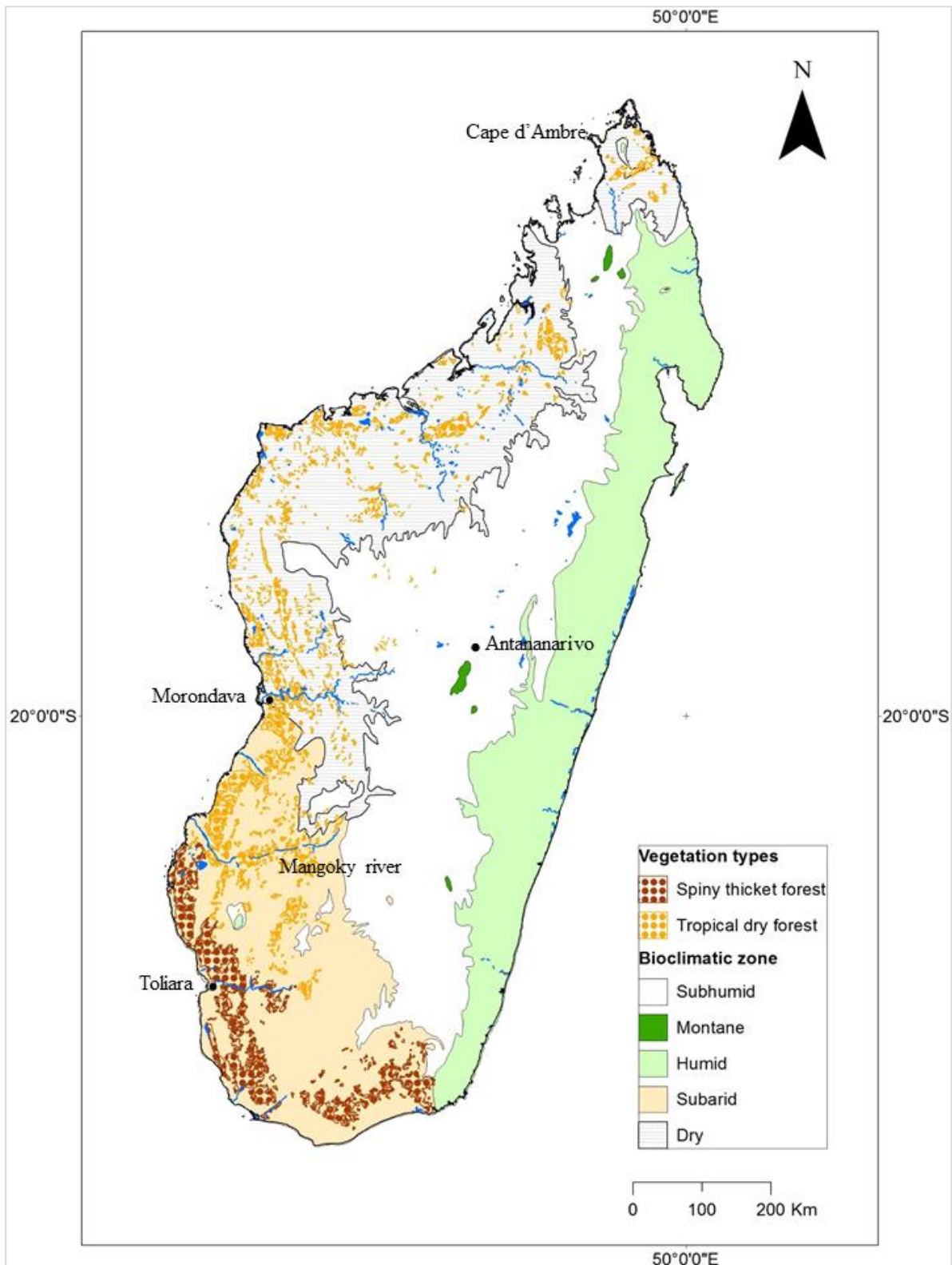


Figure 1.2: Map of the primary vegetation in the western region of Madagascar indicating the limit of tropical dry forests on the island and their presence within the sub-arid bioclimatic zone of southwest Madagascar where this research was conducted. The dry bioclimatic area receives rainfall higher than 1000 mm per year while the sub-arid bioclimat receives less than 1000 mm per year (Cornet, 1974). Main towns in the southwest, the Mangoky River and a theoretical limit of the distribution of the dry forest, are provided.

Similarly, the history of human presence and land-use across Madagascar's dry forest potentially differs significantly in different climatic zones, which may have caused the current states of the tropical dry forests and the various vegetation types within the landscape. For example, the northwest region of the dry forest is currently occupied mostly by agropastoralists while the southwest is still occupied by a community of foragers called *Mikea* in addition to agropastoralist ethnicities including *Sakalava*, *Masikoro*, *Antandroy* and *Mahafaly*. The *Mikea* people, the only foragers in Madagascar today, collect food resources during the whole year and exchange goods with their agropastoralist neighbours (Stiles, 1991; 1998; Tucker and Taylor, 2007; also see Chapter 3: Study area). In addition, seasonal cultivation of maize and cassava through slash and burn methods called "*Hatsake*" is practiced between December and March (Stiles, 1998) which consists of clearing forest and burning the biomass (Waeber *et al.*, 2015) for crop cultivation (Scales, 2012). Most of the other ethnicities in the southwest are currently agropastoralists. Intensive pastoralism was probably practiced in the southwest since AD 600 according to paleontological and palaeoecological sites in the region (Anderson *et al.*, 2018), which might have been localised. But in the last century an increase in extensive agriculture has been recorded in the southwest, especially in areas with richer alluvium and clayey soils around the Morondava basin (Fauroux, 2001; Waeber *et al.*, 2015). Those activities might impact the vegetation state especially when this results in significant forest losses. In such cases, tropical forests can shift into grassland as an alternative stable state (Dublin *et al.*, 1990; Folke *et al.*, 2004).

To elucidate the interactions between climate change and Madagascar's rich and unique human and natural communities, it is necessary to evaluate and establish the history of change in the tropical dry forests of the southwest region, where no records were previously available. Through the exploration of multiple proxies, this study investigates the impact of both rainfall variability and human land-use on the tropical dry forests in southwestern Madagascar. Given the region's lack of climate record, one of the major contributions of this thesis is generating the high resolution local and sub-regional (southwest Madagascar) rainfall record which has allowed the assessment of trends and frequency of dry and wet periods over time. Reconstruction of the vegetation and fire regime during the late Holocene was conducted using sediment cores from two lakes across the region. These changes are interpreted in terms of changes in human subsistence and are used as the basis for suggesting conservation strategies that are tailored to local context and livelihoods.

1.3. Project aim, objectives, and hypotheses

Southwest Madagascar is vulnerable to environmental change, specifically the drying of the region in the last 1000 years (Virah-Sawmy *et al.*, 2016) which affects not only the survival of the people, but also their subsistence strategies which in turn impact the ecosystem around them. In addition, ecosystems in the region have specific responses to climatic and anthropogenic disturbance which might lead to the reduction of ecosystem resilience and therefore into a shift in ecosystem states (Oliver *et al.*, 2015). This research covers a gradient of rainfall and soil fertility along southwest Madagascar and a temporal scale of about 2000 years. It presents evidence for rainfall variability, vegetation dynamics, fire history and human subsistence strategies. It investigates changes in ecosystems along the gradient at local and regional scales. The goal of this study is to understand the impact of human land-use and rainfall variability on tropical dry forests in southwest Madagascar during the late Holocene and to use this to inform conservation planning.

The four main objectives of this study are to:

- 1) Generate high-resolution regional and local rainfall records from carbon isotopes and radiocarbon dating of baobab tree rings, and to compare these with pre-existing palaeoclimate records from the western region, where the tropical dry forests occur
- 2) Reconstruct and investigate past vegetation dynamics and fire regime through pollen, carbon isotopes and charcoal analysis in the palaeoecological record from lakes in the southwest region
- 3) Assess the importance of both anthropogenic and climatic (rainfall) factors in the vegetation change during the late Holocene
- 4) Evaluate human-nature interactions and impacts through of fire usage, inferred from microscopic and macroscopic charcoal, and other activities inferred from pollen and carbon isotope analysis
- 5) Identify possible conservation and restoration opportunities that safeguard biodiversity as well as human livelihoods

To better predict the results of this research, three hypotheses with their respective research questions were established.

Hypothesis 1: Southwest Madagascar has experienced rapid decrease in rainfall in the last millennium.

- What was the climate variability across the region in southwest Madagascar over the last millennium?
- How was the distribution and variability of the rainfall at the sub-regional / landscape scale?
- What was the climate in the southwest between 2000 cal years BP and 1000 cal years BP relative to rainfall records available from the northwest region?
- What was the rainfall pattern in the western region where tropical dry forests occurred during the late Holocene?
- What is the long-term rainfall trend in southwest Madagascar over time?

Hypothesis 2: Biodiversity and taxa richness of the tropical dry forests in southwest Madagascar decreases in response to a drying climate and an increasing fire regime over time.

- How has fire changed over time?
- How has the drying trend of the climate recorded in the last millennium affected the fire regime in southwest Madagascar?
- What was the local and regional fire influx trend in these sites during the late Holocene?
- What vegetation dynamic occurred in the region during the late Holocene?
- Have rainfall and fire interacted to affect vegetation structure, composition and richness?
- Which vegetation types are the most resilient to changes in rainfall and fire regime?
- Is there evidence of shifts between alternative stable states?
- How will the vegetation types within the tropical dry forests in southwest Madagascar respond to increasing duration and severity of dry periods and increasing human activities?

Hypothesis 3: The introduction and practice of pastoralism and agriculture in human subsistence in the southwest led to an increase in fire activity but the intensities of these human activities is directly dependent on soil fertility.

- Is fire increase directly driven by aridification or human activities or both?
- What are the main subsistence practices recorded in the area and how did they develop over time?

- How would these subsistence strategies be affected by future rainfall variability?

1.4. Study design

This study combines palaeoecological and dendroclimatological approaches to assess three main parameters: rainfall variability, vegetation dynamics and human land-use, as detailed in Figure 1.3. I analysed the isotope rainfall proxy from baobab trees distributed along the southwest region within the sub-arid region to generate the first regional rainfall record in Madagascar. The novelty and uniqueness of this method for Madagascar is explored to investigate patterns and changes of rainfall over time along the western region which is then compared with previously published palaeoclimate data in the northwest. I analysed pollen and carbon isotopes in sediment cores from lakes distributed within the tropical dry forests extent to infer changes of vegetation at the local and landscape scale. These proxies are commonly used for palaeoecological investigations of ecosystem dynamics (Bjune *et al.*, 2004; Birks and Seppä, 2004; Gillson and Ekblom, 2009; Colombaroli *et al.*, 2010; Colombaroli and Tinner, 2013; Voarintsoa *et al.*, 2017a). I also analysed microscopic and macroscopic charcoal, a rigorous method to infer fire history and it has been widely used in Madagascar and elsewhere (MacPhee *et al.*, 1985; Bennett and Willis, 2001). I examined charcoal influx alongside the climate record to assess human subsistence strategies and their evolution along the southwest region over time. Because I have an independent rainfall record, I could elucidate the impacts of climate change versus human impacts on the vegetation over time and evaluate the response of the various ecosystems within the tropical dry forests in Madagascar to these factors.

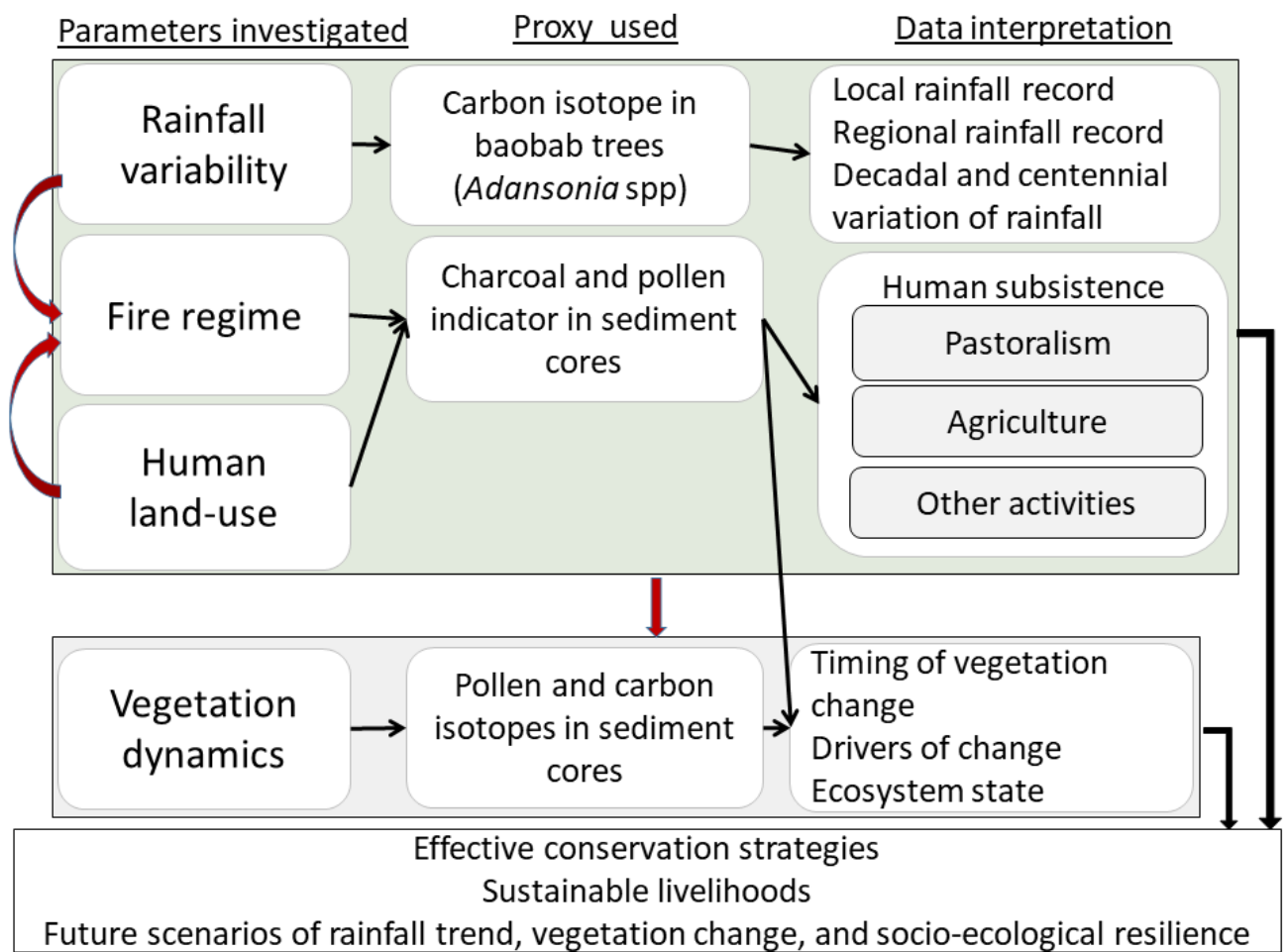


Figure 1.3: Diagram showing the design and interpretation of data generated by the present research. Red arrows indicate interactions between parameters while black arrows show the proxy or the expected outcome of the analysis.

1.5. Thesis organisation

This dissertation is structured in the following six chapters to respond to the research questions and hypotheses described above:

Chapter One: Introduction

This introductory chapter gives background information on the state of the tropical dry forests ecosystem and the drivers of change in this ecosystem. It highlights the hypotheses of environmental change in Madagascar and how this relates to the tropical dry forests of the island along the western region, with the specificity of the evidence for anthropogenic activities and climatic impacts of the southwest region. The chapter summarises the aims and hypotheses and the associated research questions that are elaborated in the thesis and guides to the designs of the study.

Chapter Two: Literature review

This chapter provides the palaeoenvironmental context in Madagascar by describing palaeoclimate and vegetation records available both on a regional and island-wide scale. Special attention is given to southwest Madagascar and gaps in the literature were identified, part of which will be the focus of interpretation in the present research.

Chapter Three: Description of study area

The first section of this chapter locates the study area of the present study within the sub-arid southwest Madagascar. It describes the contemporary state of its environment including vegetation, climate, geology, and human land-use and details the threats as well as conservation strategies that are currently in place.

Chapter Four: Methodology

This chapter describes in detail approaches and methods applied to reconstruct rainfall, vegetation and fire over time. Qualitative and quantitative data analysis is also provided in this chapter

Chapter Five: Results

This data chapter describes the results of the rainfall variability from carbon isotope in baobabs, and the results of the palaeoecological investigation of pollen, isotope and charcoal records in the sediment cores from two lake sediments cores in southwest Madagascar.

Chapter Six: Discussion

This chapter interprets and discusses the results of the rainfall reconstruction at local and regional scales. It also details the results of the western palaeoclimate comparison of rainfall and deduces the rainfall of the southwest for the last 1700 years following the available record for the northwest. The second part of the discussion deals with the drivers of vegetation change and the response of these ecosystems to anthropogenic and climatic disturbance. Particular attention is also given to the analysis of human subsistence strategies across the region.

Chapter Seven: Synthesis and conclusion

This chapter provides synthesis of the main findings conducted throughout this thesis and gives future scenarios of ecosystem change and human subsistence. It highlights the significance of this research and proposes further research projects. Furthermore, it suggests conservation strategies for the each of the ecosystems identified in the analysis and identifies the potential effect of climate on human-nature interaction.

2. CHAPTER TWO: LITERATURE REVIEW OF PALAEOENVIRONMENT AND RESEARCH IN MADAGASCAR

Palaeoecological research in Madagascar has focused on vegetation cover to explain the past extinction events in relation to human land-use and climate variability and consequently the current state of its vegetation (Burney, 1993; Matsumoto and Burney, 1994; Virah-Sawmy *et al.*, 2009a; 2009b). These studies have provided information on ecosystem dynamics, climate change and the possible impact of human arrival and settlement on Madagascar. In addition, palaeoecological studies have helped in understanding Madagascar's past vegetation for example by demonstrating the existence of an ancient grass-dominated ecosystem in the central highlands before human arrival (Bond *et al.*, 2008; Vorontsova *et al.*, 2016), and this had been subject to controversial debates. Palaeoecology has also helped to identify factors that have been strongly associated with current vegetation distribution and land-cover including the effects of climate and human disturbance. As such, an adequate understanding of these factors assists in identifying the vulnerability framework of a mosaic ecosystem and elaborate adequate conservation strategies which considers human livelihood at landscape scale as shown in Virah-Sawmy *et al.* (2016). This research showed that within the spiny thickets forest ecosystem, the gallery forest is susceptible to degradation and should be strictly included within the protected areas schemes, while resilient dry forest would provide wildlife friendly agriculture. The resistant xerophytic coastal bush provides the perfect area for livelihoods (Virah-Sawmy *et al.*, 2016).

There is an ongoing discourse around the changes in Madagascar's ecological systems, including its vegetation distribution, fire regimes, and its megafauna, as well as the influence of human contact and settlements. The initial view proposed by early botanists saw Madagascar as originally covered by forest, where fire was absent, and the megafauna were forest adapted creatures (Humbert, 1927; Perrier de la Bathie, 1936; Humbert, 1955). This has been the predominant view of ecology in Madagascar until recently (but see, for instance, Bond *et al.*, 2008). This view suggests that the present-day forest-grassland mosaics of the central highlands, for example, are anthropogenic. It further argues that habitat fragmentation caused by humans led to megafaunal extinction in the last 2000 years. However, recent research has started challenging this view using paleontological, anthropological and palaeoecological approaches (Burney, 1987a; 1987c; Matsumoto and

Burney, 1994). Around the 1980s, new artefacts and palaeoecological sites from various regions within Madagascar started emerging and provided new evidence for the islands' ecological history.

Numerous studies from different regions using materials such as sediment cores, bones, and speleothems, and using proxies such as pollen, charcoal, isotopes, and diatoms provided an alternative ecological narrative for Madagascar (Burney, 1987a; MacPhee and Burney, 1991; Virah-Sawmy *et al.*, 2010; Burns *et al.*, 2016). In fact, it is now well established that some of the grasslands are ancient, and are specifically rich in endemic taxa, resembling the African mainland grassland (Bond *et al.*, 2008; Vorontsova *et al.*, 2016). Some of the ecosystems in Madagascar were also dynamic and patchy in certain areas prior to human arrival. This can be observed in the southeast where heterogenous vegetation of littoral forest with fire prone ericoid grassland occurred prior to evidence of any anthropogenic activities (Virah-Sawmy *et al.*, 2009). Furthermore, fire which is usually associated with human land-use was recorded in the late Pleistocene and early Holocene in the central highlands. This research found that samples from these periods had a higher charcoal content than they did during the human period (MacPhee *et al.*, 1985).

Even with the modern view of the presence of mosaic vegetation in the island, and non-anthropogenic fire occurrence, the question still remains whether it was human or climate that triggered the disappearance of megafauna and changes in forest cover during the late Holocene (see Chapter 1.1: Hypothesis of environmental change in Madagascar). Not all landscape mosaics are ancient and to design appropriate conservation strategies, it is necessary to distinguish ancient grasslands and fire-prone heathlands from deforested areas. In addition, some livelihoods have persisted alongside biodiversity until recent decades, which allows possibilities for improving sustainability alongside biodiversity conservation. This chapter provides a detailed description of Madagascar's history by critically reviewing literature on rainfall variability, vegetation dynamics, human arrival, settlement and land use across various regions. This review gives special attention to the southwest region, which is the focus of this study.

2.1.Palaeoclimate records in Madagascar

2.1.1.Island wide climate record from late Cretaceous up to late Quaternary

The island wide palaeoclimate of Madagascar from the late Cretaceous up to late Quaternary is of low temporal resolution (Ohba *et al.*, 2016) but is more detailed from the late Quaternary up to the present. These Quaternary records were obtained from studies using different approaches such as modeling and palaeoecology, along with an analysis of instrumental and historical records. These investigations are aimed at understanding patterns and factors that influence the island's climate, which may have been less variable prior to the Holocene but have been accentuated with dry and wet oscillations since the Holocene (Burney, 1997).

During the late Quaternary, oscillations between dry and wet climates have been recorded for the island (Table 2.1). A dry period occurred during the full glacial peaks around 18,000 – 17,000 cal years BP with an arid period recorded for the entire island (Burney *et al.*, 2004; Mietton *et al.*, 2018), while the wettest period was recorded in the middle Holocene around 5000-3000 cal years BP (Burney, 1996). In all proxies used for palaeoclimate in Madagascar, the last millennium has been suggested to be within a dry period with a possible increase of aridity in some areas (Burney, 1987a, 1993; Gasse and Van Campo, 1998; 2001; Virah-Sawmy *et al.*, 2010). However, the resolution of these reconstructions does not allow for the evaluation of trends over time specifically in the last millennium. Analysing trends in each region would be more appropriate, considering the presence of gradients due to trade wind patterns, topography and tropical cyclone genesis that impact the rainfall distribution of Madagascar (Donque, 1972; Jury, 2016). Currently, the northeast region receives more than 3500 mm per year of rain, while the southwest of the island is the most arid with less than 500 mm per year of rain (Cornet, 1974). This southwest region mostly depends on moisture from the movement of the temperate tropical troughs (Woodborne, personal communication 2018, July) and from the Intertropical Convergence Zone which is limited at 20 °S (Figure 2.1).

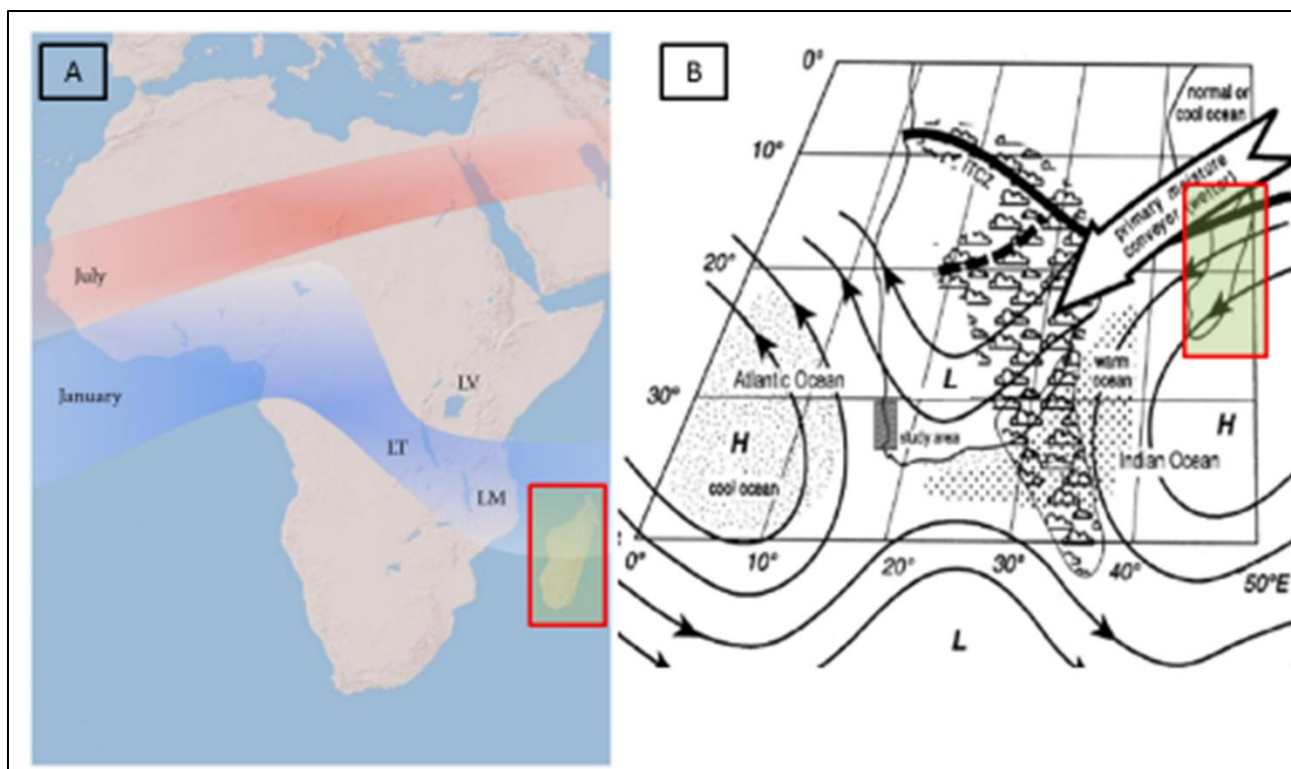


Figure 2.1: (A) Seasonal position of the intertropical convergence zone (ITCZ) with limited effect up to 20° in Madagascar. LV: Lake Victoria, LM: Lake Malawi, and LT: Lake Tanganyika. Map extracted from Danley *et al.* (2012). (B) Troughs that regulate rainfall in southern Africa including Madagascar (modified from Chase and Thomas 2007). Red boxes indicate location of Madagascar.

Table 2.1 : Inferred climate for Madagascar from the Late Cretaceous up to present modified from Burney, 1997; Virah-Sawmy *et al.*, 2010 with additional information from Wells, 2003 and Ohba *et al.*, 2016

Period	age (cal years BP)	Inferred climate	References
Holocene			
Present millennium	1000 – present	Drying trend	Virah-Sawmy <i>et al.</i> , 2010
Late Holocene	3000 – 1000	Warm, dry	Burney, 1997
Middle Holocene	6000 – 3000	Warm wet	Burney, 1997
Early Holocene	11,000 – 6000	Moderately warm, dry	Burney, 1997
Pleistocene			
Postglacial	15,000 – 11,000	Moderately warm, dry	Burney, 1997
Full Glacial	25,000 – 15,000	Cold, very dry	Burney, 1997
Interstadial	40,000 – 25,000	Cool, wet	Burney, 1997
Late Cretaceous – end of Eocene	33,9 million	Moisture restricted Moderate humidity. generally	Wells, 2003
KP Boundary (Late Cretaceous)	66 million	dry but contained distinctly humid areas	Ohba <i>et al.</i> , 2016

2.1.2. Regional palaeoclimate variability

The regional climate record and its resolution at a millennial to centennial time scale is patchy in the various regions. The northwest region is the most studied with results yielding higher resolution reconstructions, while palaeoclimate records for the rest of the island remain sparse (as is the case for the southwestern, the central highlands, and the eastern regions). The relatively high data availability for the northwest region is due to archaeological and paleontological investigations using modern techniques, for example palaeoclimate reconstruction such as isotopes in speleothems (Burns *et al.*, 2016; Voarintsoa *et al.*, 2017a; Scroxton *et al.*, 2017).

For the northwest region, climate records date back to early Holocene after the island wide aridity experienced during Late Glacial Maximum around 18,000-17,000 cal years BP (Burney *et al.*, 2004; Mietton *et al.*, 2018). During the early Holocene (9800-7800 cal years BP), the region may have been wetter but with a 100-year drought recorded at 7500 cal years BP (Voarintsoa *et al.*, 2017b). In the middle Holocene (7800-1600 cal years BP), stalagmites from the region showed a hiatus in deposition that was interpreted as an indication of a dry climate (Voarintsoa *et al.*, 2017b) with the transition to a drier period around 4000 years ago (Wang and Brook, 2013). From 3500 years ago up to 1000 cal years BP (Wang and Brook, 2013) and after 1600 cal years BP (Voarintsoa *et al.*, 2017b), the climate was possibly wetter. A high resolution 1700-year record of oxygen isotopes from speleothems at Anjohibe Cave in the northwest region was used to infer the rainfall variability in the region during the late Holocene (Scroxton *et al.*, 2017). This showed a 500-year periodicity of dry and wet spells in the region associated with the displacement of the Intertropical Convergence Zone and global climate forcing. This record suggested that the northwest regional record correlated with other records across the Indian Ocean and the east African records. This high-resolution climate record might represent the western regional record of Madagascar. The high-resolution datasets available for the last 1700 years (Scroxton *et al.*, 2017) combined with a lower resolution record from the same site in Anjohibe Cave from speleothems and stalagmites (Brook *et al.*, 1999; Voarintsoa *et al.*, 2017) showed a succession of dry and wet periods. Brook *et al.* (1999) obtained a succession of dry and wet periods from speleothems from AD 1600 (Figure 2.2) while Voarintsoa *et al.* (2017a) demonstrated that from AD 755-795 was the driest period recorded in the northwest after which the environment became wetter. These records allow us to understand the climate variability for the western region during the late Holocene.

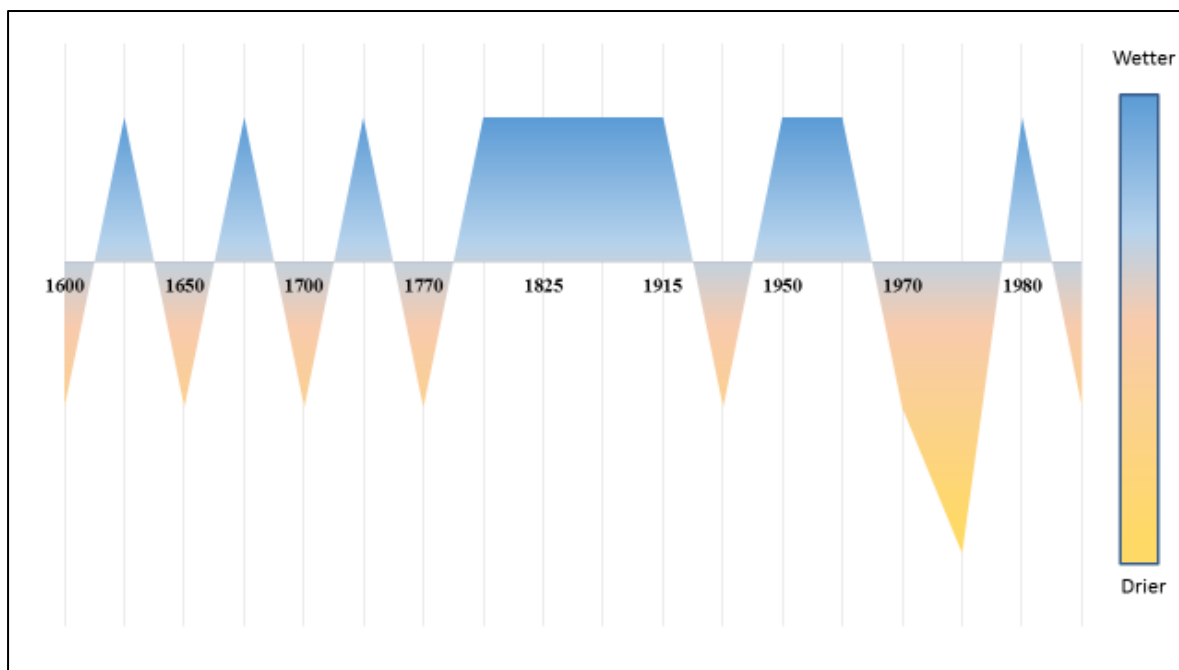


Figure 2.2: Reconstructed palaeoclimate for northwestern Madagascar from AD 1600-1990. This graph is based on speleothems reconstruction by Brook *et al.*, 1999.

Other regions in Madagascar remain poorly documented with limited temporal resolution. In the eastern region, pollen analysis from Andasibe suggests that around 100,000 years ago the temperature was cooler than present (Straka, 1996). In addition, the analysis of lake level at Lake Alaotra suggested a wetter climate favourable to peat around 30,000 cal years BP, followed by a period of relative drought around 29,690-6850 cal years BP (Mietton *et al.*, 2018). Evidence from the southeast region showed drought events around the mid-Holocene with the driest period recorded around 1200 years ago, which correlates with a synchronous desiccation from the various regions in Madagascar (Virah-Sawmy *et al.*, 2010). In the last 300 years from AD 1708-2008, a high-resolution spectral luminescence from coral reef reconstruction of river runoff in the northeast region found that the region experienced wet conditions from AD 1700-1820 with a gradual decrease until mid-1950s. Since then, there has been an increase in rainfall (Grove *et al.*, 2013). For the central highlands, climate records covering the last 30,000 years are very patchy but yield information about temperature with cooling and warming periods as shown in Table 2.2. Dry periods were recorded around 20,000 and 9800 cal years BP. Around 3500 cal years BP, wetter periods were recorded (Gasse and Van Campo, 2001). The driest period was recorded around 2500 years ago (Burney, 1987a; Burns *et al.*, 2016) after which no published climate reconstructions are available.

Climate records available for the southwestern region are very scarce and were mainly interpreted from pollen analysis. Known for its current dry and arid climate, interpretations from pollen showed that the region experienced a wet period in the early and mid-Holocene (7000-4000 cal years BP) (Virah-Sawmy *et al.*, 2016). Since then, the pollen record showed an increase in dry periods and became more pronounced in the last millennia (Table 2.2) (Burney, 1993; Virah-Sawmy *et al.*, 2016). No high-resolution palaeoclimate record is available for the area to identify the patterns, trends, and variability of the rainfall at a decadal to centennial time scale, especially in the last millennium.

Table 2.2: Palaeoclimate reconstruction for the various regions in Madagascar

Region in Madagascar	Period cal Kyr BP	Inferred climate	proxy used	References
Eastern	100 -9.5	Cooler than today	Pollen	Straka, 1996
Eastern, Central	30	Climate favourable to peat, sustain raised lake levels, associated with cooler baseline temperature which lasted until 9500 but there were warmer oscillations in 29,000 and 18,000 cal years BP	Diatoms	Straka, 1996; Mietton <i>et al.</i> , 2018
Central East	29.69 – 6.85	Period of relative drought	Diatoms	Mietton <i>et al.</i> , 2018
Southeast	5.9-5.6	Moderate drought from diatom record	Pollen, Diatoms	Virah-Sawmy <i>et al.</i> , 2009b
	3.3-3.0	Drought	Pollen, Diatoms	Virah-Sawmy <i>et al.</i> , 2009b
	1.2-0.95	Dramatic and synchronous desiccation (but synthesised for all Madagascar based on previous research)	Pollen, Diatoms	Virah-Sawmy <i>et al.</i> , 2009b; 2010;
Northwest	18-17	Arid climate and evidence of sand dune growth	Pollen and diatoms	Burney <i>et al.</i> , 2004; Mietton <i>et al.</i> , 2018
	9.8-7.8	Wet period	Stalagmites	Voarintsoa <i>et al.</i> , 2017
	7.8-1.6	Dry period	Stalagmites	Voarintsoa <i>et al.</i> , 2017
	3.5-1.0	Wet period	Speleothems	Wang and Brook, 2013
	After 1.6	Wet period	Stalagmites	Voarintsoa <i>et al.</i> , 2017
Central Highlands, Eastern, and North	around 20	Dry phase	Pollen Basin formations	Burney, 1987b,
Central Highlands	26-19	Humid and cool period	Pollen, Diatoms	Straka, 1996; Gasse and Van Campo, 1998
	16-15.1	Cooler condition		

Region in Madagascar	Period cal Kyr BP	Inferred climate	proxy used	References
Central Highlands	16.5	Warming of postglacial condition	Pollen, Diatoms	Gasse and Van Campo, 1998
	After 15 14 -13	Return of humidity in the region Warming	Pollen, Diatoms Ice	Mietton <i>et al.</i> , 2018; Reyes, 1993 Romani <i>et al.</i> , 2002 Burney <i>et al.</i> , 1987a,
	9.8	Cool and dry conditions	Pollen, diatoms	Gasse and Van Campo, 1998 Burney, 1987a,
	around 3.5	Cooler conditions with higher moisture	Diatoms, pollen	1987b; Gasse and Van Campo, 1998
	3.5-2.5	Increased moisture and lower temperature	pollen and Diatoms Nitrogen isotope on Speleothem	Gasse and Van Campo, 1998
	2.5	Driest period		Burns <i>et al.</i> , 2016 Virah-Sawmy <i>et al.</i> , 2016
Southwest	7.0-6.6	Cooler in temperature	Pollen	Virah-Sawmy <i>et al.</i> , 2016
	6.6-5.5	Wetter	Pollen Nitrogen isotope on Speleothem	Virah-Sawmy <i>et al.</i> , 2016
	2.5	Increasing drier conditions		Burns <i>et al.</i> , 2016
	2.0-1.0	Increase in arid conditions	Nitrogen isotope on Speleothem	Burns <i>et al.</i> , 2016 Virah-Sawmy <i>et al.</i> ,
	1.8-1.6	Supposed to be drier	Pollen	2016 Virah-Sawmy <i>et al.</i> ,
1.6-0.7	Drier climate	Pollen	2016	

In summary, the northwest region has the highest resolution of rainfall records over the last 1700 years while the northeast contains a 300-year record of runoff from coral reefs. The other regions in Madagascar remain poorly documented. Despite the higher spatial resolution of palaeoecological analysis for the central highlands, the temporal resolution of reconstruction from this region is very limited and there are no high-resolution reconstructions during the late Holocene particularly in the last 1000 years. Southwest Madagascar is poorly understood, and climate reconstruction is needed especially in the last millennium to understand the environmental change that occurred across the island during the late Holocene.

2.2. Palaeoecological reconstruction of the regional vegetation types in Madagascar

2.2.1. Spatial resolution of vegetation reconstruction in Madagascar

The vegetation reconstruction across Madagascar is also scarce, similar to the rainfall reconstruction discussed above as shown in Table 2.3, Figure 2.3. The evaluation of vegetation change was based on ecological association and physiognomy of the taxa recorded in pollen spectra. It included woody and herbaceous taxa variation along with grass rates, fire or/ and dry-adapted, ruderal taxa as well as isotopes ratios indicating C₃ and C₄ plant abundance, which provided the inferred vegetation. The limited available published palaeoecological records are reviewed in Table 2.3, Figure 2.3 to establish the basis for regional ecosystem change, identify the drivers of change in the vegetation of the island and explore gaps which could be filled through the present research.

Table 2.3: Palaeoecological reconstruction from Madagascar and the time period covered by these investigations with their associated vegetation types

Region	Forest type / Ecoregion	Location of core collection	Proxy	Time scale (cal years BP)	Reference
Madagascar		Madagascar	Model	66millions	Ohba <i>et al.</i> , 2016
Madagascar		except west and southwest	Pollen	Modern pollen spectra	Burney, 1988
East	Evergreen forest	Montagne d'Ambre	Pollen	100,000	Straka, 1996
East	Evergreen forest	Andasibe	Pollen	63,000	Straka, 1996
Northeast	Evergreen forest	Lake Alaotra	Pollen, sedimentology, Diatoms, paleolake levels	30,000	Reyes, 1993
Southeast	Littoral forest	Sainte Luce	Pollen, diatoms, charcoal	5200	Virah-Sawmy <i>et al.</i> , 2010
Southeast	Littoral forest	Mandena	Pollen, diatoms, charcoal	5900	Virah-Sawmy <i>et al.</i> , 2010
Central Highlands	Grassland and patch of evergreen forest	Itasy	Pollen	11,500	Straka, 1996
	Grassland and patch of evergreen forest	Vinaninony	Pollen	up to 9500	Straka, 1996
	Grassland and patch of evergreen forest	Tritrivakely	Mineral magnetic proxies for erosion	35,000	Williamson <i>et al.</i> , 1998
	Grassland and patch of evergreen forest	Tritrivakely	Pollen and charcoal	11,000	Burney, 1987c
	Grassland and patch of evergreen forest	Kavitaha	Pollen and charcoal	1500	Burney, 1987a, 1987b

Region	Forest type / Ecoregion	Location of core collection	Proxy	Time scale (cal years BP)	Reference
Central Highlands	Grassland and patch of evergreen forest	Tritrivakely	Pollen, diatoms	40,000	Gasse and Van Campo, 1998; Gasse and Van Campo, 2001
	Grassland and patch of evergreen forest	Ampasambazimba	Bones, pollen, stratigraphic columns	8000	MacPhee <i>et al.</i> , 1985
Northwest	Dry forest	Anjohibe Cave	Speleothems	AD 370 - 1300	Voarintsoa <i>et al.</i> , 2017a
	Dry forest	Anjohibe Cave	Stalagmites	AD 200 - 2000	Burns <i>et al.</i> 2016
	Dry forest	Anjohibe Cave	Speleothems	1700	Scroxton <i>et al.</i> , 2017
	Dry forest	Lake Mitsinjo	Pollen and charcoal	3500	Matsumoto and Burney, 1994
	Dry forest	Lake Amparihibe	Charcoal, sporormiella	1300	Burney, 2003
Southwest	Spiny thickets	Andolonomby (Ambolisatra)	Pollen and charcoal	7000	Burney, 1993; Virah-Sawmy <i>et al.</i> 2016

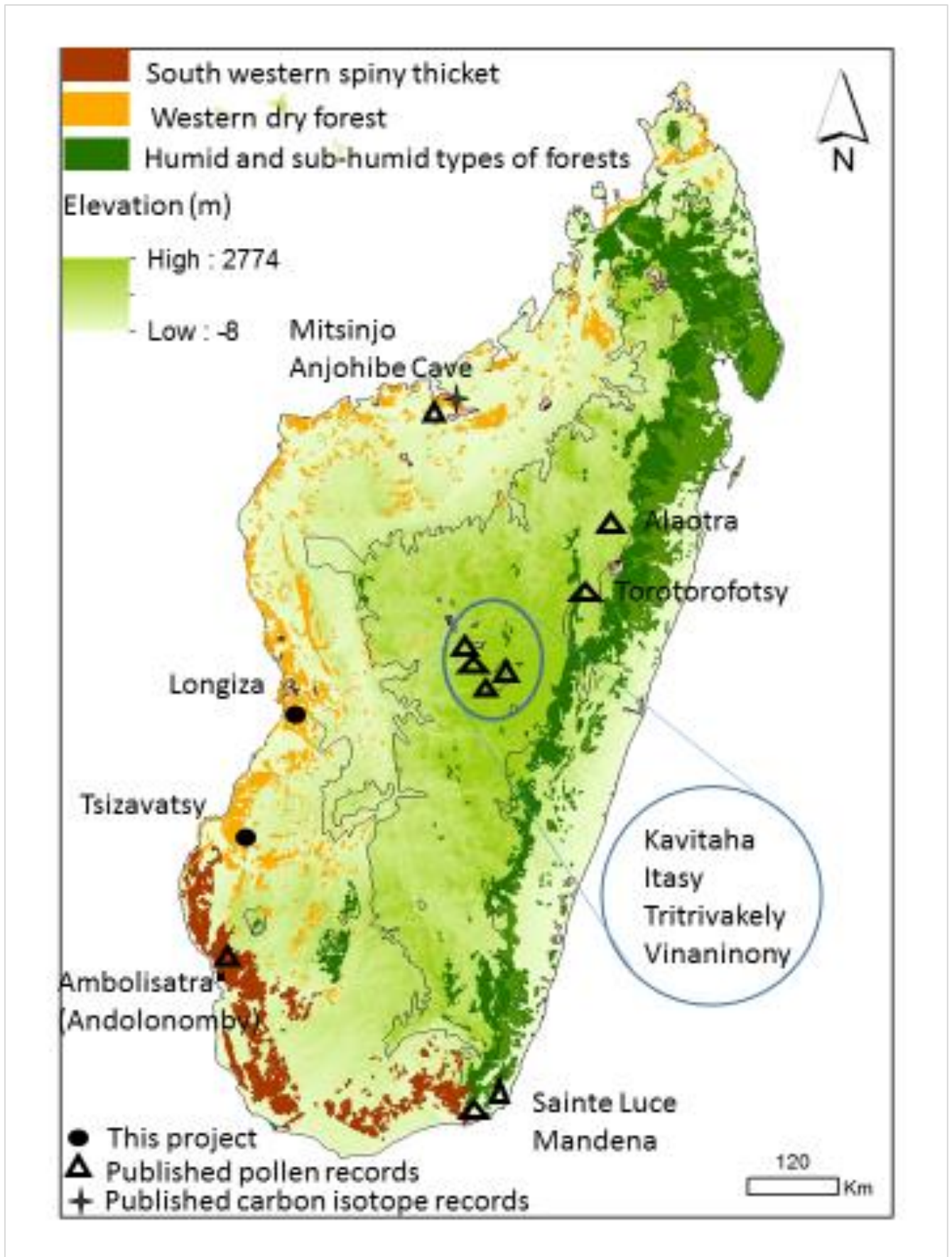


Figure 2.3: Palaeoecological sites investigated in Madagascar including the present research.

2.2.2. Vegetation dynamics of the eastern region ecosystem

The eastern region contains the largest remaining evergreen humid forest (0-1800 m ASL) (Figure 2.4), coastal forest (0-800 m ASL) and montane forest (more than 1800 m ASL) (Du Puy and Moat, 1996) in Madagascar. The published palaeoecological sites for this region are shown in Table 2.3, although other unpublished works (theses) have been conducted in Alaotra (Reyes, 1993), and Torotorofotsy (Rakotondrazafy, 1992). The only published research in the area by Straka (1996) showed that the dense forest has remained basically stable over the last 63,000 years with a variation in Ericaceae and Vaccinaceae pollen rates (Straka, 1996) (Figure 2.5). Investigations at the montane forest (Montane d'Ambre, Straka, 1996) showed that the forest composition has remained largely unchanged over the last 100,000 years (Straka, 1996). The stability of these ecosystems can be explained by the fact that these areas were among the last to be settled and changed by humans (Burney, 2003). However, additional research is needed to obtain high-resolution AMS radiocarbon dated sediments for this region as well as vegetation and climate records on a high-resolution temporal/spatial scale. This will assist in evaluating the drivers of change in these eastern dense forests.

It has been suggested that the littoral forest was patchily distributed over the past 6000 years with the succession of open thickets and open *Myrica-Uapaca* in place of the present vegetation which is *Myrica* bushland and *Erica* grassland (Virah-Sawmy *et al.*, 2010). The vegetation was naturally heterogeneous and underwent changes in its composition around 950 cal years BP (Virah-Sawmy *et al.*, 2009b). These changes were characterised as a response to environmental conditions such as drought and sea level rise (Virah-Sawmy *et al.*, 2009b).



Figure 2.4: Recent photograph of the eastern forest (Image: Andriantsilavo Razafimanantsoa)

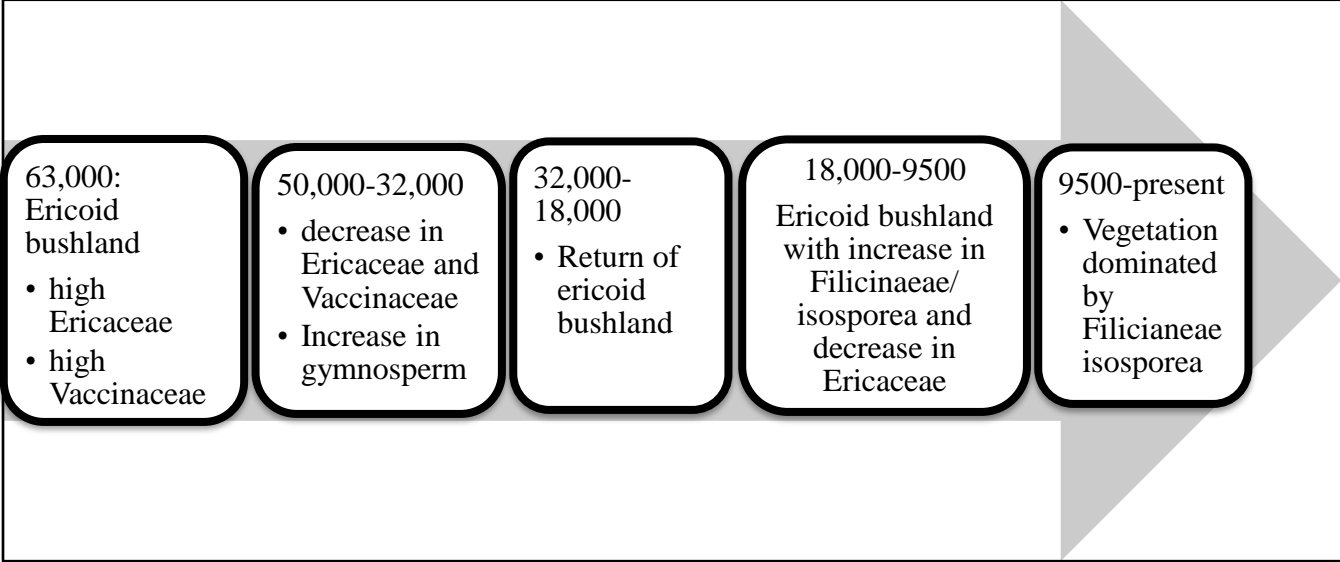


Figure 2.5: Summary of the vegetation change in the eastern dense forest in Andasibe during the last 63,000 years according to Straka (1996).

2.2.3. Vegetation dynamics in Madagascar's central highlands

The central highlands of Madagascar range between 1000 and 2700 m (Klein, 2002) and are currently covered by a forest-grassland mosaic with more than 70% of the area being occupied by grassland (Fisher and Robertson, 2002). The forest mosaic is classified as mid-elevation evergreen forest (800-1800 m) of *Tambourissa* (Cunoniaceae) and *Weinmannia* (Monimiaceae) (Humbert, 1955) with a dominance of Fabaceae, Euphorbiaceae and Myrtaceae (Faramalala, 1995). Recent analysis of the grassland showed that these ecosystems precede human settlement based on the rate of endemic species (Vorontsova and Rakotoarisoa, 2014; Vorontsova *et al.*, 2016) and their similarities with the African mainland grassland (Bond *et al.*, 2008). These results correlated with the palaeoecological record from the Pleistocene to the present from various sites around the region (Table 2.3), suggesting a dynamic vegetation with an abundance of grass. During the full glacial period (150,000-40,000 cal years BP), the vegetation was dominated by Ericoid bush with a few composites and grasses (Gasse and Van Campo, 1998; 2001; Burney *et al.*, 2004).

The early Holocene was characterised by a mixed vegetation of dry-mesic forest similar to the western forest and grassland (MacPhee *et al.*, 1985). In the mid-Holocene, the presence of mosaic vegetation was inferred from palaeoecological investigations across the region (MacPhee *et al.*, 1985; Gasse and Van Campo, 1998; Burney *et al.*, 2004). This was characterised by the decrease in ericoid pollen and the dominance of wooded grassland where taxa such as *Celtis*, *Trema*, Combretaceae, *Macaranga*-type, and *Uapaca* were recorded (Gasse and Van Campo, 1998; Burney *et al.*, 2004). Pollen reconstruction from the late Holocene at Lake Kavitaha showed an increase in the grass pollen and forbs and a decrease in pollen of woody taxa (Burney, 1987a). The last millennium is marked by a significant opening of the vegetation mostly dominated by grass in pollen spectra of the region. It could be largely attributed to an increase in man-made fire intensity and frequency (Burney, 1987a; 1987c; Gade, 1996).

2.2.4. Vegetation dynamics in the western region

The western region is 80% covered by a discontinuous band of dry forest (Guillaumet and Koechlin, 1971; Grubb, 2003). The northwest region is occupied by dry deciduous forest (hereafter dry forest) while the extreme southwest and south are occupied by spiny thicket forest. In the late Holocene, there was an expansion of xerophilous thickets and contraction of woodland vegetation or CAM plants in western and southwest regions (Clarke *et al.*, 2006).

The dry forest composed of *Commiphora*, *Dalbergia* and *Hildegardia* is distributed along the western region (Figure 1.2). The main palaeoecological sites from the dry forest are located in the northwest region within the dry bioclimatic zone at the site Mitsinjo for pollen analysis (Matsumoto and Burney, 1994). In addition, the archaeological and paleontological site in Anjohibe Cave allowed evaluation of the temporal changes in the vegetation through speleothem isotope analysis (Burns *et al.*, 2016; Voarintsoa *et al.*, 2017a; Scroxton *et al.*, 2017). Results from the palaeoecological studies suggest that the vegetation was dynamic over the last 3500 years with an increase in C₄ plants composed mainly of grass taxa which is indicative of an opening-up of the ecosystem to the present. From 3500-1200 cal years BP, the vegetation was classified as a mosaic of dry forest and grassland (Matsumoto and Burney, 1994). A gradual change in the vegetation from C₃ to C₄-dominated plants is recorded with a short recovery of C₃ plants between 1155 cal years BP (AD 795) and 1080 cal years BP (AD 870), in response to monsoonal rainfall linked to the relative position of the ITCZ. By 820 cal years BP (AD 1130), a transition into an open landscape attributed to the burning for slash and burn agriculture locally called *tavy* was recorded (Voarintsoa *et al.*, 2017a). It correlated with the pollen record where the sampled lake was surrounded by savanna (Matsumoto and Burney, 1994). Since 500 cal years BP (AD 1450), grassland with fire resistant trees and ruderal herbs have been recorded in the pollen spectra (Matsumoto and Burney, 1994). This vegetation is presently characterized by a dry-mesic woodland and forest composed by Combretaceae, Ericaceae, and Euphorbiaceae (Koechlin *et al.*, 1974).

It is worth noting that the dry forest in the southwest within the sub-arid bioclimatic zone (Figure 1.2) receives rainfall of about 600 mm inland and less than 400 mm near the coast. This has resulted in the presence of spiny thicket forest species from further south that are more adapted to drought. However, no palaeoecological research has been conducted in the area to evaluate the response of these ecosystems to rainfall change and the relative and most likely interacting drivers of the vegetation dynamics.

The spiny thicket forest in the sub-arid zone is characterized by the presence of the endemic family Didiereaceae and arborescent Euphorbiaceae (Humbert and Cours Darne, 1965). Recent reconstruction shows that the vegetation was dynamic during the last 7000 years (Table 2.4). From three cores collected in the spiny thicket forest in a small basin site called Andolonomby (previously named Ambolisatra), a tendency towards an adaptation to dry conditions was recorded (Burney, 1993; Virah-Sawmy *et al.*, 2016). These cores were initially analysed by Burney (1993) but re-evaluated by Virah-Sawmy *et al.* (2016) to increase the

temporal resolution from two to nine radiocarbon dates. These results suggested that the cores covered the last 7000 years with a hiatus from 5500 to 1800 cal years BP (Virah-Sawmy *et al.*, 2016).

During these last 7000 years, several taxa indicative of change in the ecosystem such as the presence of fire-resistant species (*Medemia nobilis*, *Hyphaene shatan*), and the appearance of endemic and characteristic species such as *Dalbergia*, *Euphorbia*, and Didiereaceae were recorded. Fire-adapted species increased in all the samples around 1000 cal years BP (Virah-Sawmy *et al.*, 2016) after which they disappear along with the other taxa characteristic of the vegetation. From 700 cal years BP to the present, the vegetation became species poor with the dominance of dry-adapted taxa such Didiereaceae. It appears that the vegetation change in the spiny thicket was a response to various factors including climate and human activities at different time-periods. Despite the difference in temporal resolution, these analyses show that there has been an increase in Didiereaceae or a hiatus recorded around 5500 to 1600 cal years BP which is associated with increasing aridity in the region (Burney, 1993; Virah-Sawmy *et al.*, 2016). In addition, changes of the vegetation in the last 2000 years might be associated with a combination of increasing aridity and extensive cattle grazing (Virah-Sawmy *et al.*, 2016).

Table 2.4: Vegetation dynamics and climate variability in the dry spiny forest obtained from reconstruction in Andolonombay in southwest Madagascar. Recent revision of the dates and analysis by Virah-Sawmy *et al.* (2016) but initially analysed by Burney (1993) (results shown at the second part of the table). None indicates that no information was available.

Date (cal years BP)	Grass	Arboreal pollen	Didiereaceae	Climate	Inferred vegetation	Reference
7000-6600	moderate 20-30%	Combretaceae, Arecaceae, Euphorbiaceae, <i>Antidesma</i> and <i>Uapaca cf. bojeri</i>	None	cooler in temperature	Grassland	Virah-Sawmy <i>et al.</i> , 2016
6600-5500	decline	increase of arboreal taxa	none	wetter	Humid woodland	Virah-Sawmy <i>et al.</i> , 2016
1800-1600	high	high	high Didiereaceae	supposed to be drier	spiny bushland with palm/ <i>Pandanus</i> savanna	Virah-Sawmy <i>et al.</i> , 2016
1600-700	none	decline and disappearance <i>Antidesma</i> , <i>Uapaca</i> and <i>Dalbergia</i>	decline Didiereaceae	drier climate	open vegetation	Virah-Sawmy <i>et al.</i> , 2016
700 - present time	None	None	increase	none	Vegetation with species-poor	Virah-Sawmy <i>et al.</i> , 2016
5500-1800	Low (10-28%)	decline especially <i>Medemia nobilis</i> and increase in other species	increase Didiereaceae	drier-warmer	Forest and woodland	Burney, 1993
3000-2000	none	increase <i>Medemia nobilis</i> , decline <i>Euphorbia</i> , Combretaceae, increase <i>Delonix</i> absent or traces / Appearance of ruderal plants (<i>Ricinus</i> , <i>Plantago</i>) and increase Urticaceae	increase Didiereaceae	increased dryness	Wooded grassland	Burney, 1993
2000	increase 60%		none	drier	Grassland	Burney, 1993

In summary, the vegetation in Madagascar was extremely dynamic over time with the presence of mosaic forest and an abundance of grass-dominated ecosystems especially in the central highlands. Changes in the vegetation across the island were associated with climate especially the variation in rainfall prior human arrival. However, the most important changes were recorded in the late Holocene, which coincided with human presence or activities across the island, while in the southwest, these changes were more linked to drying climate.

2.3. History of human presence and subsistence in Madagascar

Considered as one of the primary drivers of ecosystem change, the knowledge of early human presence and the evolution of their subsistence practices (economy) over time would provide critical information for the environmental discourse in Madagascar. Palaeoecological, palaeontological and archaeological approaches have indeed provided evidence about early human arrival and activities in Madagascar. Palaeoecology and palaeontology investigations inferred early human contact and presence on the island ranging from 10,500 to 1350 cal years. BP (Perez *et al.*, 2005; Gommery *et al.*, 2011; Hansford *et al.*, 2018; Anderson *et al.*, 2018). However, there are discrepancies between the dates, progression of humans across the island as well as the possibility of multiple arrivals which differs between regions. These discrepancies are related to the dating methods, the process of analysis and the explored proxy.

The date of human arrival in Madagascar is contentious and also varies with region. Recent analysis of cut marks from the extinct bird *Aepyornis* suggested the presence of humans in Madagascar in the southwest region as early as 10,500 cal years BP (Hansford *et al.*, 2018). Prior to that, cut marks on hippopotamus (*Hippopotamus lemerlei*) suggest human presence on the island at least 4000 years ago (2288-2035 cal years BC) in the northwest region (Gommery *et al.*, 2011; Dewar *et al.*, 2013) but this interpretation was questioned as the cuts did not present pattern of butchery (Ekblom *et al.*, 2016). In the southwest, human evidence is inferred later on around 2366-2315 cal years BP (402-204 BC) (Perez *et al.*, 2005) from cut marks on extinct lemurs *Paleopropithecus ingens*. The interpretation of cuts marks has also been highly criticized as they might have been the results of activities conducted by visitors and not settlers (Dewar, 2014). Palaeoecological investigations conducted in the central highlands have shown the presence of pollen from introduced plants *Humulus-Cannabis* around 2200 cal years BP in Triterivakely suggested as an indicator of human presence. In addition, a large increase in ruderal pollen types associated with disturbance were also

recorded at the same period (Burney, 1987a; 1987c; Matsumoto, and Burney, 1994). The eastern region is considered to be the last colonized by two waves of early human presence inferred through the increase of grass pollen in sediment cores at around 2050 cal years BP (100 BC) and 600-700 cal years BP (AD 1400-1500) (Straka, 1996). It is worth noting that few dates were conducted for these cores. The evidence from palaeoecology and palaeontology suggested independent human settlement of early human presence in the southwest at 10,500 cal years BP. Humans then expanded to the northwest (4288-4035 cal years BP) and further into the central highlands (2200 cal years BP), to finally occupy the eastern region (2050 cal years BP).

By contrast, archaeological evidence points to human presence 8000 years later than paleontological evidence, though there has been evidence from the north dated around 4000 years ago (Dewar *et al.*, 2013). This evidence was however criticized because it was based on dating of the substrate and not on the organic content of the artefacts (Hansford *et al.*, 2018). In addition, this difference could be related to the nomadic way of life of the earlier humans on the island which did not leave traces of activities (Dewar, 2014). The oldest direct human occupation has been suggested through the discovery of faunal materials with pottery in Lakaton'i Anja in the north of the island at about 1680 ± 65 cal years BP (AD 230-530) and 1300 ± 80 cal years BP (AD 620-900) (Dewar and Rakotovololona, 1992; Wright and Rakotoarisoa, 2003; Dewar *et al.*, 2013). Then, there was evidence of human presence from the southwest inferred from charcoal and pottery in Sarondrano around 1460 ± 90 cal years BP (AD 410-710) (Battistini and Verin, 1971). In the northeast in Nosy Mangabe evidence of coarse ceramic, chlorite schist and iron slag suggested the presence of humans from around 1250 ± 60 cal years BP (AD 660-990) (Dewar and Wright, 1993). Furthermore, there was evidence from the southeast which indicated that the earliest settlements date to be around 1150 cal years BP (AD 800) (Rakotoarisoa, 1997). Evidence for human occupation in the south was only dated around 920 ± 90 cal years BP (AD 1020-1210) (Burney *et al.*, 2004). The central highlands are suggested to be the last settled, which had evidence of human population around 750 cal years BP (AD 1200) (Wright and Rakotoarisoa, 2003). The evidence presented here provided a picture of the early presence of humans from separate settlements of Austronesian or east African origin. It first occurred in the north, then continued in the southwest as well as the northeast, to finally point to human occupation in the southeast, south and the central highlands (Blench, 2008; Beaujard, 2012).

Dewar (2014) suggested that the early people in Madagascar might have had distinctive practices for their livelihood, hence creating a diversity of regional human subsistence or economies depending on their origin. For example, archaeological artefacts in one of the oldest villages near Mananara and on Nosy Be in the north indicates that farmers could have practiced slash and burn agriculture and also exploited native plants and animals around 1300 cal years BP (AD 700) (Wright and Fanony, 1992). By the end of the first millennium AD or the beginning of the second millennium, further archaeological evidence suggested that Islamized traders, Bantu-speaking people from east African coast introduced livestock on the island (Dewar and Wright, 1993; Beaujard, 2012). In the eastern region, linguistic studies have shown multiple introductions of rice and other plants such as yam adapted to humid tropical ecosystems around the first millennium (Beaujard, 2012) where their subsistence strategies were probably based on agriculture. Archaeological artefacts from various early villages in the southeast point to the evolution of fishing and agriculture in the eastern region (Rakotoarisoa, 1997) at around 1150-750 cal years BP (AD 800-1200). Subsequently, around 750-450 cal years BP (AD 1200-1500), cattle herding became part of their subsistence. It was only around 450 cal years BP (AD 1500), according to archaeological evidence, that irrigated rice farming formed part of their subsistence. In the central highlands, there is evidence of cattle bones only from around 750 cal years BP (AD 1200), indicating the presence of herding or pastoralism in the area (Wright and Rakotoarisoa, 2003), even though, interestingly, the arrival of livestock dates to 1400 cal years BP (AD 530-750) in Kavitaha and 960 cal years BP (AD 900-1200) in Tritrivakely (Burney, 1987b). Nevertheless, there is consistent evidence in most of the region except the southwest of the cultivation of rice paddies and animal husbandry around 450 cal years BP (AD 1500-1800) (Wright and Rakotoarisoa, 2003).

The southwest region which is the focus of this research, is thought to have been occupied by Bantu hunter-gatherers on the basis of linguistics analysis (Blench, 2010; Beaujard, 2012) but recent analysis suggested the presence of agropastoralism in the region since AD 600 (Anderson *et al.*, 2018). This was demonstrated through the analysis of bone cuts and charcoal peaks in sediments dated to around 1000 cal years BP (AD 950) and at 500 cal years BP (AD 1450) which in both cases was linked to the expansion of pastoralism across the region (Virah-Sawmy *et al.*, 2016). Analysis from historical records showed that before 1950, the population from southwestern region were exclusively practicing intensive zebu farming subsistence (Fauroux, 2001; Scales, 2011). But later on, due to a range of factors, including national policies, political and socio-economic factors, human subsistence shifted from

exclusively pastoralism to include agriculture. This led to a rapid transformation of the landscape since 1900 (Fauroux, 2001). These changes were motivated by three successive booms of crops such as rice (1940 and 1980), butter beans (1915-1922), and maize (1934-1940 and 1992-1994) which were mainly practiced by migrants from the southeast, and extreme south. Interestingly, there is still a community of foragers in the region called “Mikea” which lives by hunting wild pigs, lemurs and birds and collecting wild tubers (Stiles, 1998).

Studies of human arrival and the development of human subsistence strategies in Madagascar have received a great interest due to the massive environmental change that the island has experienced in the last 2000 years. It is important to note the discrepancies among the disciplines which specifically concern the dates of early arrivals but also the development of the society and their impact on the environment where more evidence is still needed. Most of the evidence justifying human subsistence across Madagascar has been based on archaeological and linguistic evidence. Landscape transformation at different spatial and temporal scale could be related to the change in local and regional human subsistence strategies. These changes could be better understood through long-term analysis of both ecosystem changes and human subsistence which can be inferred from palaeoecological proxies. This is critical especially in the southwest region where human subsistence such as foraging and agropastoralism still co-exists. Few investigations conducted in the island, have considered these changes in human subsistence across regional scale.

2.4. Summary

This literature review summarises environmental changes and human subsistence practices in Madagascar from various disciplines. It shows that the environmental change on the island is fraught with conjecture and there is still an ongoing debate among scientists regarding the nature and timing of environmental change, as well as the drivers of change. Some important elements to draw attention to concern: i) the lack and insufficient climate records available and their resolution for the whole island and the possibility of regional differences due to strong climatic gradients across the island; ii) inconsistencies in the dates of early human arrival, their subsistence practices and their impacts; and iii) the uneven distribution of vegetation reconstructions and their resolutions within the various eco-regions of the island. The research presented here brings additional knowledge to the history of the island, by focusing in the southwest region on the tropical dry forest ecosystems during the late

Holocene. It aims at providing vegetation reconstruction as well a high resolution of rainfall variability for the southwest region from a separate proxy for rainfall. Last, this investigation will attempt to interpret the change in fire influx in terms of change or evolution of human land-use and subsistence and its interaction to climate.

3. CHAPTER THREE: STUDY AREA-CONTEMPORARY ENVIRONMENTS OF SOUTHWESTERN MADAGASCAR

3.1. Location and setting of the study area

This research was conducted in southwest Madagascar within the sub-arid bioclimatic zone. Along the north-south transect within the sub-arid zone, there are variations in geology, rainfall and human land-use, which have shaped the vegetation over time (Figure 3.1). This chapter describes the contemporary environments of the study area including geology, climate, and existing vegetation along the north-south transect in southwest Madagascar. It gives an overview of the human subsistence and land-use, focusing on traditional practices that involve the use of fire, which can be used to guide explanations of the charcoal influx in sediment samples, and its consequence on the vegetation. Finally, conservation strategies that have been adopted in the study area are described to better understand the relationship between climate variability, vegetation change, and conservation efficiency.

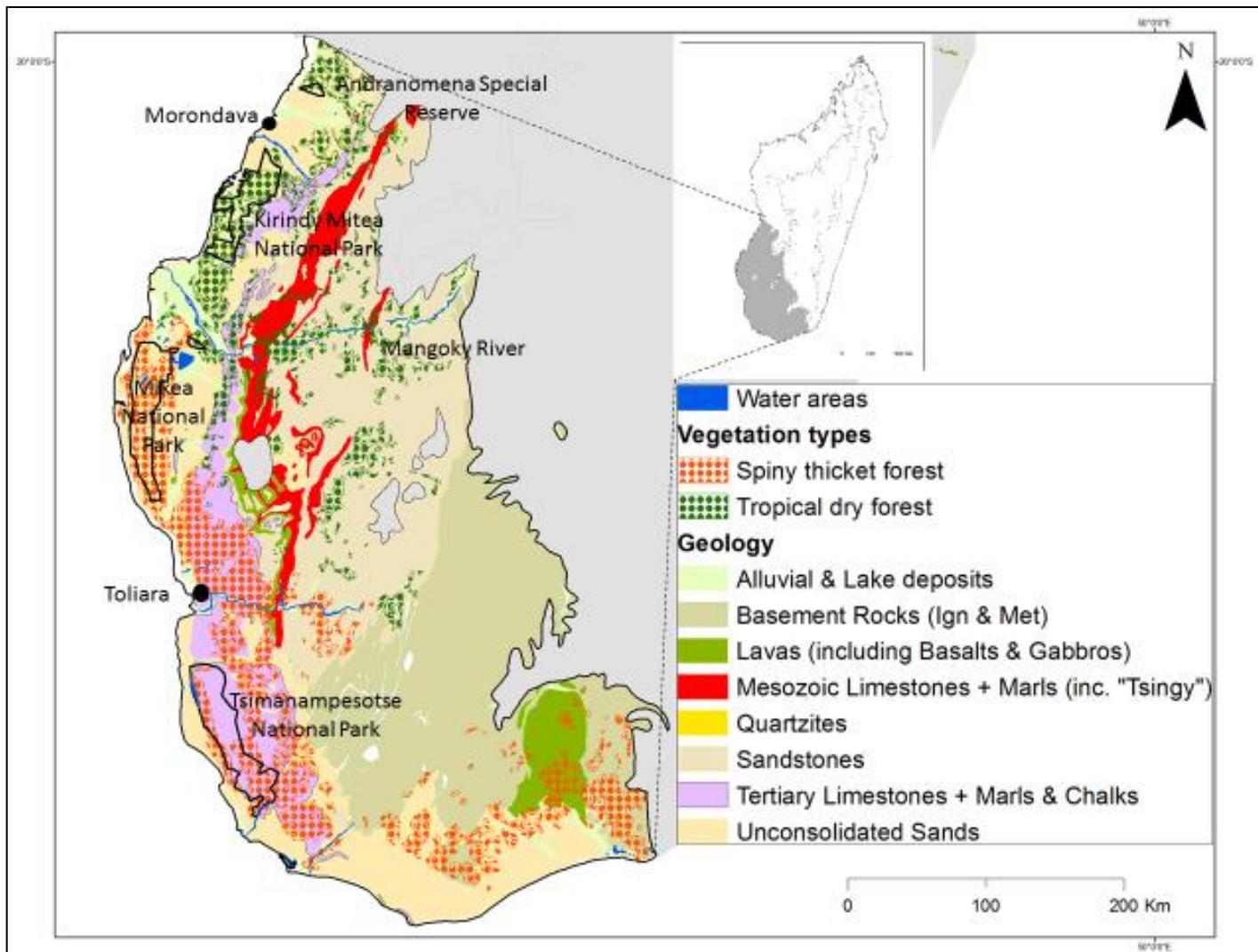


Figure 3.1: The sub-arid bioclimatic zone and its associated geology, main vegetation types and protected areas mentioned in the text, including the Mikea National Park occupied by the Mikea people, forager communities in the southwest region in Madagascar.

3.2. Geology

The geomorphology of southwest Madagascar was formed at the end of the Tertiary and during the Quaternary periods (Dixey *et al.*, 1959). It comprises an extensive formation of sandstone eroded from the Precambrian basement and a limestone plateau within the Morondava Basin (Du Puy and Moat, 1996; Grubb, 2003; Moat and Smith, 2007). The basin is composed of unconsolidated sandstone, limestone, and alluvium (Figure 3.1). The unconsolidated sandstone with deeper sand or sand clay soils of various consistencies occupies areas around plains (Sourdat, 1970). While white sands are distributed along the littoral, ferruginous soil or red sand are also encountered. These are the topsoils that constitute the substrate of the dry forest (Du Puy and Moat, 1996). There are also tertiary limestones of marls and chinks from marine facies which are less eroded and were formed during the Eocene approximately 54-38 mya (Du Puy and Moat, 1996). These tertiary limestones generally occur near the coast between 0 and 300 m above sea level (ASL) and are a substrate to the xerophytic bush or the spiny thicket forest. The limestone plateau often has depressions, which are filled with ferruginous soil and provide a substrate for both dry forest and spiny thicket forest (Du Puy and Moat, 1996). The southwest region also has a high frequency of alluvium with finer grain texture than the unconsolidated sand. These have high nutrient values and are associated with the water availability in riverine areas, providing substrate to tall riparian forests (Du Puy and Moat, 1996).

3.3. Climate

The southwest region is the driest in Madagascar because of trade winds and the topography (see Chapter 2.1: Palaeoclimate record in Madagascar) resulting in declines in both the quantity of rain and duration of the rainy season towards the west and south (Battistini, 1964; Donque, 1972; Cornet, 1974). The climate of the southwest is characterized by semi-arid conditions with a pronounced seasonality (Donque 1972). There is little to no rain between April to November and a rainy season from December to March (Koechlin *et al.*, 1974; Sorg and Rohner, 1996). There is a precipitation gradient across the sub-arid southwest, manifested by a decreasing rainfall from north to south. The mean annual precipitation is 800 mm per year in the north (Sorg and Rohner, 1996), and the south which receives less than 600 mm of rainfall per year, declining to 400 mm per year near the coast (Stiles, 1998). The dry season can extend for several years (Dewar and Wallis, 1999), but an increase in rainfall has been recorded in the last century (Ganzhorn, 1995). Temperatures remain relatively

similar across the region and vary between a mean of 23 °C to 26 °C annually with high humidity during the wet season (Du Puy and Moat, 1996; Elmqvist *et al.*, 2007).

3.4. Vegetation of southwest Madagascar

The southwest region of Madagascar is included in the sub-arid bioclimatic zone (Cornet, 1974), based on the species distribution and climate variation (Humbert, 1955; Humbert and Cours Darne, 1965; Cornet, 1974; White, 1983; Faramalala, 1995; see also Figure 3.1). It covers two main vegetation types, namely dry forest and xerophytic spiny thicket forest, with a mosaic of other vegetation types. Dry forest is the dominant vegetation type in the north while spiny thicket forest dominates in the south in addition to dry forest up to the Mangoky River (Figure 3.1). Both vegetation types have traits characteristic of drought resistance. This section describes the vegetation present in the southwest and its dominant taxa, which are named following the binomial nomenclature and verified using Tropicos Madagascar (2009). Species adaptation to drought in the vegetation of the southwest Madagascar is manifested in the presence of water storage in the stem such as *Adansonia* spp., roots, bulbs or tubers such as *Gyrocarpus* sp., as well as the presence of small leaves, which are more common in the dry deciduous forest (Koechlin *et al.*, 1974). Dominant species and the number of deciduous species differ within the dry forest and the spiny thicket forest (Table 3.1). The mosaic vegetation of wooded grassland is characterised by low diversity and endemism. Mangrove vegetation occurs near the estuaries (Phillipson, 1996), while riverine forest dominates water courses and rivers (Rabesandratana, 1984; Phillipson, 1996; WWF, 2001).

Table 3.1: Characteristics of the dry forest and the spiny thicket forest vegetation types in southwest Madagascar

Description	Dry forest	Spiny thicket forest	References
Distribution	to Cape D`Ambre in the north down to Mangoky River in the south	North of Mangoky River to Tolagnaro in the south	Moat and Smith, 2007
Elevation	0-800 m	0-300 m	Faramalala, 1995
Geology	White sand, red sand, and limestones	White sand, red sand, and limestones	Du Puy and Moat, 1996; Grubb, 2003
Rainfall	Mean annual precipitation: 800 mm per year	Mean annual precipitation: 300-600 mm per year	Ganzhorn, 1995; Sorg and Rhoner, 1996; Ratovomanana <i>et al.</i> , 2013
Dominant species	<i>Commiphora</i> spp., <i>Cedrelopsis grevei</i> , <i>Colvillea racemosa</i> , <i>Dalbergia</i> spp., <i>Adansonia rubrosipa</i> , <i>Adansonia grandidieri</i> and <i>Adansonia za</i>	<i>Jatropha mahafaliensis</i> , <i>Euphorbia antso</i> , <i>Alantsilodendron</i> , <i>Grewia grewei</i> , <i>Cedrelopsis grewei</i> , <i>Operculicarya decaryi</i> , <i>Pachypodium meridionalis</i> , <i>Gyrocarpus americanus</i> , <i>Bauhinia grandidieri</i> , <i>Chadsia grevei</i> , <i>Bauhinia madagascariensis</i> , <i>Terminalia seyrigii</i> , <i>Senna leandri</i> , <i>Uncarina</i> spp. and <i>Boscia</i> spp.	Rabesandratana, 1984; Ratovomanana <i>et al.</i> , 2013; Waeber <i>et al.</i> , 2015
Adaptation to drought	Bottle-shaped trees, small leaves	Bottle-shaped trees, small leaves, succulent trunks	Koehler <i>et al.</i> , 1974; Grubb, 2003
Maximum canopy height	Up to 20 m	2 - 6 m tall occasionally 10 m	Humbert and Cours Darne, 1965; Grubb, 2003; Raheison and Grouzis, 2005, Moat and Smith, 2007
Conservation status		30% under formal protection	Moat and Smith, 2007
Others	A small set of trees highly adapted to fire	High incidence of evergreen species	Grubb, 2003

3.4.1. Dry deciduous forest

The dry deciduous forest or dry forest (Koechlin *et al.*, 1974; Faramalala, 1995; Figure 3.2) where the appellation depends on the authors as western dry forest (White, 1983) or seasonally dry deciduous forest (Du Puy and Moat, 1996; Moat and Smith, 2007) or dry evergreen forest (Grubb, 2003) covers 31,800 km². It has reduced in size by almost 40% since 1970 due to deforestation (Moat and Smith, 2007; Whitehurst *et al.*, 2009; Waeber *et al.*, 2015). It is included with the tropical dry forests (Miles *et al.*, 2006) and is encountered from Cape D`Ambre in the north to the Mangoky River in the south from sea level to about 900 m ASL across the region. The dry forest has survived in isolated patches due to its higher resilience to disturbance and is considered to be the local climax vegetation of the region (Bloesch, 1999). It is floristically rich with more than 200 spp. (Abraham *et al.*, 1996) and associated with an abundance of *Dalbergia*, *Commiphora* and *Hildegardia* and other common genera and species as indicated in Table 3.1 (Humbert and Cours Darne, 1965; Baum *et al.*, 1998). There are patches of grassland savanna with the forest with a small set of tree species highly adapted to fire such as *Arecaceae* (cf. *Medemia nobilis*) (Grubb, 2003) and patchy sclerophyllous forest which contains *Arcolan oblongifolia*, *Asteropeia labatii* and *Leptolaena* spp. (Moat and Smith, 2007). The forest has three distinct layers with the canopy reaching up to 20 m, sub-canopy of 3 to 8 m and the forest floor including herbaceous plants and grasses, which are less than 3 m in height (Raherison and Grouzis, 2005).



Figure 3.2: Dry deciduous forest at Andranomena Special Reserve (Image: Estelle Razanatsoa)

3.4.2. Spiny thicket forest

The appellation of the spiny thicket forest often changes depending on authors (Gautier and Goodman, 2003), such as Bush a *Didierea* (Perrier de la Bathie, 1921), Serie a Didiereaceae et Euphorbia (Humbert, 1955), Fourre xerophile a Didiereaceae et Euphorbiaceae (Cornet and Guillaumet, 1976), dry forest with *Didierea* and *Euphorbia* (Faramalala, 1995), deciduous, dry southern forest and shrubland (0-800 m) (Du Puy and Moat, 1996), southwestern dry spiny forest thickets (White, 1983) and spiny succulent thicket and spiny forest (WWF, 2001). It covers 15,491 km² but had been reduced by 30% since 1970 (Moat and Smith, 2007). The spiny thicket is found from north of Mangoky River to Tolagnaro in the south (Figure 3.3; Table 3.1). It is considered one of the most important ecosystems for biodiversity conservation as it contains 52% of the local endemism with a total of over 1000 species (Phillipson, 1996). It is dominated by endemic xerophytic plants that are adapted to high water stress, especially members of the Didiereaceae family, from the genera *Alluaudia*, *Alluaudiopsis*, *Didierea*, *Decarya*, and some Euphorbiaceae from the genus *Euphorbia* (Rabesandratana, 1984; see also Table 3.1). The vegetation is also characterized by the presence of bottle-shaped trees such as *Delonix* and *Adansonia*; succulent taxa that are not only present on rocky terrain but also on plains (Grubb, 2003). The spiny thicket forest is purported to have a higher incidence of evergreen species than the dry deciduous forest (Grubb, 2003).



Figure 3.3: Recent photograph of the spiny thicket forest (Image: Estelle Razanatsoa)

3.5. Human land-use and subsistence in southwest Madagascar

The southwest region (the focus of this research) is currently occupied by foragers (Mikea people) and agropastoralist ethnicities. Though other ethnicities such as Vezo (fishermen) and Bara (located more inland) are also present in the region, this study focuses on the terrestrial and the distribution of the tropical dry forest ecosystems. Only subsistences that have direct or indirect relationship with this vegetation are described below.

3.5.1. Foraging subsistence by the Mikea community

Foraging was suggested to be the first human subsistence in Madagascar (See literature review section). One community in the southwest called Mikea are still foragers and are practicing resource partitioning in symbiosis with farmers (Stiles, 1998). Initially, they were thought to have practiced an immediate return system where their food is consumed just after it is acquired (Stiles, 1991), however later research found that from July to November, they collect and dry food resources for the coming season (Stiles, 1998). In addition, they cultivate maize and cassava through slash and burn methods called “*hatsake*” during the transitional seasons (Figure 3.4). Stiles (1998: 132) stated that, “these hunter-gatherers have a well-developed system in living in the forest with a structured annual cycle”. However, their main food is based on wild tubers belonging to the genera *Dioscorea*, *Colocasia*, *Ipomoea*, and *Tacca*. As a source of protein, they hunt feral cats, various birds, tenrec, lemurs, and tortoises (Stiles, 1991; Tucker and Taylor, 2007). Currently, some of the Mikea (people living in the forest) have mixed with other ethnicities, such as the Masikoro (agropastoralists). These links have been made through marriage or other forms of exchange which gives them the opportunity to trade goods such as honey and tubers with their neighbours in exchange for fish, tobacco, rum and iron objects such as axes and knives. Nevertheless, Stiles (1998) also noted the presence of groups that are exclusive hunter-gatherers all year round.

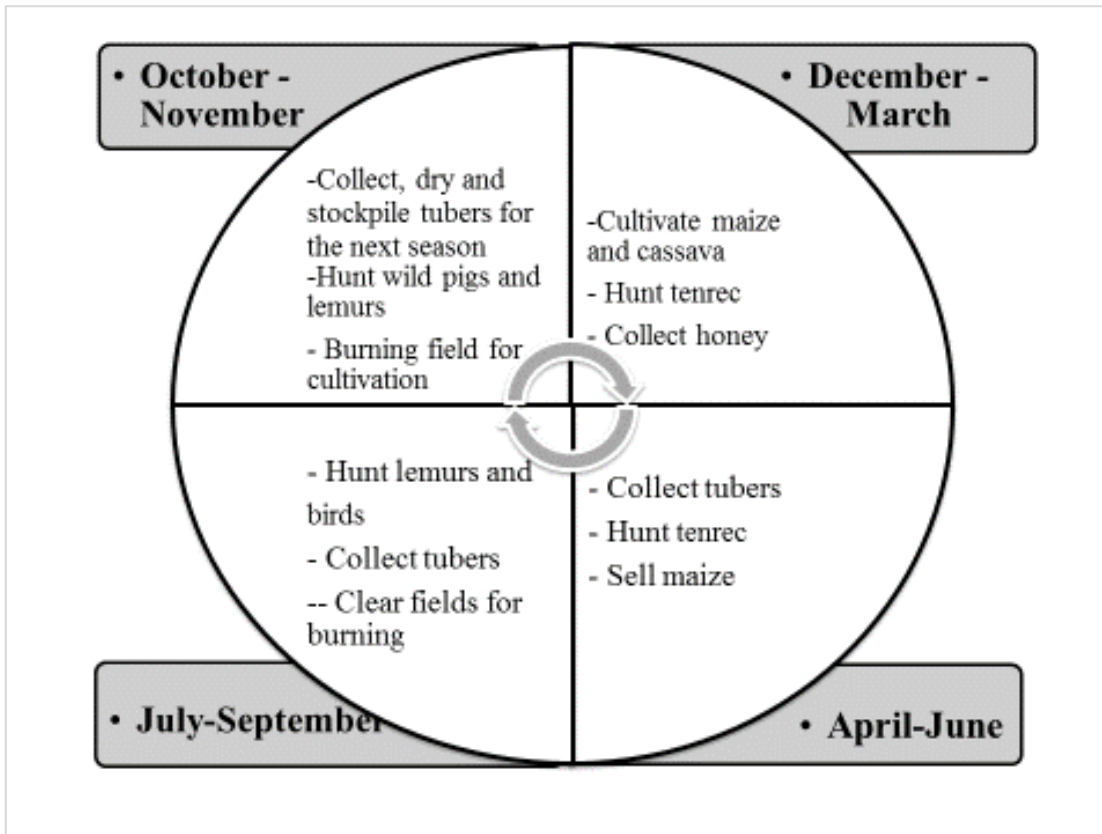


Figure 3.4: Annual cycle of subsistence strategies by the Mikea, a forager community in southwest Madagascar within the southern site of the present study. Adapted from Stiles (1998).

3.5.2.Pastoralism

Pastoralism has an important economic and cultural value to all the ethnicities in southwest Madagascar (Fauroux, 1989; Razanaka *et al.*, 2001). Cows have critical significance in rituals such as marriages and serves as safety to overcome famine (Razanaka *et al.*, 2001; Waeber *et al.*, 2015; Hänke and Barkmann, 2017). The accumulation of cattle is associated with higher social status. Much research has disregarded the importance of pastoralism to the economy in the region (Hänke and Barkmann, 2017). The rural economies, specifically the poor households are mostly sustained through livestock herding (Kaufmann and Tsirahamba, 2006), based on cattle and goat pastoralism which often serves a hedging function especially during lean periods (Dewar and Richard, 2012; Hänke and Barkmann, 2017). Zebu pastoralism is traditionally conducted on open abundant grasslands during the rainy season (Blanc-Pamard, 2009) and zebu transhumance is practiced with long distance migration during water and food scarcity (Feldt, 2015; Hänke and Barkmann, 2017). This is performed because herders often consider the forests as sacred and would only use it as a mode of extraction of important materials (for medicinal or construction purposes). During the last

century, the number of zebus has surpassed the number of inhabitants of the region (Kauffmann and Tsirihamba, 2006). With the increasing number of livestock, the reduction of land available for pasture and insecurities with zebu thieves in the region, increase in forest clearing for new pasturelands has been recorded even though such practice is uncommon in the southwest (Casse *et al.*, 2004; Waeber *et al.*, 2015).

3.5.3. Agriculture

Extensive agriculture has only been part of southwestern subsistence economy in the last century (Fauroux, 2001; Waeber *et al.*, 2015). Prior to that, foraging and pastoralism dominated the region with lowland agriculture. Local communities only grew rice in lowland and near watercourses, rivers and near the gallery forests where the soil is suitable, and water is abundant (Sourdat, 1970). No evidence has been found suggesting when such activities started to be practiced. Recently people have shifted into extensively irrigated cultivation to grow both domestic and cash crops. This is associated with the increasing aridity and drying of several lakes in the region and the increase of international trade. Like the forager communities (Mikea), these crops are often cultivated on cleared land through a process called “*hatsake*”. “*Hatsake*” consists of clearing forest to acquire new space for agricultural purposes or pasture, and in some cases, serves as a form of land acquirement. It functions by cutting down trees and burning the biomass (Waeber *et al.*, 2015) to transform the ash into nutrients for the soil for crop cultivation (Scales, 2012). Once cleared, rain fed crops such as maize are planted for the first three years and when the production drops to 80%, other crops such as butter beans and groundnuts are cultivated on the land (Scales, 2012). After this the soil is abandoned in the form of what is locally called “*monka*”. *Hatsake* is mostly practiced by the Antandroy and Mahafaly from the south of Madagascar (Bloesch, 1999) and is often blamed for forest destruction (Fauroux, 2001). With the increase in population (Sussman *et al.*, 1994), the exploration of more arable land for agriculture has resulted in greater pressure on the forest. In parallel, the conflict of land regulations in Madagascar led the “*Zanantany*” or land owners in the northern area of the southwest region to increase the practice of *hatsake* for land ownership purposes even though it was regulated by local taboos for several generations (Bloesch, 1999).

Vegetation change through the practice of hatsake

The *hatsake*, which is a human-induced forest burning, is known to significantly impact on forest regeneration and recovery (Sourdat, 1970; Zinner *et al.*, 2014). Research has investigated the impact of fire activities on the dry and spiny thicket forest and the associated wooded grassland present in the southwest region (Bloech, 1999; Razanaka *et al.*, 2001; Raharimalala *et al.*, 2010). *Hatsake* conducted on primary dry forest may lead to the growth of secondary vegetation with low species diversity and homogenous flora (Bloech, 1999) and repeated fire events (3-4 times) in 15 years would transform the dry forest into savanna (Bloech, 1999; Razanaka *et al.*, 2001). In such situations, the dry forest on red sand is transformed into grassland savanna dominated by *Aristida barbicollis* while the forest on white sand becomes shrubland savanna without *Aristida* species. The grassland savanna of *Hypparhenia* ecosystem with regular burning and overgrazing would be converted into savanna of *Heteropogon contortus*, and subsequently into savanna of *Aristida barbicollis*. If the *monka* that are the results of *hatsake* are protected from repeated fire and abandoned, recovery of forest is possible. Research has shown that dry forest are more resilient to disturbance, such as fire, than other ecosystems because of the preponderance of fire-adapted species (Bloech, 1999; see also Table 3.1). However, tree regeneration is low in the red soil and their use by farmers is irregular (Raharimalala *et al.*, 2010; Zinner *et al.*, 2014). In general, an increase in the species diversity and composition would occur after 21-30 years of recovery with abundance in pioneer woody species such as *Albizia bernieri*, *Diospyros perrieri*, and *Ziziphus mauritiana* (Raharimalala *et al.*, 2010).

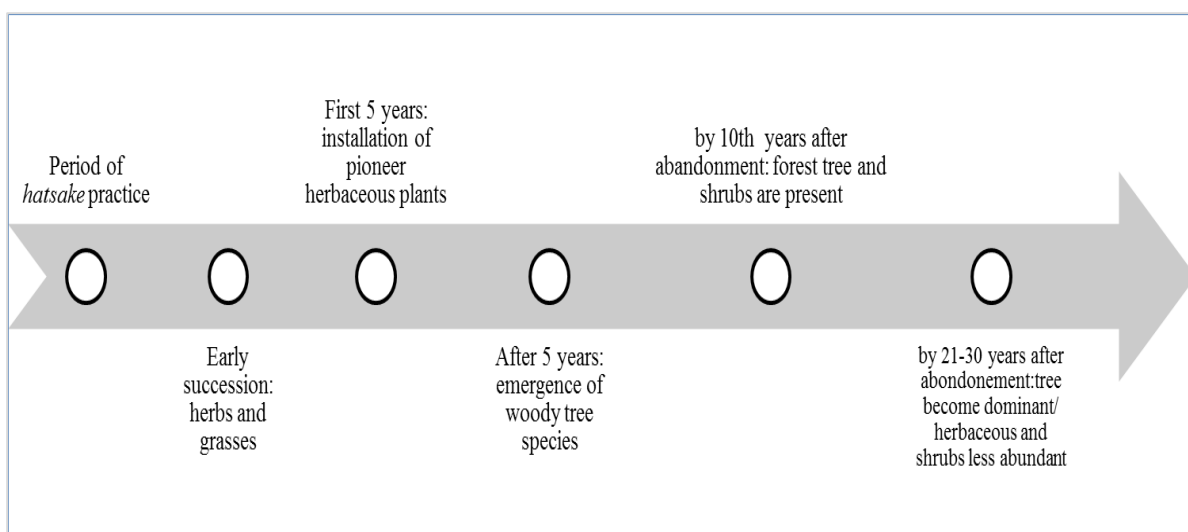


Figure 3.5: Regeneration process of dry deciduous forest after *hatsake* (slash and burn) activities in southwest Madagascar (adapted from Raharimalala *et al.*, 2010).

3.5.4. Activities with little to no use of fire

Forest degradation by people in southwest Madagascar is not limited to burning (Bloech *et al.*, 1999). Such degradation ranges from selective logging at the household scale to massive destruction for mineral and oil exploitation at an industrial scale (Waeber *et al.*, 2015). Selective logging for construction and woody charcoal production are practiced to increase income especially during dry periods and are considered as a safety net for the population (Gardner *et al.*, 2016). This activity alters the vegetation structure and composition over time by reducing the tree component of the forest due to active selection of species such as *Dalbergia* spp. and *Acacia* spp. depending on the availability of such taxa (Razanatsoa, 2012; Randriamalala *et al.*, 2016). In addition, exploitation of aquatic plants for trade such as *vondro* (*Typha angustifolia*) and *bararata* (*Phragmites mauritianum*) has also been recorded in the southwest region (Gardner and Davies, 2014). At an industrial scale, mining and agribusiness are also developing in the region which directly affects large scale changes in the vegetation. Mining activities are prominent in southwest Madagascar due to mineral abundance. Several minerals have been recorded in the region such as ilmenite (Blanc-Pamard, 2009), which is exploited by the Toliara Sands Project. Agribusinesses in the region are also contributing to forest clearance to establish new areas of plantations to produce agrofuel such as the cultivation of *Jatropha mahafaliensis* (Waeber *et al.*, 2015). These projects are often in conflict with conservation projects (Waeber *et al.*, 2015) and the long-term extent of their impact is poorly documented.

3.6. Conservation action

The dry forest and the spiny thicket forest in southwest Madagascar were the least represented in the protected areas system in Madagascar despite the high endemism and their importance to the local population (Tengö *et al.*, 2007). Only 3.2% of the spiny forests were under protection prior to the Durban Vision (WWF, 2001). In November 2003, at the Vth International Union for Conservation of Nature (IUCN) World Parks Congress in Durban, the president of the republic, Ravalomanana Marc, proclaimed an initiative to triple the surface of protected areas in Madagascar from 1.7 million ha to 6 million ha by 2012 (Raik, 2007; Gardner *et al.*, 2018). This brings the country in line with the IUCN standard of having 10% of the total land area under protection (Raik, 2007; Gardner *et al.*, 2018). Several protected areas focusing on multiple use models, a livelihood-based approach and shared governance with local communities and NGO's were implemented (Gardner *et al.*, 2018).

Within the sub-arid zone in and around the tropical dry forest areas where this study was conducted, several protected areas with different degrees of protection status and conservation history exist. Some examples include the forest in Andranomena which started management of wood exploitation in 1958 and is currently in the protected area system as the Andranomena Special Reserve managed by Madagascar National Parks (Grubb, 2003; Raselimanana, 2008). There is also the Kirindy Mitea National Park (625,000 ha) and the Mikea National Park (184,630 ha), approved as a national park in 2008. As part of the new protected areas generations, it is co-managed with local communities (Blanc-Pamard, 2009). The area within the Mikea National Park is occupied by the forager community, the Mikea (Stiles, 1998; see also Figure 3.1). Lakes investigated in this research were not part of any formal protection, however conservation through traditional management has also been recorded in the area and has proved effective in the region.

Communal management in the area

The success of traditional management in the form of taboos has been reportedly beneficial for conservation in Madagascar (Jones *et al.*, 2008). Taboos are social fencing that limits access to, and therefore exploitation of, an entire habitat (Tengö *et al.*, 2007; Jones *et al.*, 2017; Elmqvist *et al.*, 2007) down to a species level (Jones *et al.*, 2008). The disrespect of the taboos could result in direct payment to the community or divinity sanctions that are believed to affect personal success and prosperity in life. These taboos come with a gradient from open access to almost complete entry prohibitions (Tengö *et al.*, 2007). For instance, several forest, savanna, and lacustrine sites are recorded as sacred in Tsimanampesotsa National Park in the south within the spiny thicket forest (Fritz-vietta *et al.*, 2017). Tree species, such as *Tamarindus* spp. or *Adansonia* spp. (baobabs) are often considered as a sacred meeting place with ancestors (Stiles, 1998). Some endangered animals (as per the IUCN Red List of Threatened Species) are also protected by taboos, such as lemurs (Loudon *et al.*, 2006) and tortoises (Lingard *et al.*, 2003), as well as terrestrial (Tengö *et al.*, 2007) and marine habitats (Langley, 2006) in southwest Madagascar. Due to migration, there is a weakening of these taboos as new migrants often fail to integrate them in their practice (Scales, 2012). These taboos and social beliefs have been suggested by several studies to be legitimate and incorporated in conservation strategies (Tengö *et al.*, 2007; Jones *et al.*, 2008).

4. CHAPTER FOUR: METHODOLOGY

This research investigated vegetation change, fire history, and rainfall variability over time in southwest Madagascar. Field work was conducted in the southwest region with permission from the Ministry of Water and Forests (Ministere des eaux et forets; MEF) and Madagascar National Parks (permit number 211/15/MEEMF/SG/DGF/DAPT/SCBT) (Appendix 3, Figure 3.1). This research uses dendroclimatological and palaeoecological approaches and they are described in detail in this chapter as follows:

- Dendroclimatological approach was conducted to reconstruct the past rainfall of the area by analysing the carbon isotope ratios ($\delta^{13}\text{C}$) of baobab rings from four (4) specimens across the southwest region.
- A palaeoecological approach was used to evaluate the dynamics of dry forest and fire regime in the region during the late Holocene. Proxies such as pollen and stable carbon isotope ratios were used for vegetation analysis while microcharcoal and macrocharcoal influx of the sediments were evaluated for fire activities.

4.1. Rainfall reconstruction through dendroclimatological approach

4.1.1. Isotope fractionation in plants

4.1.1.1. Carbon isotope and plant

Carbon isotopes, specifically ^{13}C , in plants records the environmental condition of its surroundings from the selective fractionation of isotopes through their photosynthetic pathways. The fractionation is regulated by stomatal conductance and the rate of photosynthesis. A decrease in water availability will reduce the stomatal conductance and consequently water loss but also CO_2 uptake, leading to ^{13}C -enrichment of the internal CO_2 and increased $\delta^{13}\text{C}$ values in leaf tissue (Ehleringer, 1989). Soil moisture (rainfall) and relative humidity are the main factors determining water availability in drier areas, whereas temperature and summer irradiation are important in wetter areas (McCarroll and Loader, 2004). During photosynthesis, carbon isotope fractionation varies depending on photosynthetic pathway. Massive discrimination of ^{13}C against ^{12}C during the process yields differences in the $\delta^{13}\text{C}$ of various plants whether they are C_3 or C_4 or CAM plants (Ehleringer and Vogel, 1993). C_3 plants (trees, shrubs, herbs, forbs, cool season grasses and sedge) with Calvin Benson cycle have a $\delta^{13}\text{C}$ value between 24‰ - to -34‰ while the $\delta^{13}\text{C}$ value of C_4

plants (aquatic, desert, salt marshes and tropical grasses) with Hatch slack cycle is -6‰ to -19‰ (Ehleringer and Rundel, 1988), relative to Vienna Pee Dee Belemnite or VPDB (McCarroll and Loader, 2004). CAM plants which include both C₃ and C₄ pathways have intermediate value of δ¹³C and they mostly include succulent species (Ehleringer and Rundel, 1998). This study is focusing on the fractionation steps occurring in C₃ plants as it investigates the isotopic composition of tree rings in Baobabs. As the study takes place in a dry area (rainfall less than 1000 mm per year) the results are interpreted mainly in terms of changing rainfall, rather than temperature, as explained above.

4.1.1.2. Isotope fractionation in C₃ plants

Fractionation is the change of the ratio of δ¹³C from the air unto the plants and is determined by the response of the tree to its environment (McCarroll and Loader, 2004). In C₃ plants, there are two phases of fractionation which occur during diffusion and carboxylation. For both of these stages, there is preferential uptake of the lighter (¹²C) isotope compared with the heavier isotope (¹³C). This leads to depletion of δ¹³C during the uptake of CO₂ into the plant, during CO₂ absorption process and stomatal conductance (O'Leary, 1988). The preferential intake of ¹²CO₂ than ¹³CO₂ is due to differences in their atomic mass, where the lighter isotope enters the stomata more easily than the heavier isotope (McCarroll and Loader, 2004). In addition, during water stress, the stomata tend to close to prevent water loss and consequently reduce entrance of CO₂ from the atmosphere. This will force the plants to use the intercellular carbon available, leading to an increase of the δ¹³C. Increases in δ¹³C are thus associated with drier conditions. This fractionation related to diffusion is about -4.4‰. The second phase of fractionation is the discrimination during the photosynthesis process by the ribulose di-Phosphate-carboxylase. This enzyme has preference for ¹²C over ¹³C and this fractionation is about -27‰ (McCarroll and Loader, 2004).

These fractionations can be expressed the by the following formula according to Farquhar *et al.* 1982:

Equation (1):

$$\Delta\text{‰} = a + (b-a) ci/ca$$

Where *a*, and *b* are constant values related to diffusion and carboxylation fractionation, respectively -4.4‰ and -27‰.

The isotopic composition of C₃ plants depends on ci/ca where ci is the internal concentration of CO₂ and ca the concentration of atmospheric CO₂. So, if ci is higher compared to ca , as occurs in wet conditions, then stomatal conductance will be much higher than photosynthetic rate and will result in strong carboxylation discrimination. This will result depletion of ¹³C and a low value of $\delta^{13}\text{C}$ carbon isotopic composition. But in contrast, if the rate of stomatal conductance is low, as occurs in dry conditions, then the concentration of internal CO₂ will be low and consequently less discrimination against ¹³C will occur during carboxylation, leading to with higher values of $\delta^{13}\text{C}$ (McCarroll and Loader, 2004). As such, the limiting environmental factors of the tree should control the ratio of carbon isotope ratios in the rings with the regulation of stomatal conductance and photosynthetic rate. In dry areas such as that of the current study, the amount of rainfall (rather than temperature) will be the main determinant of $\delta^{13}\text{C}$.

4.1.1.3. Carbon isotope as a rainfall proxy

The application of carbon isotope as a climate proxy is based on the variation of the two steps of fractionation during photosynthesis, which is regulated by environmental factors. These steps of fractionation depend on the ratio ci/ca (internal CO₂ and the atmospheric CO₂ concentration) and affect directly the isotope composition of the tree, with variation along the tree ring sequence in response to changing water availability. Many factors could control the stomatal conductance and the enzyme of carboxylation depending on the environment (Farquhar *et al.*, 1989; Tieszen, 1991). As the present study focus in a semi-arid/ arid ecosystem, water stress affects the stomatal conductance, reduces the ratio ci/ca and consequently increases the $\delta^{13}\text{C}$ values of plants (more positive). In fact, in a region of low rainfall, where the trees are growing far from a water source (e.g. underground aquifer or permanent water body), the only water available for the trees is the soil moisture derived from rainfall (Farquhar, 1982). The isotopic composition of a specific ring could then indicate the rainfall condition for the period when the ring was formed. Recent studies have shown that the isotopic composition of baobab ring and amount of rainfall are negatively correlated (Woodborne *et al.*, 2015; 2016). As such, low $\delta^{13}\text{C}$ values suggest a higher rainfall, and high $\delta^{13}\text{C}$ indicate low precipitation. Tree records from southern African baobabs which were replicates of the method applied in this study show decadal, multi-decadal and centennial variability of rainfall over the last 1000 years and demonstrate the physiological response of baobab trees to water stress (Woodborne *et al.* 2015; 2016).

4.1.2. Tree sampling

Tree sampling was conducted along the southwest region of Madagascar which covers the gradient of rainfall from 800mm in the north to less than 300 mm per annum in the south along the coast. A Hagl6f CO600 increment borer was used to obtain a uniform core from the bark towards the centre of the tree. Despite the slight compression of the core from the increment borer, collected cores were suitable for analysis because this study is interested in the isotope composition of the rings but not the key features of ring formation, such as ring width. Trees were selected based on their large size (>7 m in circumference) and their location (>1 km) far from any possible surface water source, such as marshes and lakes that would obscure the rainfall signal due to the buffering effects of local hydrology. After coring, trees were sealed with a tree sealer to prevent damage by insects or fungi. A collection of 15 trees were sampled in total along the rainfall gradient described above (Appendix 4.1). Four individual trees belonging to two endemic species of baobab (*Adansonia grandidieri* and *Adansonia za*) were chosen for isotopic analysis. Both species (*A. grandidieri* and *A.za*) used in this study are endemic to Madagascar and occur in dry deciduous forest especially close to seasonal rivers, lakes, and waterholes (Baum, 1995; Baum *et al.*, 1998; Razanamaro *et al.*, 2015). They can also be found in savanna and scrubland (degraded or not) and agricultural land for *A.grandidieri* while in the spiny forest for *A.za* (Baum, 1995). These species are suggested to survive in dry environments using their deep root to accumulate water during rains and then surviving leafless through dry periods using the water stored in their trunks (Chapotin *et al.*, 2005). All species of baobabs including the mainland African species are succulents with C₃-like photosynthetic pathways (Szarek and Troughton, 1976; Baum *et al.*, 1998; Chapotin *et al.*, 2006). The choice of the four cores were based on their distribution along the southwest region which covers the north-south gradient of rainfall (Figure 4.1), and the length of the core (Table 4.1). These cores should reflect similar environmental conditions in the sub-arid region of Madagascar, with the effect of local conditions super-imposed. Based on the assumption that the isotopic composition of baobab rings represents local soil moisture (rainfall) in dry areas when trees are located far from water sources (McCarroll and Loader, 2004), time series samples from the along the cores of the four trees show depleted in ¹³C isotopes indicative of wetter conditions in the southwest Madagascar while enriched isotope values indicate drier periods (Woodborne *et al.*, 2016).

The four trees that were analysed were distributed along the southwest and represented two local sites. The northern site (in the north of the sub-arid region up to River Mangoky)

includes baobabs named DFL and DFS and the southern site (from the Mangoky River to the south) with baobabs named GTR and TSP (Table 4.1; Figure 4.1). These sites are subject to the north-south rainfall gradient in Madagascar (Donque, 1972; Jury, 2016). The northern site has higher mean annual precipitation of about 743 mm compared with 310 mm in the southern site based on instrumental records from 1960-2008 (Meteorological Station in Madagascar), at stations Morondava and Toliara respectively (Figure 4.1).

Table 4.1: Core information from two species of endemic baobab (*Adansonia grandidieri* and *Adansonia za*) sampled along a north-south transect in southwestern Madagascar.

Site	Name	Baobab species	Coordinates	Length of core (cm)	Tree circumference at breast height (m)	Diameter (m)
Northern site (north of the sub-arid region up to Mangoky River)	A. gran 01 – DFL	<i>A. grandidieri</i>	-20.2224167 °S 44.42775 °E	97.5	8.8	2.8
	A. gran 04 – DFS	<i>A. grandidieri</i>	-20.8207222 °S 44.394 °E	92	11.9	3.8
Southern site (from Mangoky River to the south)	A. gran 05 – GTR	<i>A. grandidieri</i>	-21.8602778 °S 43.8670556 °E	91	12.2	3.9
	A. za – TSP	<i>A. za</i>	-23.8863889 °S 44.2583889 °E	139	7.7	2.5

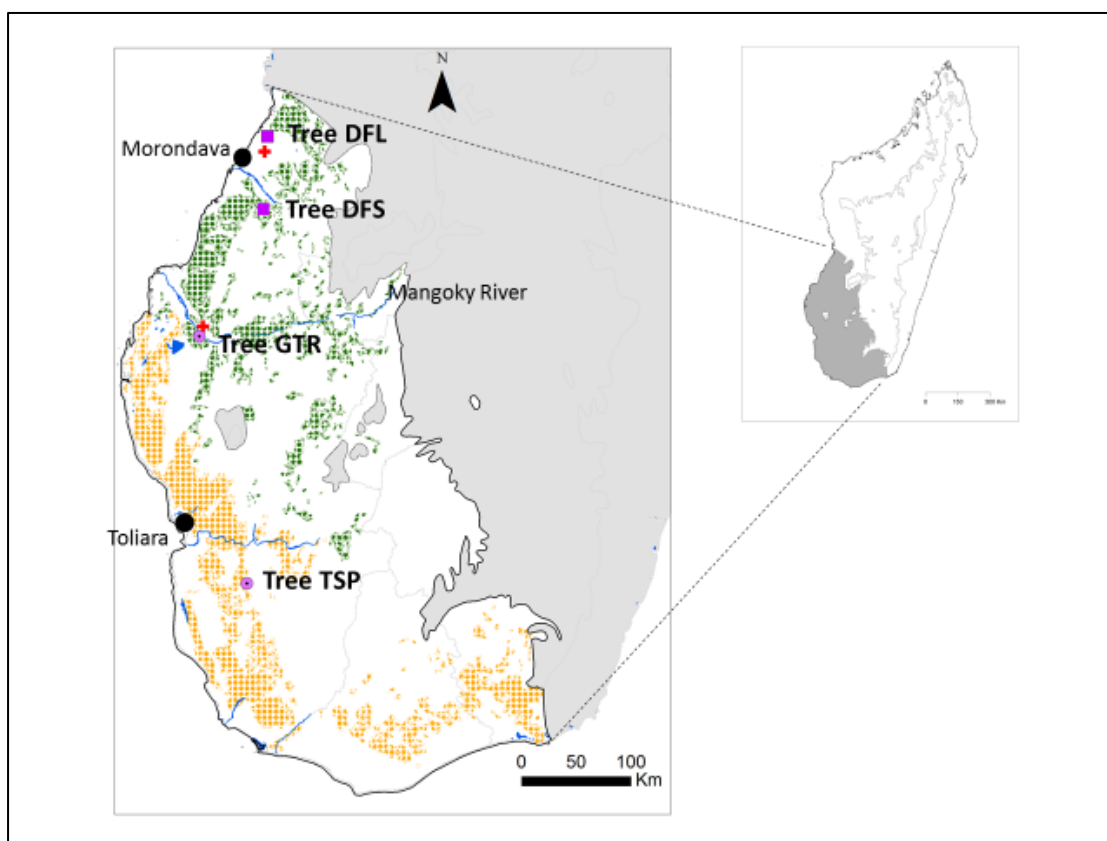


Figure 4.1: Map showing the location of the trees sampled and analysed in the present research. Violet indicates trees while red crosses indicates the sediment cores. Main town with the location of meteorological stations (Morondava and Toliara) are indicated.

4.1.3. Tree chronology

Chronologies of the tree cores were constructed using a series of AMS radiocarbon dates, a method that has been extensively used dating baobab trees (Patrut *et al.*, 2015; Woodborne *et al.*, 2015). 53 AMS radiocarbon dates were run on the remaining pre-treated samples from isotope measurement at the iThemba LABS facility in Johannesburg (South Africa). The measured AMS radiocarbon dates were calibrated with the 2013 Southern Hemisphere calibration from the online calibration programs version 7.10 (Hogg *et al.*, 2013) and the Calibomb program (<http://calib.org/CALIBomb/>) of the Queens University, Belfast, which uses the bomb carbon dataset of Hua *et al.* (2013).

The age model of the trees investigated in the current study was conducted by Dr. Stephan Woodborne using a linear model for interpolation of the chronology in the non-dated section of the cores. The dates of the trees for this research were combined with other dates from trees across southern Africa (Woodborne *et al.*, 2015; 2016) and a wiggle matching between the trees were conducted. The aliquot at the bark of a given core is attributed a date of the

start of austral growth year (July-June) and the last aliquot (from the center of the tree) would correspond to the age of the highest probability in the results of AMS dates. All the trees with all the dates are then grouped in one excel file and modelled together so that the linear interpolations of all four trees give a similar pattern in time. Wiggle matching is limited to linear interpolation at points that lie within the 1-sigma radiocarbon age. The “wiggles” are limited by obvious large excursions (like a cyclone signal) that are patently common in all the records. Events that are reflected in different trees are assigned the same age. Using a large number of dates from different cores reduces the effect of linear interpolation. Within the 53 calibrated radiocarbon ages obtained, one outlier (GTR_450) was excluded from the age model due to the level of uncertainty and the difference of age compared to its neighbouring samples. The ages interpolated for each aliquot are subject to uncertainties, estimated to be ± 5 years for baobab trees as demonstrated in previously published research (Woodborne *et al.*, 2015). This is due to different factors such as the growth of trees in dry areas which often do not produce an annualised ring (Woodborne *et al.*, 2016). There is also uncertainty associated with the process related to the establishment of the age model, which extends the range of the attributed age depending on the choice of the endpoint for the linear interpolation. Furthermore, performing wiggle matching between the trees might change the preliminary linear age associated with the individual tree, emphasizing the offset. This is particularly problematic in the comparison of annualised records where a lag of one or two years could create a direct offsetting between records. Nevertheless, the 21-year biweight mean performed on the record resolved this issue. By smoothing the data with the weighted contribution of the isotope values for the 10 years prior and after any particular year, uncertainties in the age model and any localised effect of environmental conditions are reduced (Woodborne *et al.*, 2015). The calculation of the biweight mean allows to retain the high frequency original data, and the biweight mean is overprinted to guide the decadal-scale trend. This similar to moving average but is less affected by outliers and therefore more adapted for climatological data (Lazante, 1996).

4.1.4. Alpha-Cellulose isolation and isotopic measurement from the tree rings

The analysis of stable carbon isotopes ($\delta^{13}\text{C}$) was carried out at the Mammal Institute Laboratory at the University of Pretoria under the supervision of Dr. Grant Hall. The cores were mounted in a half-round recess groove in a pine wood backing plank so that the axial orientation of the core was visible. The exposed half of the core was sub-sampled in 1 mm aliquots based on the visible orientation of the tree growth ring from the bark to the centre,

leaving a witness section comprising the other half of the core. The samples were prepared according to the method in McCarroll and Loader (2004) (Figure 4.2). Isolation of alpha cellulose was done by treatment with a solution of 2:1 toluene and ethanol in a soxhlet apparatus. This eliminated the mobile and soluble components of the wood including latex and resins. The soxhlet solvent was replaced with pure ethanol to remove the toluene, and then the samples were dried at 70 °C overnight. The samples were then treated with sodium chlorite (NaClO_2) as well as sodium hydroxide (NaOH) at different concentrations (10% and 17%) for alpha cellulose reduction. Sodium chlorite solution was used to remove the lignin from the wood which was reflected by the colour or the bleach in the samples and sodium hydroxide solutions (10% and 17%) were added to eliminate the hemicellulose of the wood. The samples were covered with a 1% Hydrochloric acid (HCl) solution for 10 minutes, rinsed till neutrality with distilled water, and dried overnight at 70 °C. Once dry, 0.05-0.06 mg aliquots of each sample were massed in aluminium foil capsules for the Mass Spectrometer (Figure 4.2).

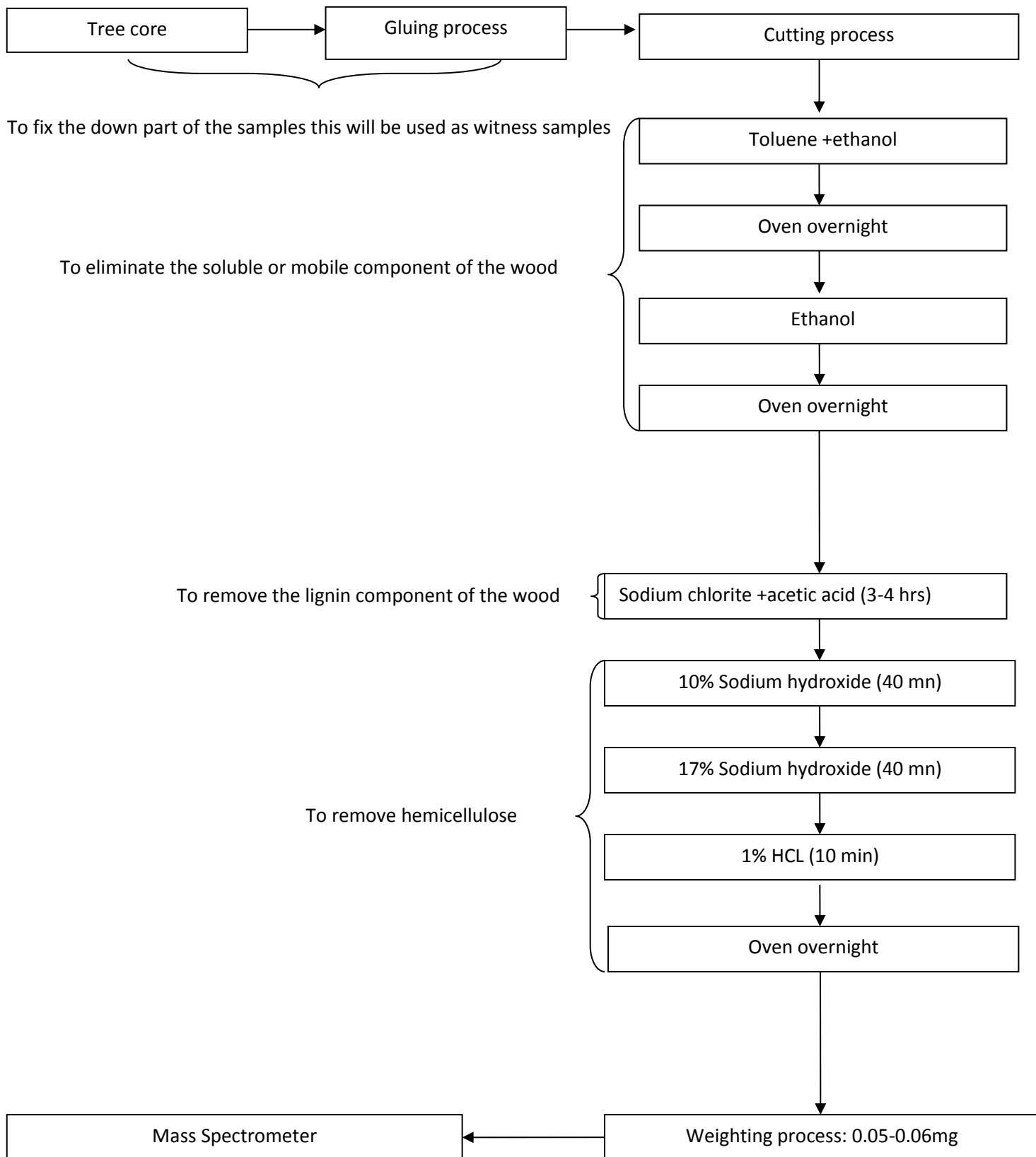


Figure 4.2: Laboratory pre-treatment for the stable carbon isotope analysis of tree rings.

All isotopic analyses were done using an elemental analyzer (Flash EA 1110 Series) coupled to a Delta V Plus stable light isotope ratio mass spectrometer, via a ConFlo III system (all equipment supplied by Thermo Fischer, Bremen, Germany), housed at the UP Stable Isotope Laboratory, Mammal Research Institute, University of Pretoria. The system yields a quantitative conversion of cellulose into CO₂ by full combustion of the samples enabling the isotopic measurement. An in-house-standard of Malaysian wood with an isotopic value of -28.4‰ was used (Hall *et al.*, 2009; Woodborne *et al.*, 2015). A blank and standard sample were run after every 12 samples. The results were reported in $\delta^{13}\text{C}$ relative to a standard fossil belemnite from the Peedee Formation of South Carolina (Vienna-PDB or VPDB) and expressed as per mille according to the following formula:

$$\delta^{13}\text{C} = (\text{R}_{\text{sample}} / \text{R}_{\text{standard}} - 1) * 1000$$

Where $\delta^{13}\text{C}$ is the isotopic composition of the sample and R indicates the ratio of ¹³C/¹²C in the sample and the international standard Vienna-PDB. Sample replication including sample pre-treatment and error in the analysis were <0.2‰. The raw data was then corrected to compensate for the increase in atmospheric CO₂ and the water use efficiency of each individual as in Farquhar *et al.*, (1982).

4.1.5. Data handling

4.1.5.1. Correction associated with the stable carbon isotope data from tree rings

The physiological response of trees to their environment is reflected in changes in the stable carbon isotope ratios ($\delta^{13}\text{C}$) of the wood, which is regulated through photosynthetic processes (McCarroll *et al.*, 2009). Such regulation recorded in the tree ring isotopic composition justifies the use of stable carbon isotopes as a climate proxy (McCarroll *et al.*, 2009). However, the raw isotope value obtained from the measurement contains non-climate information such as the change in isotopic ratio of atmospheric CO₂ which directly affects the isotopic composition of the tree. The initial correction applied to the measured isotope values is associated with the change in isotopic ratio of atmospheric CO₂ since industrialization (1795). This change was recorded in a 1000-year published record of the Southern Hemisphere atmospheric $\delta^{13}\text{C}$ which has significantly decreased since 1795 (Francey *et al.*, 1999). This first correction compensates for the $\delta^{13}\text{C}_{\text{atmospheric}}$ decrease recorded by Francey *et al.* (1999) as suggested by McCarroll and Loader (2004). In addition to the measured change in $\delta^{13}\text{C}_{\text{atm}}$, there is also an increase in the concentration of carbon in the air (C_a) which affects

linearly the intercellular CO₂ concentration (c_i) and intrinsic water-use efficiency (iWue; Wang and Feng, 2012). This concerns the second correction. An increase in CO₂ concentration inside leaves (c_i), will create faster carbon assimilation with reduced water transpiration during photosynthesis, and would increase the iWue of the plant. The correction associated with iWue in this research followed the method applied by Woodborne *et al.* (2016) which has been demonstrated to be the equivalent to the PIN correction method (Woodborne, personal communication 2018, July).

4.1.5.2. Comparison of the isotopic data with instrumental and historical records of rainfall, drought and cyclone

For each individual tree, the corrected isotope record reflects the quasi-annual variability of rainfall, while a 21-year biweight mean was calculated for the decadal and multi-decadal interpretations. The latter considers the weighted contribution of the isotope values for the 10 years prior and after any particular year, which accounts for the uncertainties in the age model and reduces the localised effect of rainfall that is recorded in each isotope record (Woodborne *et al.*, 2015). By applying the calculation of the biweight mean, the high frequency original data is retained, and the biweight mean is overprinted to guide the decadal-scale trend. This is similar to moving average but is less affected by outliers and therefore more adapted for climatological data (Lazante, 1996). The data obtained from the isotope values of the baobab ring is interpreted as a proxy for local soil moisture (rainfall) in dry regions, provided the trees are located far from water sources, that might buffer the effect of local rainfall variability (McCarroll and Loader, 2004).

It has been suggested that a more negative value is associated with wetter conditions while a less negative value indicates drier periods (Woodborne *et al.*, 2016). This negative relationship was assessed through the comparison with the local instrumental rainfall records available in the region. The quasi-annualised and biweight isotope records were compared with instrumental records of summer rainfall during period 1960-2008 from Morondava Station in the northern site (-20.28869 °S; 44.31782 °E) and Toliara station in the southern site (-23.35 °S; 43.66667 °E) (data supplied by the Service of Meteorological Station in Madagascar) (Figure 4.1). These stations were chosen because of the continuity of their instrumental record as well as their locations to the trees along the north-south transect with the closest and furthest being about 13 km and 100 km away respectively. In addition to these instrumental records, historical records of drought (Fenn and Rebara, 2003; Middleton and Beinart, 2005; Elmqvist *et al.*, 2007; Randriamahefasoa, 2013; Von Heland and Folke, 2014;

Jury, 2016; Gaspard *et al.*, 2018) and cyclone events (Nash *et al.*, 2015) in the area during the 20th century were assessed in the isotope record. Cyclones passing over the western, southwest and south were identified in historical records to assess the representation of extreme events in the isotope record.

4.1.5.3. Sub-regional and local rainfall record

The construction of sub-regional (southwest) and local (northern and southern sites) rainfall records was based on the quasi-annualised isotope record as well as the 21-year biweight mean reflecting the decadal variation of the rainfall. The isotopic composition of all four trees was averaged according to the respective age of each aliquot to provide the regional record. Locally, the DFL and DFS isotope records were combined to yield a northern site while GTR and TSP isotope records were combined to represent a southern site. Identification of monotonic trends within the record was conducted using a non-parametric Mann-Kendall trend test. The trend test has been widely used for climatological and hydrological records to detect the presence of monotonic increasing or decreasing trends (Nasri and Modares, 2009; Pohlert, 2018). A Least Squares Regression was performed to evaluate the rate of change in rainfall per year based on the sub-regional and the regional records, and a Pearson correlation was used to measure the relationship between the variables. Statistical analyses were considered significant at a level of 0.05.

The corrected isotope record was transformed into a z-score to standardize the data for local and regional records to compare between the northern and southern sites as well as the climate record available for the western region in Madagascar where tropical dry forests occur. The sub-regional record of southwest Madagascar generated here was compared with the only published record of oxygen isotopes in speleothems from Anjohibe Cave in the northwest that were considered to represent the western regional rainfall record and covers the last 1700 years (Scroxton *et al.*, 2017; see also Figure 2.4). This was conducted to extend the rainfall record of the southwest through the analysis of patterns between both records during the period covered by the present research. This information is valuable for the interpretation of vegetation change and fire regime during the late Holocene inferred from pollen, carbon isotope and charcoal analysis.

4.2. Sedimentary analysis of the past vegetation and fire analysis in southwest Madagascar through palaeoecological approach

To investigate changes in vegetation and fire regime in two sites (northern and southern sites) in the southwest, sediment cores from lakes were collected and dated. This was followed by laboratory extraction of proxies such as pollen, and charcoal after the physical description of the sediments. This physical description was conducted following the classification of Troels-Smith (Troels-Smith, 1955; Kershaw, 1997), which refers to the physical features and components of the sediments. The colours of the sediment were inferred from the Munsell soil color charts (Munsell color company, 1954). The organic carbon and carbonate content of the sediment cores were measured through Loss on Ignition (LoI) on 2-4 cm³ of samples (Benett and Willis, 2001; Heiri *et al.*, 2001). Relative abundance, diversity indices, and statistical analysis were then calculated.

4.2.1. Sediment coring

Sediment coring was conducted on lakes with abundant organic content and a total of 13 sediment cores were collected from the southwest region (Appendix 4.2). Within these collected cores, two were analysed (Figure 4.3), one from the northern site and one from the southern site. These cores were chosen after preliminary physical description of the core and pollen extraction which were performed to assess the abundance of pollen grains within the samples.

For these lakes, which were permanent wetlands (with sediment > 50 cm deep), a D-section corer called a Russian corer (Aaby and Digerfeldt, 1986) with a 6 cm diameter and 50 cm long core chamber was used to collect the cores. It was chosen based on practical use and handling of the material in remote areas. Sediment cores were extracted in 50 cm sections, up to a depth of 1.5 m. Each core was wrapped in cling wrap and aluminium foil to avoid damage and compaction during transport and on return to the laboratory. It was stored at 4 °C to inhibit microbial activity until laboratory analysis (De Vleeschouwer *et al.*, 2010). The short description of the cores is provided below and in Table 4.2 and the sampling locations are indicated in Figure 4.3.

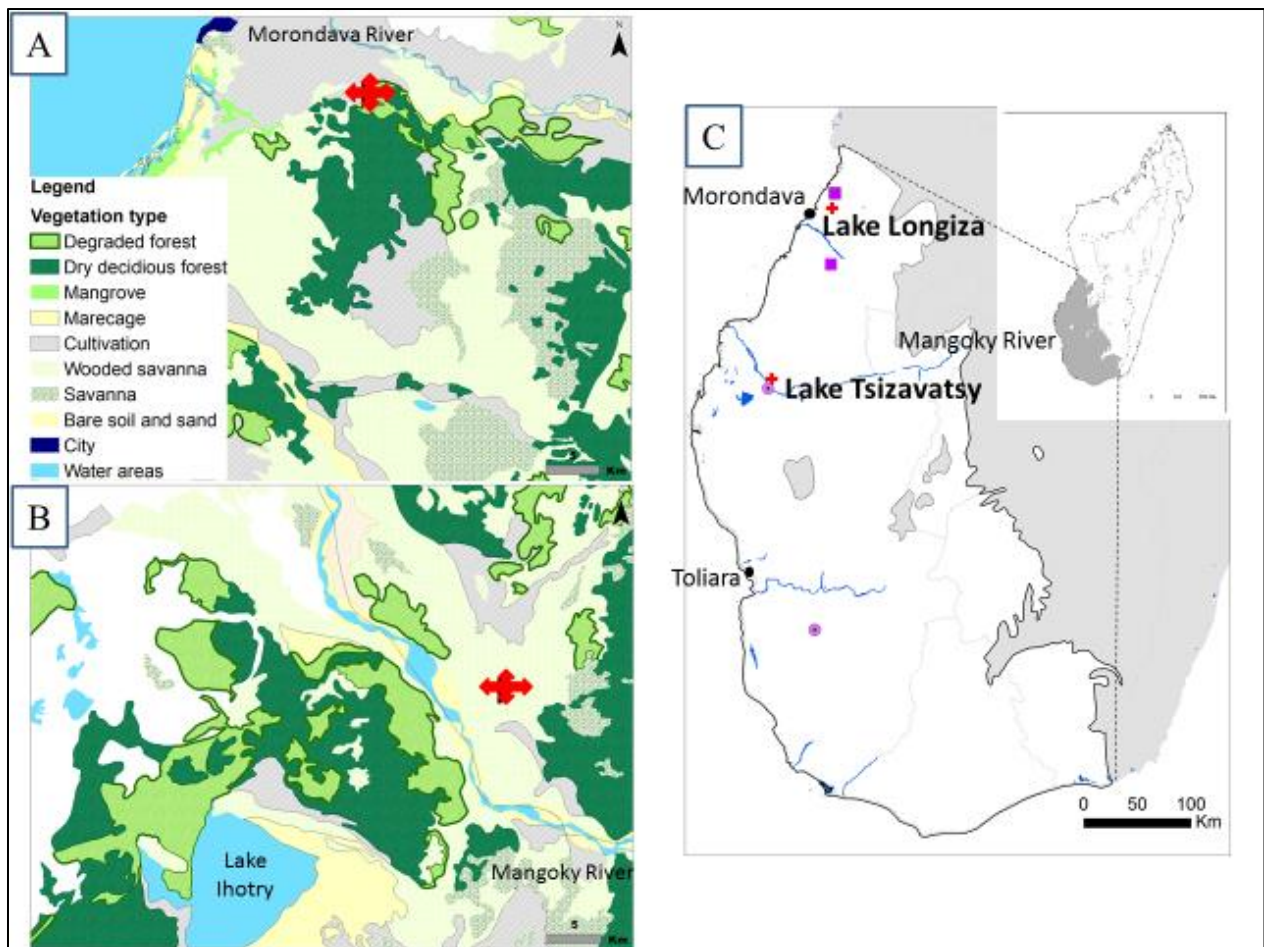


Figure 4.3: Map showing the location of the sediment cores and their surroundings. Panel (A) shows the surrounding of Lake Longiza in the northern site and panel (B) indicates the vegetation around Lake Tsizavatsy in the southern site. Panel (C) shows the map of the study area within the sub-arid region. Purple points indicate tree cores while red crosses show the sediment cores. Main towns and rivers are indicated (Morondava and Toliara).

Lake Longiza: northern site, core LNG

LNG core from Lake Longiza is from the northern part of the study area (hereafter referred to as the northern site). This is a 3 km diameter lake with a maximum depth of approximately 4 m surrounded by small patches of rice fields (Figure 4.4). The coring was recovered 150 m from the edge of the lake. A sediment core of 96 cm was collected. The core is very clay-rich with several distinctive layers of charcoal. The immediate vicinity of the lake is surrounded by rice fields, with a largely intact dry forest, degraded dry forest, agricultural lands and wooded savanna in the wider landscape (Figure 4.3A). Less than 5 km to the north of this lake is the Morondava River where riparian vegetation exists on alluvium and fertile soils. The vegetation within the immediate surroundings of the lake contained taxa such as *Typha angustifolia* (Typhaceae), *Phragmites mauritianum* (Poaceae), *Oryza* spp. (Poaceae), *Musa*

paradisiaca, *Zyziphus* spp. (Rhamnaceae), *Acacia* spp. (Fabaceae), *Adansonia grandidieri* (Malvaceae), *Androya decaryi* (Scrophulariaceae), and *Anacardium* spp. (Anacardiaceae).



Figure 4.4: Lake Longiza with the coring site at 150 m far from the limit of the rice field. (Image: Lindsey Gillson)

Lake Tsizavatsy: southern site, core TSZ

Lake Tsizavatsy is approximately 500 m diameter shallow lake with less than 0.5m water during our field work (Figure 4.5). It is located in the southern part of the study area (hereafter southern site) and is known by the local community to recede to half its capacity during the dry season. A core of 47 cm was retrieved from the lake. This coring site is surrounded by Cyperaceae at the lake edge and is encompassed by wooded savanna with the further presence of degraded and intact dry forest in the wider landscape. It is located less than 5 km from the Mangoky River and was considered being within the southern site due to its proximity to the tree record in the southern site (Figure 4.3B). Within and around the lake, taxa such as *Phragmites mauritianum* (Poaceae), *Cryptostegia madagascariensi*, *Acacia morondavensis* (Fabaceae), *Tamarindus indica* (Fabaceae), *Quivisianthe papinae* (Meliaceae), *Antidesma madagascariensis* (Euphorbiaceae), *Mimosa delicatula* (Fabaceae), *Stereospermum nematocarpon* (Bignoniaceae), *Zyziphus* spp. (Rhamnaceae), *Hyphaene shatan* (Arecaceae),

Tabernaemontana coffeoides (Apocynaceae), *Azima tetraantha* (Salvadoraceae), and *Euphorbia* spp. (Euphorbiaceae) are found.



Figure 4.5: Lake Tsizavatsy during the field work in August 2015 (Image: Estelle Razanatsoa)

Table 4.2: Description of the sediment cores and AMS dates analysed in this research. Sediment cores are distributed within the tropical dry forests in southwest Madagascar

Site	Name	Coordinates	Length of the core (cm)	Number of AMS date
Northern site	Lake Longiza_	-20.34666667°S	96	9
	Core LNG	44.40244444°E		
Southern site	Lake Tsizavatsy_	-21.77977778°S	47	4
	Core TSZ	43.89797222°E		

4.2.2. Sediment chronology

The chronology of the two sediment cores (LNG and TSZ) was established based on AMS radiocarbon dates, a technique widely used in palaeoecological studies (see Gasse and Van Campo, 2001; Colombaroli *et al.*, 2010) and proven to have higher precision in dating than the traditional beta decay (MacPherson, 2017). Subsamples weighing between 5-10 g in the desired section were wrapped in aluminium foil. Precautions were taken to avoid any contamination by carbon during sub-sampling. Samples were acid washed to remove carbonates and the bulk organic fractions were dated, because of its association with pollen deposition (unlike macrofossils which have a different taphonomy). Bulk sediment was thus considered appropriate in increasing coherence between age-depth models and pollen diagrams. The laboratories used for the sediment radiocarbon dates in this research were: iThemba LABS facility in Johannesburg (South Africa); Beta analytic Inc, Laboratory in Florida (USA) and 14CHRONO labs in Belfast (UK). The two sediment cores investigated in this research had at least four radiocarbon dates each of bulk sediments (Table 4.2) to establish a good age-depth model and identify sediments accumulation change over time. Age-depth models were performed using the package Clam 2.3.1 (Blaauw, 2010). Calibrated values of the dates in calendar years (BCE/CE) and before present (BP) were provided. The age-depth model was constructed using linear interpolations of the calibrated dates which is based on age point estimates for depths on weighted means of the dated levels and the age model is processed with 10,000 iterations. All ages were expressed in BC/AD for all cores in reference to BCE/CE.

4.2.3. Pollen and charcoal extraction

Pollen analysis is a widely used method in Quaternary science as it provides unique insights into past changes in terrestrial and aquatic environments (Birks and Seppä, 2004). Pollen was used to reconstruct the past vegetation at Lake Longiza and Lake Tsizavatsy in southwestern Madagascar. In addition, microcharcoal (<150 µm) and macrocharcoal (>150 µm) were used for the study of Quaternary fire history and provide data on contemporary fire regimes (Blackford, 2000; Scott, 2000). Specifically, macrocharcoal gives a strong signal of local fire history (Carcaillet *et al.*, 2001), which can often be interpreted as a signal of anthropogenic burning (Virah-Sawmy *et al.*, 2016). Pollen and microcharcoal analysis followed the same procedure of extraction while macrocharcoal was recovered by sieve prior to the Hydrofluoric acid (HF) step.

Pollen and microcharcoal, and their extraction from sediments for this study followed the analysis established by Berglund and Ralska-Jasiewiczowa (1986) refined by Faegri and Iversen (1989) as described and reviewed in Bennett and Willis (2001). This method consists of extracting palynomorphs elements in the sediments smaller than 150 μm . 1 cm^3 sub-samples were taken from the cores using a calibrated syringe or two razor blades where the volume was estimated using volumetric displacement. Two tablets of exotic *Lycopodium* spores, Batch number 3862 produced by Department of Quaternary Geology in Lund with a concentration of 9666 *Lycopodium* spores per tablet were added to each test tube. This allows the evaluation of the quality of the preparation, measures the sedimentation rate of the core and calculates the pollen concentration of the sample (Benett and Willis, 2001). The steps that follow consist of several physical and chemicals treatments. Sodium hydroxide (NaOH) is used to remove acid components of the sediments while Hydrochloric acid (HCl) and Hydrofluoric acid (HF) are used to remove carbonates and silicates. Finally, an acetolysis mixture (a combination of 1/9 sulfuric acid and acetic anhydride) is used to remove organic debris cellulose, proteins, lipids and carbohydrates from the surface of the pollen grains (Erdtmann, 1960; Low *et al.*, 1989). After each treatment, washing with deionized water, and centrifugation at 3500 RPM for 5min were conducted. All the reaction took place in a 40 cm^3 test tube.

Pollen and microcharcoal were counted using a Leica microscope DM750 with 4x, 10x, 40x and 100x objective lenses. Most of the identification was done using the 400x magnification but to identify the texture and the ornamentation of the exine, 1000x magnification with an addition of immersion oil was used. Pollen grains were pictured using LEICA ICC50 HD and Leica LAS EZ (V 2.1.0) software. Pollen counting software Froyd Lab Tools Version 1.1, an independent software included in JAVA-Version 8, copyright © 2015 was used to record all the pollen types and their respective pictures. Categories were created to differentiate the pollen from the spores. Pollen grains were classified into ecological and vegetation association groups and physiognomy such as trees/shrubs and herbaceous, forest taxa and dry-adapted (xerophytic) taxa. A minimum of 250 grains of terrestrial pollen (Scott and Woodborne, 2007; Quick *et al.*, 2011) was counted for each level in the sediment depth to ensure 95% confidence intervals for statistical analysis (Maher, 1972). In total, 18 levels were counted for the northern site at LNG while 14 levels were counted at TSZ in the southern site.

Pollen identification was based on published pollen references such as the Australian pollen database (Australasian Pollen and Spore Atlas[APSA], 2007) and other published references (Vincens *et al.*, 2007; Gosling *et al.*, 2013). In addition, slide references from the Palynology Unit of the Department of Ecology and Plants Biology (University of Antananarivo) with newly established pollen references for the southwest tropical dry forests were also used. Anthers of trees and shrubs specific to the region were collected from the herbarium (TAN-Herbarium Tsimbazaza Madagascar) and acetolysis was performed at the University of Cape Town (Palaeoecology Laboratory).

Microcharcoal analysis was conducted following the point count method established by Clark (1982). This method has been reported to be one of the most efficient in analysing fire activities using microcharcoal in sediments samples (Finsinger and Tinner, 2005). It consists of point counts of charcoal particles that touch directly one of the 22 major points in the graticule contained in each field of view. The same microscope slide used during pollen analyses was used for the microcharcoal except for some samples where extra slides were needed to meet the sum of *Lycopodium*-charcoal needed. A minimum of 200 counts of *Lycopodium* and charcoal were counted (Finsinger and Tinner, 2005) excluding any ambiguous particles to allow the comparison of all the levels. A total of 24 samples was counted for the LNG core while 14 samples were counted for the TSZ core.

Charcoal samples >150 μm recovered from the pollen analysis were used to count the macrocharcoal content of the sediments. The sample was transferred into a petri dish. Where the number of charcoal particles are low, the entire petri dish was counted, otherwise it was subdivided in eight equal proportions and four of them were counted. The total charcoal count is obtained by multiplying that value with the total proportions. The counting is processed using a dissecting microscope at x10 magnification.

4.2.5. Isotope measurement of sediments

Plants have specific values of isotope depending on their photosynthetic pathways and this provides signatures into sediment deposits allowing for the abundance between C_3 and C_4 plants to be distinguished over time (Ehleringer and Rundel, 1988; Tieszen, 1991; McCarroll and Loader, 2004). Carbon isotope measurement was conducted on the bulk organic content of the sediment cores. Results were plotted alongside the pollen diagram to evaluate the dynamism of the vegetation. Samples were acid washed with HCl 10% several times and soaked for 24 hours. Samples were dried in a 50 °C oven. Aliquots of 10-20 mg of sediments

were weighed and wrapped in a tin capsule foil adapted for isotope measurement. Finally, samples were combusted in a mass spectrometer where the stable isotope ratios of the samples were reported in $\delta^{13}\text{C}$ per mil. The analysis was conducted at the Stable Light Isotope Laboratory at Archaeology Department, University of Cape Town with Mr. Ian Newton.

4.2.5. Data handling

4.2.5.1. Pollen diagram

Pollen percentages and concentration were plotted and compared using C2 Version 1.7.7. (Juggins, 2003). Percentages of pollen were calculated using the formula demonstrated in Equation (2). The relative abundance of pollen data was plotted as this considers the abundance of other taxa and the results showed similar interpretation to the concentration data (Appendix 2.2 and 2.4). This method is widely used for pollen diagrams (see Colombaroli *et al.*, 2010; Virah-Sawmy *et al.*, 2010).

The relative abundance of taxa was calculated using the following formula:

Equation (2)

$$FRi = \frac{n_i}{N} \times 100$$

Where:

- FR_i: relative frequency of the taxa i
- n_i: absolute frequency of i
- N: total pollen counted, for all samples I counted 250 pollens grains

4.2.5.2. Zonation

Pollen concentration and percentages were used to evaluate the changes in the pollen assemblage over time. Percentage data higher than 2% were limited to this value to reduce bias from rare taxa and is a common palaeoecological approach (see MacPherson, 2017). All data analyses were conducted using R studio version 3.5.1 (R Core Team, 2018). Data transformation was performed using the function “decostand” through the method of “Hellinger” as it considers the presence of the zero values in the data. Temporal variation of vegetation over time was identified through clustering techniques, as commonly performed in palaeoecological analyses (see Gillson and Ekblom, 2009; Gil-Romera *et al.*, 2010) and it allows identification of significant stratigraphic changes in the pollen assemblage (Legendre

and Birks, 2012; MacPherson, 2017). Cluster analyses were done using the package “Analogue” (Simpson, 2018) through the function `chclust` using the method “CONNIS” with the Euclidean distance (Birks and Gordon, 1985). The Euclidean distance measure the similarity between the sediment samples analysed in the core where samples with similar taxa composition and abundance were grouped first. In addition, Conisss (Constrained incremental sum-of-squares cluster analysis) is a stratigraphically constrained cluster analysis that allows analysis of group of samples within their relative age and zones were identified with the function “`cutree`” (Birks and Gordon, 1985; Grimm, 1987).

4.2.5.3. Rarefaction analysis and compositional turnover

The change in the diversity of the vegetation over time was assessed through the measure of rarefaction analysis and beta diversity. Rarefaction analysis is used to estimate the palynological richness, which is an indicator of plant diversity (species richness) in the landscape. It assumes similar pollen sum counts for all samples (Birks and Line, 1992), which is based on a minimum sum of 250 pollen grains per sample excluding aquatics in this research. This method has been used by several studies in palaeoecology (Colombaroli *et al.*, 2009; Gil Romera *et al.*, 2010). However, because the number of taxa can be influenced by a few dominant species, detrended pollen richness was calculated by including the PIE evenness (probability of interspecific encounter) (Hurlbert, 1971). The PIE measures the probability that two randomly selected pollen grains will be of different taxa and it is not affected by the sample size or the pollen diversity. PIE values range between 0 and 1 where 0 indicates that all pollen grains in a sample are the same and 1 indicates they all differ. This was used to calculate the detrended pollen richness, which is the residual of the regression of the pollen rarefaction and the pollen evenness distributed around a mean of the pollen rarefaction. In addition, compositional change (or beta diversity along temporal gradient) (Birks, 2007) was obtained from detrended canonical analysis first axis (DCA axis 1) of the square root transformed pollen percentages (Birks, 2007; Colombaroli *et al.*, 2009). Results were then transformed using Hill’s transformation to evaluate the change on a positive axis. The combination of these different diversity measures ensures that the interpretation of the data reflects the change in the vegetation in the landscape.

4.2.5.4. Charcoal analysis

Charcoal concentration was calculated using the Equation (3). Charcoal data were then transformed into charcoal influx, which reflect the variation of the abundance according to the sediment accumulation rate obtained from the age model. A result that provided a similar trend to the concentration data. This influx of charcoal was calculated following the formula in equation (4).

Microcharcoal concentration was calculated according to the following formula (Bennett and Willis, 2001) and is expressed in $\text{cm}^2 \cdot \text{cm}^{-3}$:

Equation (3):

MicroCharcoal concentration

$$= \frac{\text{No field of view} \times \text{no charcoal hits}}{\text{no points}} \times \frac{\frac{\text{Lycopodium added}}{\text{Lycopodium counted}}}{\text{Sediment volume}}$$

Where

- No field of view: number of fields of view within all the slides counted for each sample
- no charcoal hits: number of charcoal that had touched the major tick in the graticule in all of the field of view analysed
- no points: maximum number of point count in all the slides for one sample
- Lycopodium added: estimated number of lycopodium added at the beginning of the sample preparation. Two tablets of lycopodium were added which estimates the number of 19332 spores added, (9666 spores times two *Lycopodium*)
- Lycopodium counted: lycopodium counted
- Sediment volume: initial volume analysed 1 cm^3

Equation (4)

$$\text{Charcoal accumulation (Influx)} = \frac{\text{Charcoal concentration}}{\text{Depositional time}}$$

Charcoal concentration calculated from Equation (3) and depositional time is inferred from the age model.

4.2.5.5. Multivariate analysis

Non-metric Multidimensional Scaling (NMDS) was applied to the pollen data to identify if there were trends or major changes of vegetation through temporal or spatial scale or if there were relationships between taxa. Only taxa with relative abundance higher than 5% were

considered in the analysis to reduce bias from rare taxa. Non-metric multidimensional scaling (NMDS) (Kruskal, 1964; McCune *et al.*, 2002) is considered as the most robust method of unconstrained multivariate ordination in community ecology (Minchin, 1987) and its advantages in analysing pollen data has been demonstrated (see Broothaerts *et al.*, 2014; MacPherson, 2017). It does not require normally distributed data and there are no ‘hidden’ dimensions as the number of dimensions are determined *a priori*, reducing losses of ecological information (McCune *et al.*, 2002; Broothaerts *et al.*, 2014). A dissimilarity matrix of the pollen percentage data was first calculated using the Bray-Curtis method. Numbers of dimensions to be included in the ordinations were determined by calculating ‘stress’. Stress value is an inverse measure of fit between rank orders of the original dissimilarity matrix and the NMDS ordination space data (MacPherson, 2017) ranging between 0 and 1 where values < 0.05 are considered excellent, <0.1 are good, values < 0.2 are usable while those between 0.2-0.3 must be interpreted with caution (Clarke and Warwick, 2001; Kruskal, 1964; McCune *et al.*, 2002). For the two cores investigated here, two dimensional solutions were enough to produce a stress value less than 0.2 and an increase in the dimension did not improve the model. Regression analyses of fire influx were plotted with the NMDS two-dimensional model to assess the response of different taxa and assemblages to fire. Regression analysis was conducted and plotted against pollen abundance of the taxa group representing similar physiognomy or ecological function. Variation of pollen rarefaction and detrended pollen richness in response to increasing charcoal influx were also evaluated.

5. CHAPTER FIVE: RESULTS

The main goal of this research is to investigate the long-term dynamics of the tropical dry forests in southwest Madagascar and its relationship to rainfall variability and fire regime. This chapter describes the results of the analysis of dendroclimatological and palaeoecological approaches at two sites (northern and southern site) in southwestern Madagascar. First, the description of the isotope record from tree rings and the inferred local (northern and southern site) and regional rainfall record of the southwest is provided. It is then followed by the results of pollen, carbon isotope and charcoal analysis of the sediments collected at Lake Longiza in the northern site and at Lake Tsizavatsy in the southern site.

5.1. Isotope record of local northern, southern site and sub-regional southwest

Madagascar

The lack of palaeoclimate record in Madagascar as described in Chapter 2 highlights the need for climate proxies that are independent of the pollen record to avoid circular reasoning when attempting to reconstruct the effects of climate change on vegetation. This section responds to the objectives of reconstructing past rainfall for the region. The $\delta^{13}\text{C}$ isotope variation of trees should reflect local changes in soil moisture (McCarroll and Loader, 2004) which reflects to rainfall in drier areas such as the southwest of Madagascar. Enriched isotope ratios (more positive values) in the growth rings of trees are expected to indicate drier conditions while depleted isotope ratios (more negative values) are indicative of wetter conditions. For the southwest region, pollen record suggests an increasing aridity in the last 2000 years which became more pronounced in the last 1000 years (Burney, 1993; Virah-Sawmy *et al.*, 2016). From such expectations, this research generates high resolution sub-regional southwest and local rainfall data from carbon isotopes of radiocarbon dated baobab tree rings over the last 700 years and compares this with a record available in the northwest from Anjohibe Cave which spans the last 1700 years (Scroxton *et al.*, 2017). This data will be used to interpret pattern of rainfall at a regional scale within the tropical dry forest ecosystems for the last 2000 years.

5.1.1. Chronology of the trees

The linear interpolation and wiggle matching of the radiocarbon dates obtained for the four baobab trees provided the age models as shown in Figure 5.1. The assigned age and the

calibrated age indicate an age model in which the majority of the assigned ages fall within one sigma error (Appendix 1). The four trees covered about 700 years (AD 1240-2015) of record (Table 5.1). Within the 53 dates run for radiocarbon dates analysis, one date GTR 450 which yielded a very young age of about AD 1950 was not considered in the analysis due to the difference in the age obtained to its neighbouring samples of around AD 1310 at one sigma error (Appendix 1). The age model allowed an interpolation of the age for each sub-sample, providing a basis for reconstructing a temporally continuous regional rainfall proxy record for the last 700 years based on isotopic analysis.

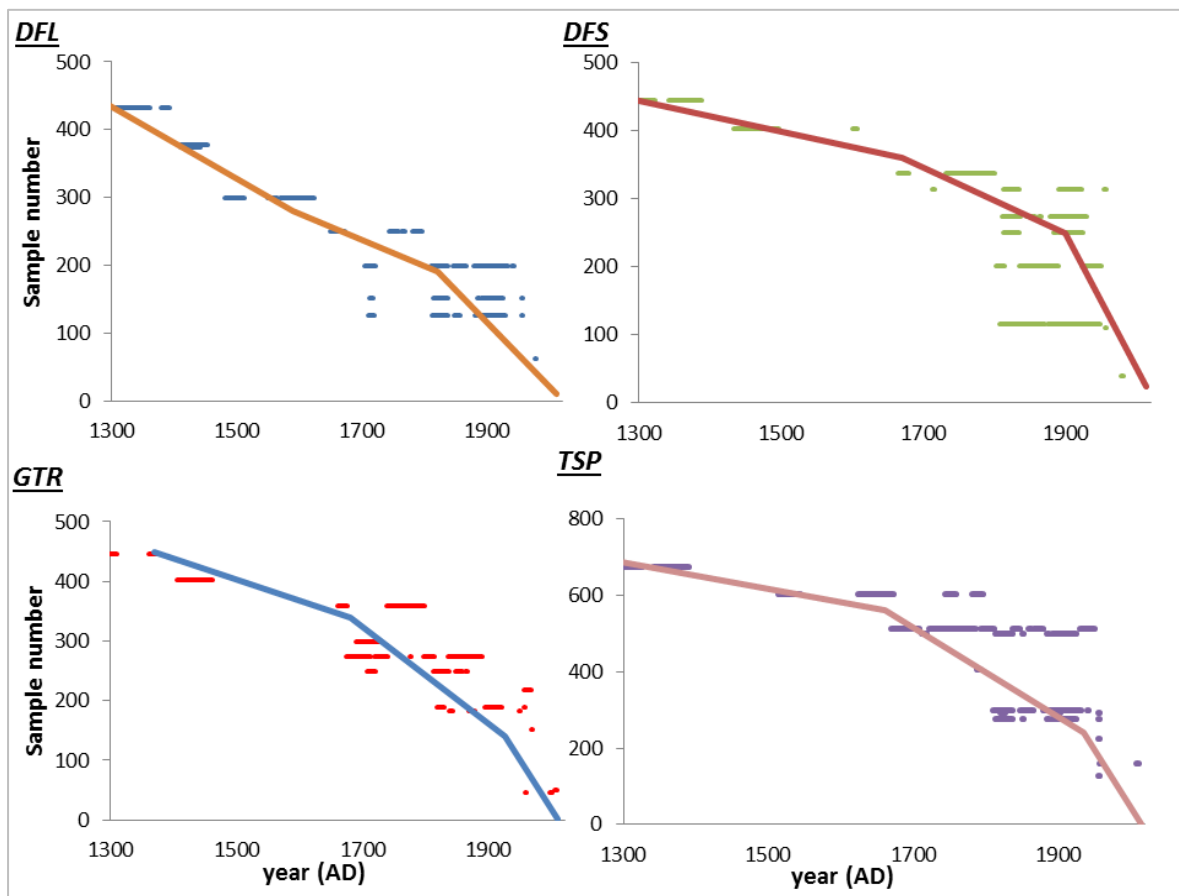


Figure 5.1: Age-model of each replicate tree based on 52 radiocarbon dates. Top: trees from the northern site; bottom: trees from the southern site of the study area. The y-axis indicates the sequential aliquot number starting with 1 at the bark and increasing towards the inner part of the tree. The x-axis is the calendar age. The horizontal lines are the 1-sigma calibration intervals for the radiocarbon dates. The bold line represents the age model which attempts to intercept the 1-sigma calibration range of each of the radiocarbon date.

Table 5.1: Period covered by the trees from north to south of the study area

	Trees	Year (AD)	Time covered (years)
Northern site	DFL	1302-2010	708
	DFS	1384-2010	626
Southern site	TSP	1240-2015	775
	GTR	1250-2015	765

5.1.2. Corrected $\delta^{13}\text{C}$ of the trees

The four cores yielded 2034 sub-samples with a precision of the isotope measurement that was less than 0.2‰. The recorded minimum and maximum $\delta^{13}\text{C}$ values are c. -27.9‰ and -22.8‰ respectively (Table 5.2). The mean $\delta^{13}\text{C}$ value is -25.5‰ for all the trees with about 0.2‰ higher in standard deviations and variance for the trees in the southern site compared to the northern site. In addition, these trees presented the highest $\delta^{13}\text{C}$ values within the record with values of about -22.8 and -23.8‰ for GTR and TSP respectively as shown in Table 5.2.

Table 5.2: The average (mean \pm SD) and range of stable carbon isotope ($\delta^{13}\text{C}$; ‰) values from the tree ring samples per baobab along the north-south transect in southwest Madagascar.

	Northern site		Southern site	
	DFS (n = 433)	DFL (n=445)	GTR (n=450)	TSP (n=706)
Mean \pm SD	-25.4 \pm 0.5	-25.8 \pm 0.6	-25.5 \pm 0.7	-25.6 \pm 0.7
Min	-26.9	-27.5	-27.9	-27.6
Max	-23.9	-24.2	-22.8	-23.8

5.1.3. Comparison of the isotopic data with the meteorological record and historical record of drought and cyclone

There is a negative correlation between the stable carbon isotope record for all trees and the instrumental record (Table 5.3). This confirms the inverse relationship between rainfall and carbon isotope in trees where relatively positive isotope values are associated with dry periods and relatively negative isotope values with wet periods. The relationship between these two variables along the transect (Figure 5.2) shows that some dry years such as 1973 in Morondava with the lowest summer rainfall record (359.8 mm) corresponded to the highest isotope value (-24.1‰) while the wet years for example in 1982 (1173 mm) had more negative value of isotope of about -26.3‰ in the DFL tree (Figure 5.2A) which is in line with the theoretical expectation (McCarroll and Loader, 2004). This is also reflected in the 21-year-biweight comparison in the period 1980-1990 where high rainfall values coincide with a

low isotope record along with the inverse pattern between these variables (Figure 5.2). The non-significant correlation for TSP could be associated with the accuracy and the precision of the age model as one-year error might offset completely a dry or wet year as well as the localised rainfall experienced by the tree (Table 5.3).

Table 5.3: Coefficient of correlation associated with the instrumental record and the stable carbon isotope record

	Tree	Location station record	Data compared	Correlation coefficient r	p-value
Northern site	DFL	Morondava	Quasi-annual	-0.35	0.01
	DFS	Toliara	21-year biweight	-0.41	0.02
Southern site	GTR	Toliara	21-year biweight	-0.51	0.03
	TSP	Toliara	21-year biweight	-0.27	0.14

In addition, the comparison of extreme events with the isotope record in the last century (Figure 5.3) showed that most drought events were reflected in the dry periods of the regional isotope record. This was the case for the drought recorded around 1930, 1941-1942 and since 1980. There were also droughts that occurred within relatively wet period such as in 1956 and 1973. For cyclones, those recorded at the beginning of the century (1902, 1905, 1907) are not reflected in the rainfall record, after which most of the recorded cyclone events in the western region were reflected in the isotope data. This was the case in 1953, 2004 and 2010.

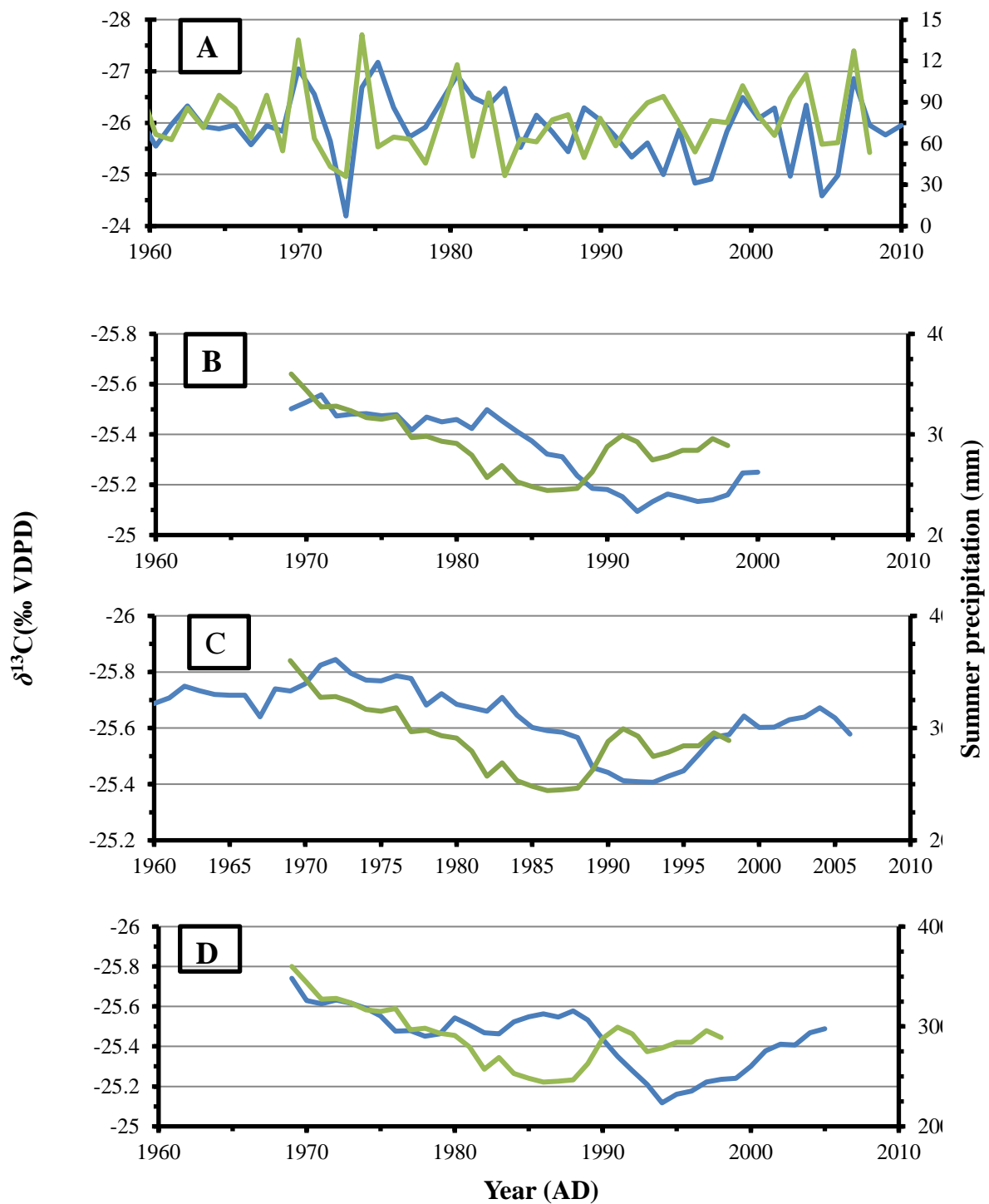


Figure 5.2: Time series comparison of the stable carbon isotope data (blue) and instrumental rainfall record (green) from meteorological stations in southwest Madagascar for trees DFL (A), DFS (B), GTR (C) and TSP (D). An enriched isotope value corresponds to low rainfall whereas a depleted isotope value corresponds to high rainfall.

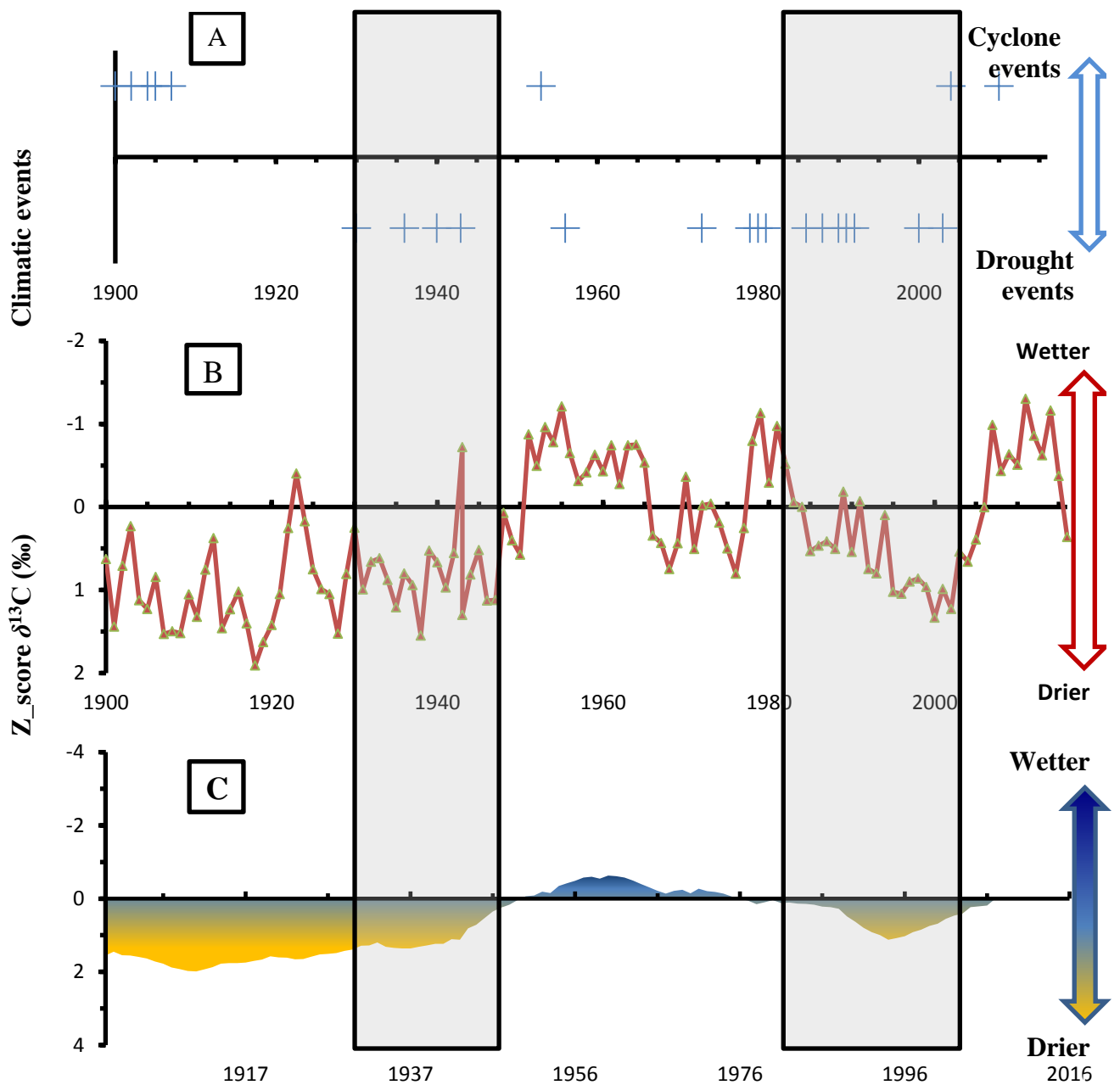


Figure 5.3: Comparison of the available historical records of climatic events and the carbon isotope data (this research) for the twentieth century (A): Historical record of cyclones events and drought events (B): Quasi-annual record of the carbon isotope data and (C) indicates the decadal isotope record with orange for dry periods and blue for wet periods.

5.1.4. Local (northern and southern sites) and sub-regional rainfall record for southwestern Madagascar

5.1.4.1. Local variability of rainfall

The isotope record from the northern site indicated highly variable rainfall at quasi-annual to decadal scale, which is combined with the shortening of wet periods at multi-decadal to centennial scale and an overall decreasing trend in rainfall (Table 5.4). On a decadal scale, there is a highly variable period of rainfall between AD 1620-1850, with pronounced dry periods around AD 1700 and AD 1750, followed by a very brief wet period around AD 1800 but still fluctuating (Figure 5.4A). On a centennial scale, the northern site experienced a succession of wet periods with reducing duration over time and recurring dry periods with duration of about 80-100 years. Wet periods are recorded from AD 1350-1450 spanning 100 years, then AD 1550-1635 for 85 years followed by 30 years wet period between AD 1790-1820 and AD 1950-1980. Dry periods, in contrast, remained relatively constant in duration as observed from AD 1450-1550, AD 1700-1780, and AD 1850-1950, but an increase in its severity especially in the last two dry cycles (Figure 5.4B). A dry phase is observed since 1980 to the present but towards a tendency of increase in rainfall.

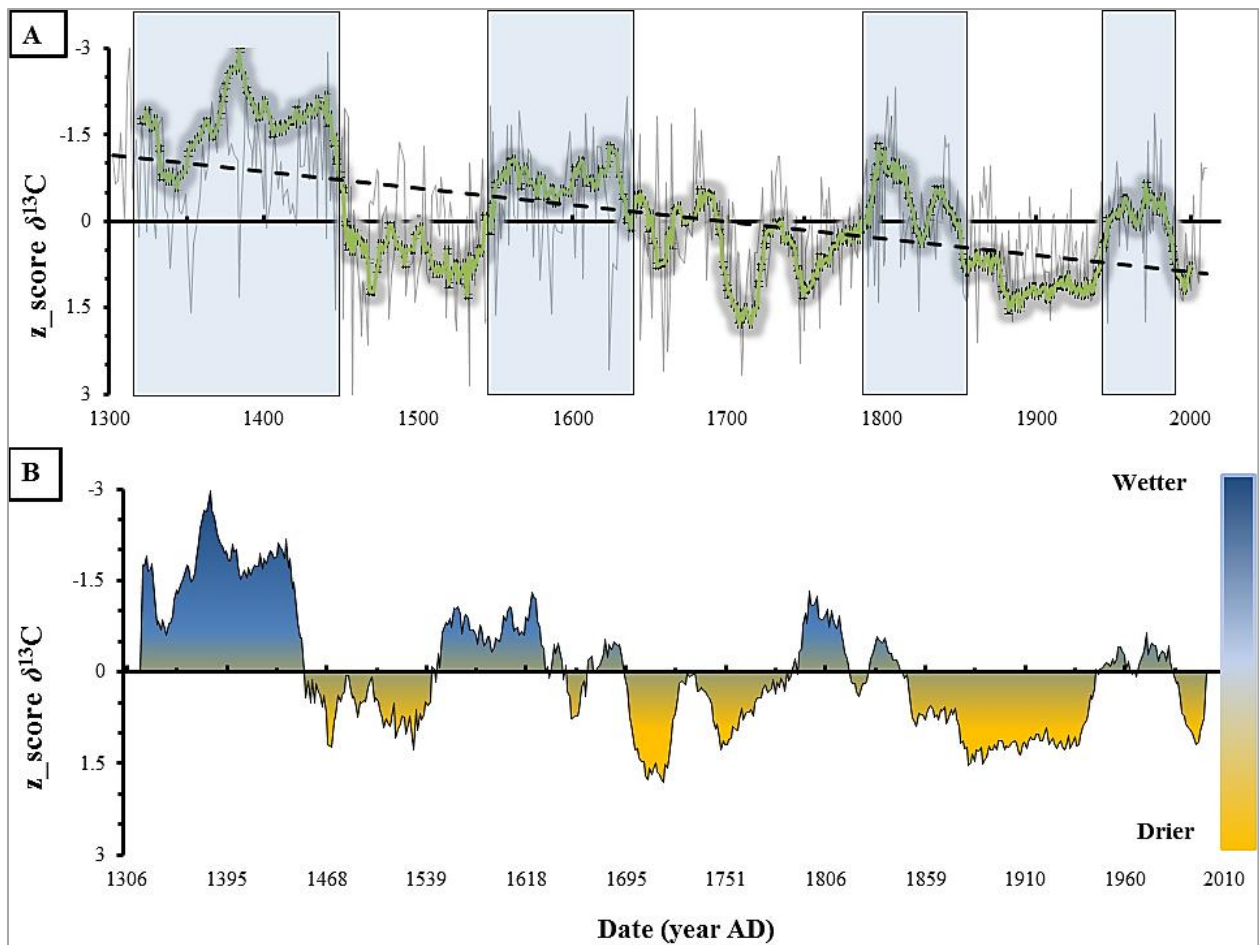


Figure 5.4: Rainfall record for the northern site of the study area. (A) grey line indicates the quasi-annualised record and grey boxes indicate wet periods, green bold indicate the 21-year bi-weight mean reflecting decadal variability. Dashed line shows the decreasing trend over time. (B) multi-decadal and centennial variability of the rainfall.

At the southern site, there is a monotonic decreasing trend in the rainfall record with a higher rate (0.001‰ per year, $p < 0.05$) compared with the northern site (Table 5.4) in addition to higher variability at a centennial scale (Figure 5.5). There is also a tendency towards a shortening of wet and dry periods over time. The wet periods are from AD 1300 to 1617 for about 300 years, then <100 years from AD 1762 to 1860 to about 30 years of a wet period from AD 1950 to 1980. Three wet periods were identified within these wet phases mainly around AD 1400, AD 1850 and AD 1950. The dry periods are recorded around AD 1617 to 1762 for about 145 years, AD 1860 to 1950 for about 120 years. The driest period in the region was recorded around AD 1300, AD 1700, and AD 1920. Since the drought in AD 1920, there is an increase in rainfall at a decadal scale leading to a peak in a wet period around AD 1950. In the current period, despite the slight decrease in rainfall relative to the previous century, the records show a decadal slow increasing trend of rainfall.

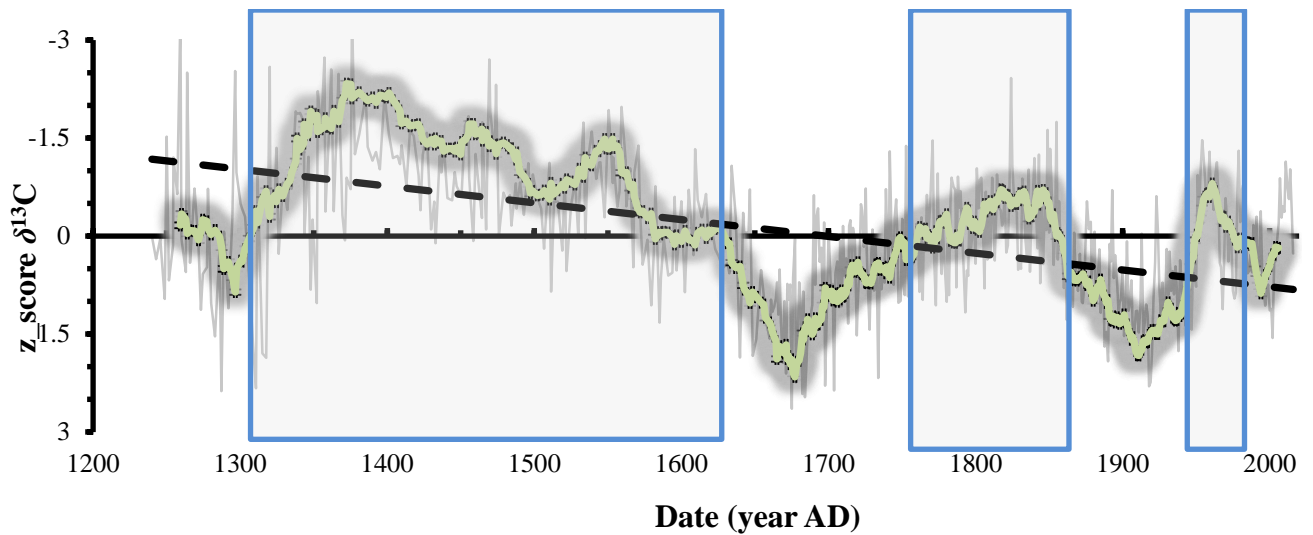


Figure 5.5: Quasi-annual to decadal variability of the rainfall at the southern site. Grey indicates the quasi-annualised record and green indicate the multi-decadal to centennial variability based on the 21-year biweight mean. Blue boxes mark wet periods while the dashed line indicates the decreasing trend identified in the area.

For both local sites, the record shows significant drying trends (Table 5.4). The northern site has been marked by the decrease in the duration of wet periods and more severe and prolonged dry periods. Overall, both regions have the same pattern of decreasing rainfall except around AD 1450 to 1673 where at first wet period has been recorded for the southern site while a dry period was recorded in the northern site until 1550 and then the pattern was inverted from AD 1550 to 1673.

Table 5.4: Trends analysis and rate of change in the carbon isotope record of baobab rings over time

Site/Statistic parameters	Mann-Kendall trend test			Regression analysis			
	Mann-Kendall Statistics (S)	Kendall's Tau	p-value (two tailed test)	Interpreted trends	Slope	t-value	Significance (p-value)
Northern site	-614,585	-0.61	<2.2e-16***	decreasing	0.0008	-146.82	< 2e-16 ***
Southern site	-792,091	-0.6	<2.22e-16***	decreasing	0.001	-132.61	< 2e-16 ***
Sub-regional southwest	-854,035	-0.65	<2.22e-16***	decreasing	0.0009	-174.753	<2e-16 ***

***highly significant

5.1.4.2.Southwest rainfall record

Quasi-annual to decadal variability of rainfall

The quasi-annual to decadal (21-year biweight mean) sub-regional record rainfall proxy shows high variability over the last 700 years (Figure 5.6). Variation at annual or decadal scales reflect that there were periods dominated by wet or dry years. Wet years dominate from AD 1300 until AD 1450 and dry years dominate from AD 1620 to 1750 and AD 1850 to 1960. The maximum records of wet and dry years have been identified within these periods such as the wet years around AD 1350 and the drought around AD 1700. There was also variability of rainfall at quasi-annual to decadal scales identified in the record. These periods from AD 1450 to 1620, AD 1750 to 1850, and AD 1960 to 2015 are marked with high fluctuations of rainfall from years to decades with no distinct trends and/or patterns. Since AD 1960 there has been a tendency of reduction of this fluctuation from quasi-annualised to a more decadal scale (Figure 5.6B).

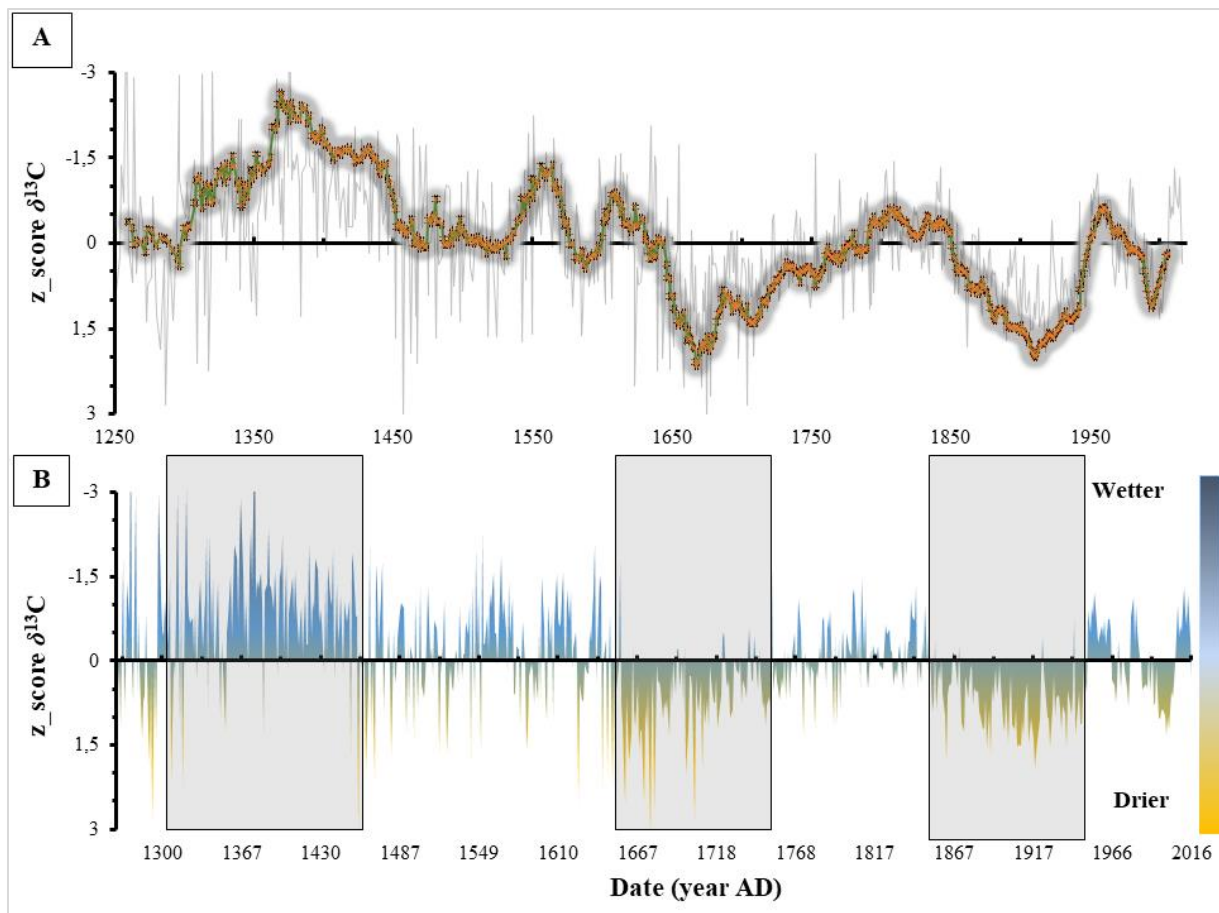


Figure 5.6: Regional rainfall record of southwestern Madagascar from $\delta^{13}\text{C}$ record of baobab trees standardised into z_score. (A) 21-year biweight mean (in orange) record with quasi-annualised record (grey). (B) Quasi-annual to decadal variability, grey box indicates wet/dry predominated periods with low fluctuations of rainfall within years to decade. Note the inverted Z-score scale which depicts high rainfall at the top of the plot, and low rainfall at the bottom of the plot

Multi-decadal to centennial variability of the rainfall in southwest Madagascar

The multi-decadal and centennial variation of rainfall is identified through the change in 21-year biweight mean over time. Based on all four records, there has been a significant decreasing trend of rainfall in southwest Madagascar in the past 700 years ($S=-854,035$, $p < 0.05$). Within this overall drying trend, three cycles of extended drier and abbreviated wetter periods were identified (Figure 5.7). The beginning of the record is marked by the wet period from AD 1300 to 1630. The wettest period was recorded for about 150 years around AD 1300 to 1450 and the extent of this wet period was not reached in any of the following wet phases (Figure 5.7). There is a difference of about 0.6‰ in the isotope value of the wet period from AD 1300 to 1450 and those recorded later in the record. This wet period is followed by a decrease in rainfall leading to the driest recorded period in the last 700 years indicated by the

change in the isotope record from -25.2 ‰ (AD 1300) to -24.2‰ (AD 1700). The duration of wet periods has reduced gradually from 330 years (AD 1300 to 1630) to about 60 years (AD 1790 to 1850) to 30 years (AD 1950 to 1980). Multi-decadal to centennial scale dry periods occurred from AD 1630 to 1790 for 120 years and AD 1850 to 1950 for about 100 years. From these results, there is a reduction in the length of wet periods over time, associated with a continuous decrease in rainfall (Table 5.4). The current period is within a dry period since AD 1980 but the isotopic record indicates a tendency towards a wet period since AD 2000.

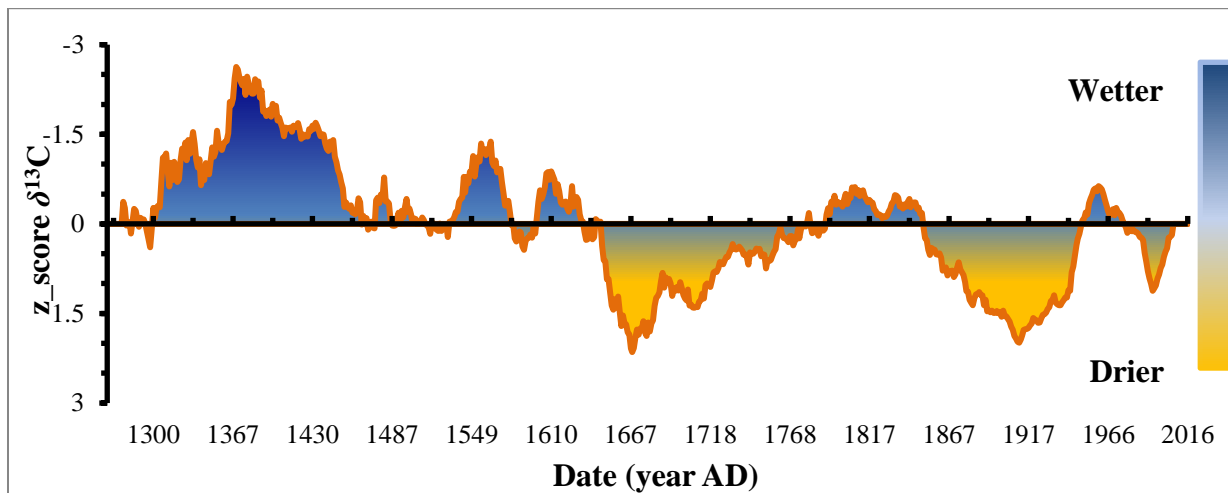


Figure 5.7: Multi-decadal to centennial variability of rainfall in southwest Madagascar over the last 700 years. The orange bold represent the multi-decadal variability, blue represent wet period and light orange represent dry periods.

5.1.5. Comparison of rainfall record available for the western region of Madagascar

The comparison between the sub-regional tree ring $\delta^{13}\text{C}$ record from the southwest (this study) and the speleothem $\delta^{18}\text{O}$ record from Anjohibe Cave in northwest Madagascar (Scroxtton *et al.*, 2017) shows a weak significant negative correlation $r = -0.18$, $p = 0.0005$ ($n=363$) for the last 700 years (Figure 5.8). Two distinct periods are identified in the record (Figure 5.8). Prior AD 1700, there is an inverse rainfall pattern with wet periods in the southwest corresponding to dry periods in the northwest ($r = -0.70$, $p < 0.005$). The wettest period recorded in the southwest around AD 1320 to 1450 corresponded to a dry period in the northwest and the driest period in the southwest around AD 1640 to 1690 corresponded to a wet period in the northwest. After about AD 1700, similar trends of rainfall are recorded for both regions ($r = 0.56$, $p < 0.005$). For example, the wet periods around AD 1800 to 1850 and around AD 1950 and the dry periods towards the end of AD 2000 coincide.

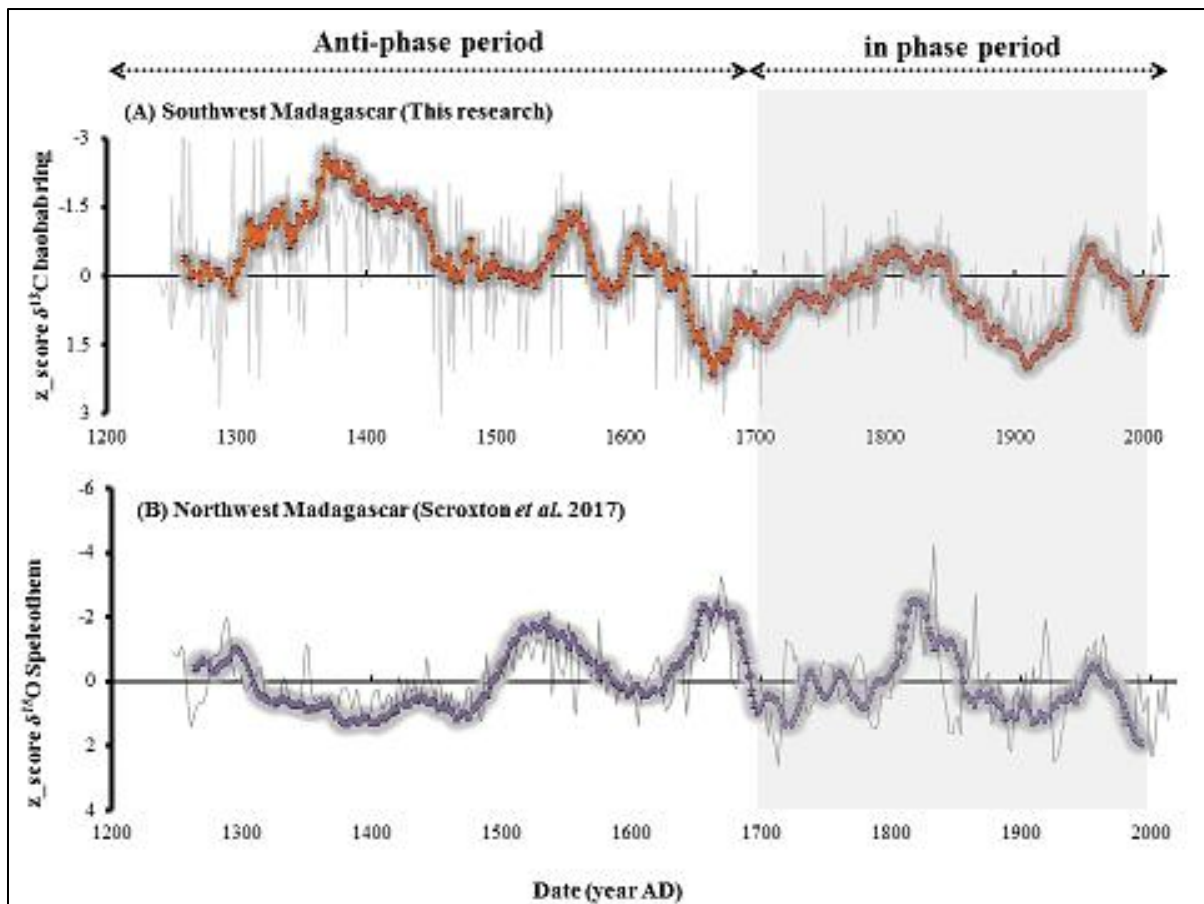


Figure 5.8: Comparison of isotope records from baobab rings with other published record in western Madagascar with all data transformed in z-score: (A) baobab $\delta^{13}\text{C}$ record from southwest Madagascar, this study. Grey indicates the quasi-annualised records; orange is the multi-decadal record. (B) Speleothem $\delta^{18}\text{O}$ record from Anjohibe Cave in northwest Madagascar (adapted from Scroxton *et al.*, 2017), grey indicates the quasi-annualised data; purple indicates the decadal and multi-decadal variability. Grey box indicates the in-phase period identified in the western region record.

5.1.6. Summary

The four trees investigated in this research provide an approximate 700-year of carbon isotope records which is confirmed to reflect rainfall variability at local (northern and southern site) and sub-regional (southwest) scale. Trees from the southern site seems to have been more impacted by climate variability as demonstrated through the high variance within the isotope record for the trees GTR and TSP. This could be related to the higher trends of decreasing rainfall recorded for the southern site compared to the northern site. Similarly, the southwest sub-regional record reveals a drying trend of rainfall in the last 700 years with a succession of dry and wet period. The period from AD 1300-1400 was the wettest in the record, followed by a decreasing but still wet period until AD 1600. Then the period from AD 1600-1800 represents the driest period, peaking around AD 1700. This was then followed by a relatively

wet period of about 50 years and another 100-year dry period. The last period from AD 1985-2000 was within a relatively wet period. The comparison of this record with the northwest oxygen isotope speleothem record shows that there were two period of change in the pattern of rainfall along the western region. The period from AD 1300-1700 demonstrated a rainfall dipole between the northwest and the southwest region. Since AD 1700 up to present, both regions show similarity in their rainfall patterns. Such information is valuable to infer the rainfall of the southwest corresponding to the length of the record in the northwest which is 1700 years. This would assist in interpreting change in the vegetation and its response to rainfall variability during the late Holocene.

5.2. Vegetation reconstruction and fire history at Lake Longiza and Lake Tsizavatsy in southwest Madagascar

Vegetation reconstruction of tropical dry forests in the northwest region revealed changes in the abundance of trees and opening of the ecosystem as reflected through the variation of pollen abundance and $\delta^{13}\text{C}$ values in the bulk organic component of the sediments in the last 2000 years (Matsumoto and Burney, 1994; Burns *et al.*, 2016; Voarintsoa *et al.*, 2017). Yet, it has been demonstrated that there is a difference in climate and human land-use across the western region where these vegetation types occur, which might have impacted the ecosystem differently (see Chapter 1: Introduction). In addition, no vegetation reconstruction is available for the tropical dry forests in the sub-arid region of southwest Madagascar (see Chapter 2: Literature review). The vegetation reconstruction of the tropical dry forests in southwest Madagascar is conducted in two lakes that are located respectively within the northern site at Lake Longiza and the southern site at Lake Tsizavatsy. This analysis responds to the second objective of this research which is to reconstruct and investigate past vegetation dynamics and fire regime around these two lakes through pollen, carbon isotope and charcoal analysis. This provides information on the vegetation change and fire regimes in the period covered by the cores and would be later used to interpret the drivers of these changes over time in relation to human and climate.

5.2.1. Lake Longiza, (LNG core) in the northern site

5.2.1.1. Longiza age model

The radiocarbon dates of the LNG core are shown in Table 5.5 and plotted in Figure 5.9. Nine dates were performed on the 96 cm sediment core, and calibration was done using the

Southern Hemisphere calibration curve "SHCal13.14C" (Hogg *et al.*, 2013) for older dates and post-bomb curve "postbomb_SH1-2.14C" for younger dates post 1950 (Hua *et al.*, 2013). The age model presents an age reversal at 96 cm and 80 cm which might be due to rootlet contamination in these sections. An age reversal also happened at 65 cm which presented the highest error. Dates associated with these depths were considered as outliers as also suggested by the results from rBacon. The uncalibrated basal date of this core at 92 cm depth is 2280 ± 30 BP years followed by two other pre-bomb radiocarbon dates at 70 cm, and 56 cm of 1160 ± 30 BP, 611 ± 32 BP. The calibrated ages of these dated are 327-208 cal years BC, 948-1017 cal years AD, and 1381-1426 cal years AD respectively. The postbomb dates at 39 cm, 30 cm and 25 cm are 105.36 ± 0.60 PMC, 121 ± 0.48 PMC and 113.60 ± 0.65 PMC and had the highest accumulation rate within the core. Sediment accumulation rates range from 0.18 mm. yr^{-1} for the oldest section of the core from 380 cal years BC until 985 cal years AD (380 BC – AD 985) to ca. 5 mm. yr^{-1} at the top of the core (Figure 5.9).

Table 5.5: Radiocarbon age of LNG core at the northern site in southwestern Madagascar with the uncalibrated and the calibrated calendar year (AD) and BP provided.

Depth (cm)	Sample code	Lab ID	Uncalibrated radiocarbon dates (Conventional dates – BP)	$\delta^{13}\text{C}$ (‰)	95% Calibrated radiocarbon dates (cal years BP)	Probabilit y (%)	95% calibrated calendar dates (cal years AD)	Probabi lity (%)
25-26	LNG_25	IT-C-1588	113.60±0.65PMC	-23.7	-	-	1951-1955	95
30-31	LNG_31	BETA_498 745	121.28±0.45PMC	-19.8	-	-	1951-1955	95
39-40	LNG_39	IT-C-1485	105.36±0.60PMC	-22.8	-	-	1951-1955	95
56-57	LNG_56	UBA_3567 0	611±32	-	524-569	95	1381 - 1426	54.6
65-67	LNG_65	IT-C-1586	1310±44	-21.3	1074-1275	94.4	675 - 876	95
70-71	LNG_70	BETA_498 746	1160±30	-18.9	933-1002 - 956	95.4	948-1017	56.4
80-81	LNG_80	BETA_498 747	610±30	-20.3	521-570	95	1380 - 1429	55.2
91-92	LNG_91	BETA_435 567	2280±30	-21.9	2158-2277	60.2	Cal BC327 – 208	67.5
94-96	LNG_94	IT-C-1587	900±33	-25.9	685-804-	95	Cal AD 1146 - 1265	84

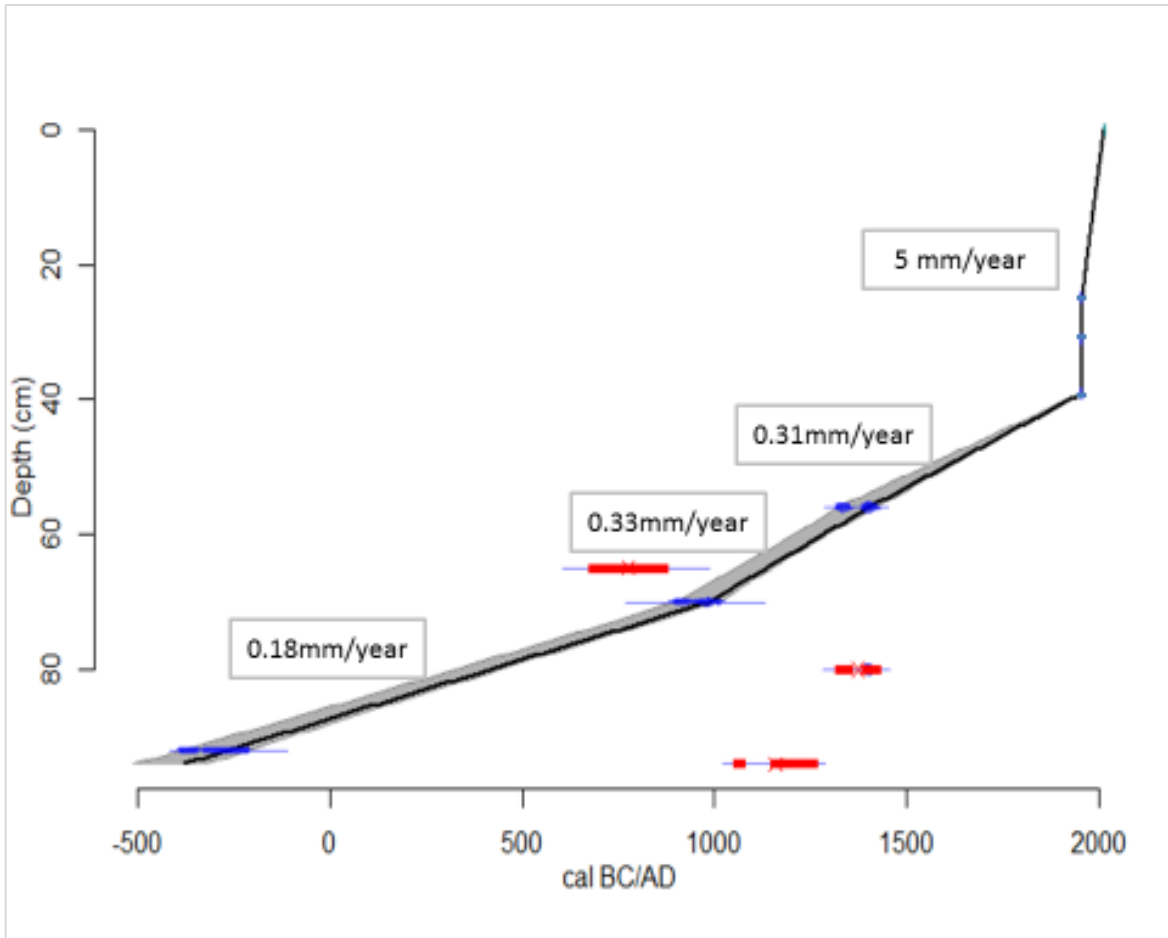


Figure 5.9: Age model for the LNG core from the northern site of southwestern Madagascar with outliers in red. Grey shading indicates an interval of confidence at 95% with the associated accumulation rate for each section.

5.2.1.2. Longiza sediment description

The description of the lithology of the core LNG from Lake Longiza in the northern site is based on a modified version of Troels-Smith (1955). Five (5) stratigraphic units are observed along this core of 96 cm depth named LNG_strat-1 to 5 from the bottom to the top (Figure 5.10). These units have similar colours with varying shades of grey along the core and contained various components with different proportions of clay, sand and plant fragments (Table 5.6). The entire core has an abundance of clay or *As* (*Argilla steatodes*) with grain sizes <0.002 mm (Table 5.6). LNG_strat-1 had the highest proportion (50%) of fine sand *Ga* (*Grana arenosa*) while 25% of the main part of LNG_strat-2 was composed of coarse sand or *Gs* (*Grana minima*). Apparent plant and animal material classified in coarse roots of herbaceous origin > 5 mm or *Th* (*Turfa herbacea*), *Dh* (*Detritus herbosus*) plant or animal fragments > 2mm, *Dl* (*Detritus lignosus*) plant or animal fragments > 2mm, are present in the unit LNG_strat-3 and LNG_strat-4. These plant materials were in the form of charcoal fragments in the unit LNG_strat-4. LNG_strat-5 is quite different from the entire core due to

traces of ferruginous iron oxide particles, *Lf* (*Limus ferrugineus*), <. 0.1 mm found at the upper level of the core which made up 25% of the samples.

Higher inorganic carbon (TIC) than organic carbon (TOC) content is recorded in core LNG which reaches as maximum as respectively 14% and 10%. Both TOC and TIC displays similar trends along the depth of the core (Figure 5.10). The maximum carbon content in the sediment is recorded in LNG_strat-2 (from 80-50 cm) after which it decreases significantly from 7% and 10% to 4% and 7% in LNG_strat-3 respectively for TOC and TIC. The carbon content of the sediment then increases to 5% and 7% (for TOC and TIC) at the beginning of LNG_strat-4 around 32 cm and stabilises until the top of the core at LNG_strat-5.

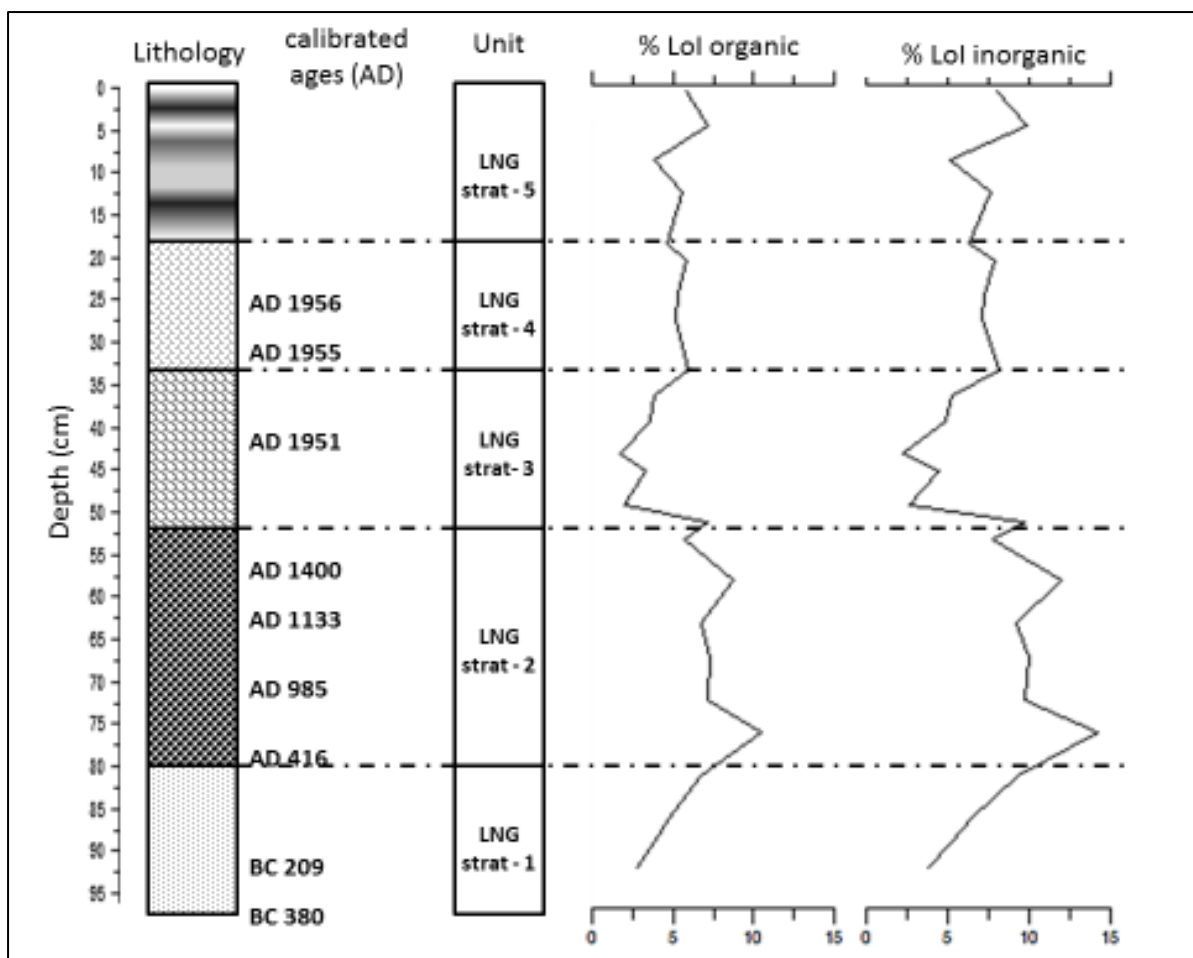


Figure 5.10: Lithology, calibrated ages and description of LNG core from the northern site of the study area in southwest Madagascar. Loss on Ignition (LoI) indicates the organic and inorganic content of the core.

Table 5.6: Troels-Smith description of LNG core from the northern site in southwestern Madagascar

Depth (cm)	Unit	Troels-Smith	Description	Munsel code	Color
16-0	LNG_strat-5	As3 Lf1 Th ⁺	Clayey and ferruginous deposit	10YR 4/2	Dark greyish brown
32-17	LNG_strat-4	As2 Dh1 Th1	Clayey samples with detritious and some discernible plants rootscomponents	2.5Y 4/1	Dark grey
50-33	LNG_strat-3	As2 D11 Th1	Clayey with some detritious of herbaceous and ligneous. Traces of charcoal	2.5Y 3/2	Very dark greyish brown
76 – 51	LNG_strat-2	As3 Gs1	Clayey and occasional coarse sand	2.5Y 4/2	Dark greyish brown
96 – 77	LNG_strat-1	As1Ga2Gs1	Fine sand and clayey deposits with occasional occurrence of coarse sand.	2.5Y 4/1	Dark grey

5.2.1.3. Longiza pollen analysis

Pollen zones identified through cluster analysis

Using stratigraphically constrained cluster analysis with Euclidean distance (Grimm, 1987), three statistically significant clusters are identified in the pollen assemblage of the LNG core (Figure 5.11). These clusters represent zones with major shift in vegetation structure based on the ecological association and abundance of the taxa recorded in the sediment. Temporal boundaries of each zone have been assigned to the midpoint date between the terminal samples of each zone. Each zone LNG_1, LNG_2, and LNG_3 corresponds to periods 450 BC-AD 1250, AD 1250-1985, and AD 1985-2010 respectively.

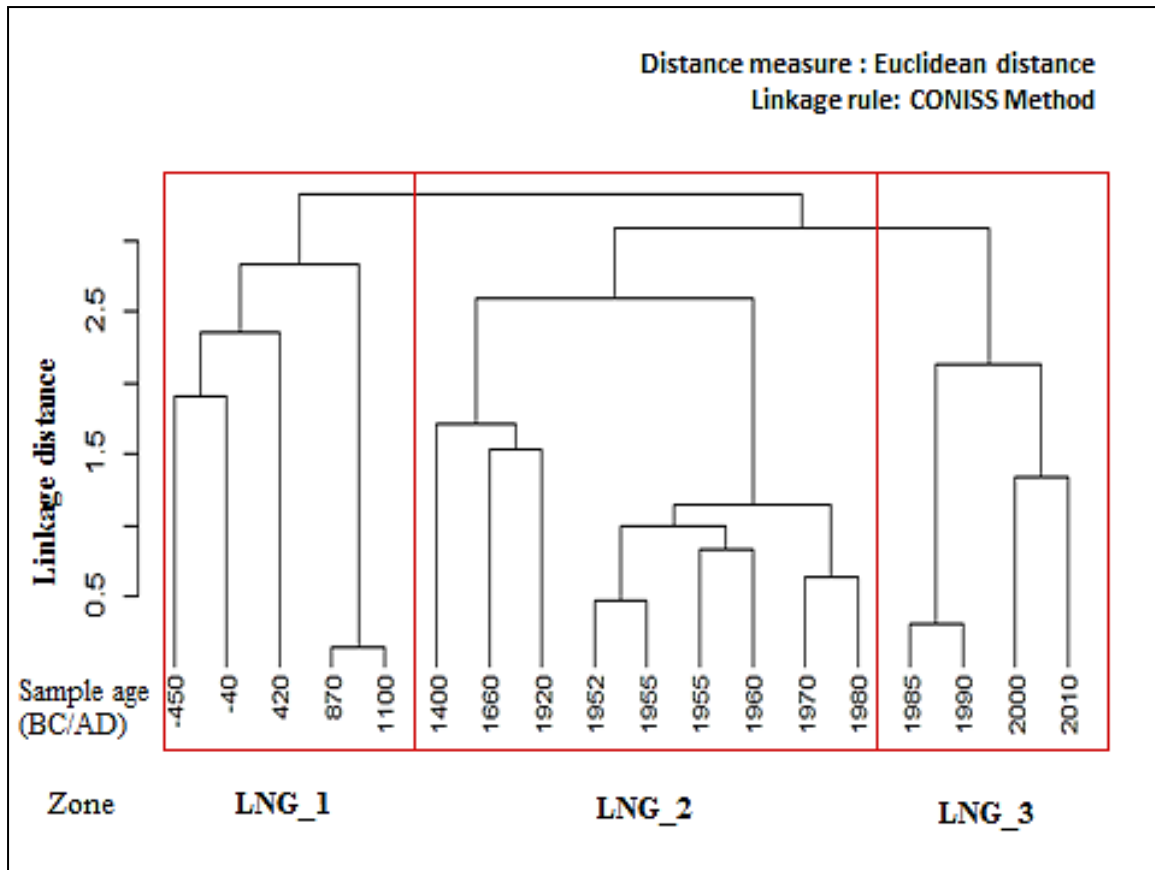


Figure 5.11: Hierarchical clusters of the LNG core from the northern site with red box delimiting statistically significant pollen zones

➤ **Longiza pollen diagram**

The pollen assemblage zones indicate major shifts in the vegetation over the last 2400 years. A pollen diagram of terrestrial taxa with higher abundance than 2% is shown in Figure 5.12 and the detailed pollen diagram of all taxa from the LNG core is given in Appendix 2.1.

LNG_1: BC 450 to AD 1250: Dry forest with mosaic of *Podocarpus* (Podocarpaceae)-Myrtaceae riparian forest

This period is marked by the abundance of taxa associated with dry forest such as *Acacia* (Fabaceae), with a mean relative abundance of $3.8 \pm 2.4\%$ and reaching its highest value around AD 870 (7%). The *Arecaceae* family also reaches its maximum abundance (17%) at this time. Other trees such as *Gnidia* (Thymelaeaceae), *Ficus* (Moraceae), *Trema* (Ulmaceae), were abundant with a mean frequency higher than 2% of the total pollen sum (TPS). The xerophytic component of the dry forest such as *Acalypha*, *Phyllanthus* and *Securinega* remained low during this period (on average less than 1%) except around 450 BC and AD 420 where their total abundance exceeded 2%. This period was also marked by the abundance of riverine trees such as *Podocarpus* reaching its maximum proportion (10%) at

450 BC and Myrtaceae with a mean of $3.9 \pm 1.1\%$. Of the herbaceous group, Poaceae covered $48 \pm 6.4\%$ of the TPS with a peak around AD 410 where its abundance reached 59.6%. All the other taxa remained relatively low during this period except Urticaceae type with a relative abundance of $2.6 \pm 1.2\%$. This period is then characterised by a dry forest with mosaic of *Podocarpus*- Myrtaceae riparian forest

LNG_2: AD 1250 to 1985: Open ecosystem with mosaic of dry forest and *Pandanus* (Pandaceae) riparian forest

This period was marked by a decrease in dry forest taxa such as Fabaceae, and riverine forest such as *Podocarpus* and Myrtaceae, and an increase in Poaceae. Some dry forest taxa such as *Arecaceae*, *Gnidia*, *Trema*, *Celtis*, and *Acacia* remained abundant during this period with a mean frequency higher than 2% despite a decrease in proportions compared to the previous period. Decreases in *Podocarpus* ($1.3 \pm 1.4\%$) and Myrtaceae ($2.7 \pm 1.1\%$) were recorded for the riverine taxa in contrast with *Pandanus* which reached its maximum around AD 1950 (7.1%). All the riverine taxa had higher proportions at the beginning of this period around AD 1250 but decreased over time until AD 1985. Similarly, in the herbaceous group, taxa such as *Acanthaceae*, *Menispermaceae* and *Urticaceae* had high relative abundance at the beginning but decreased over time. Poaceae, however, increased over time during this period from 51% around AD 1400 to 67% around AD 1985 with a mean abundance of $58.1 \pm 7.8\%$.

LNG_3: AD 1985 to 2010: Mosaic of xerophytic-degraded dry forest/ Myrtaceae riparian forest

This period is characterized by an increase in dry forest taxa especially those associated with an adaptation to drought (also called xerophytic taxa) as well as the herbaceous taxa. Xerophytics were abundant with a mean abundance of 3.2% in this period. Taxa such as *Securinega*, *Acalypha*, and *Phyllanthus* reach their maximum during this period (respectively 2%, 2.3%, and 2.7%) around AD 1985 and AD 2000. Some taxa that characterise the dry forest such as Fabaceae showed an increasing rate of $2.8 \pm 1.5\%$ and reached their maximum at the present time (AD 2010) (4.4%). In addition, other trees such as *Moraceae* ($2.2 \pm 1.3\%$) including *Ficus* ($2 \pm 1.6\%$), and *Celtis* ($2.5 \pm 0.7\%$) had higher relative abundance during this period. However, some other trees showed a decrease in proportions compared to the previous period. This is the case for *Gnidia* type (from $2.6 \pm 2.2\%$ to $1.8 \pm 1.3\%$) as well as *Arecaceae* from $6.5 \pm 2.5\%$ to $4.8 \pm 2.4\%$ at the present period (AD 2010). Riverine taxa such as Myrtaceae (3.1%) increase in abundance during this period while *Podocarpus* and *Pandanus* became traces. For the herbaceous group, Poaceae decreased to $52.4 \pm 8\%$ in

comparison with the previous period ($58.1 \pm 7.8\%$) but taxa such as Asteraceae cf. *Ambrosia* type became abundant with a mean of $3.8 \pm 3.2\%$ and peaking at the surface sample representing the present period (8.8%). This also applies to Menispermaceae type which increased and reaches its maximum in this zone ($2.2 \pm 1.7\%$).

➤ **Longiza pollen rarefaction, detrended pollen richness and compositional turnover**

Pollen rarefaction and detrended pollen richness shows the variation of pollen diversity within LNG core over time, associated with compositional turnover (beta diversity) of the area (Figure 5.12). The maximum pollen richness of 33 pollen types was recorded around AD 1920 and the minimum value at the present period around 2010 with 23 pollen types. The mean value through the entire core is 28 ± 2 pollen types. Three maximum turnovers of taxa around Lake Longiza were recorded in each zone associated with a reduction of pollen richness. The first zone showed the maximum change in the composition for the entire period recorded around AD 870 with a value of 2.63 SD which marked the decrease in richness from 31 pollen types to 24 pollen types. During this period, taxa such as *Acalypha*, *Gnidia*, *Phyllanthus*, *Securinega*, and Fabaceae became scarce. A short recovery of the richness is recorded around AD 1100 after which another turnover of 2.30 SD is recorded around AD 1400 in the second zone. The last zone LNG_3 is marked by decreasing pollen richness and is reflected in the compositional turnover of 1.83 SD around AD 1985. By the end of this zone (the near present period), several taxa in the dry forest tree group such as *Dichrostachys*, *Trema*, *Securinega*, Arecaceae and, Malvaceae, became present only in trace quantities. All taxa from the riverine trees group also decreased significantly or became scarce.

➤ **Longiza sediment $\delta^{13}\text{C}$**

The analysis of the $\delta^{13}\text{C}$ isotope values in the LNG core collected in the northern site had a mean value of $-22 \pm 1.7\text{‰}$ in the last 2400 years. The minimum value of about -25.4‰ is recorded around AD 2000 while the maximum value is recorded around AD 870 with -19.3‰ . The first zone LNG_1 from 450 BC to AD 1250 had a mean value of $-21.6 \pm 1.6\text{‰}$ with a more negative value (approximately -22‰) until around AD 410 (-20.7‰). Then there was a sudden short change around AD 980 (-24‰) followed by a more positive value of about -19‰ until the end of this period. The second zone from AD 1250 to 1985 (LNG_2) had a similar mean value ($-21.4 \pm 1.2\text{‰}$) over time but was more positive (~ -19 to -20‰) until AD 1920 where there is a gradual decrease of the isotope value to -21 to -23‰ . The near present period in zone LNG_3 from AD 1985 to 2010 was marked by a decrease in the

isotope value (mean $-24.5 \pm 1.1\text{‰}$) reaching the lowest value during the period covered by the core (-25.4‰) (Figure 5.12).

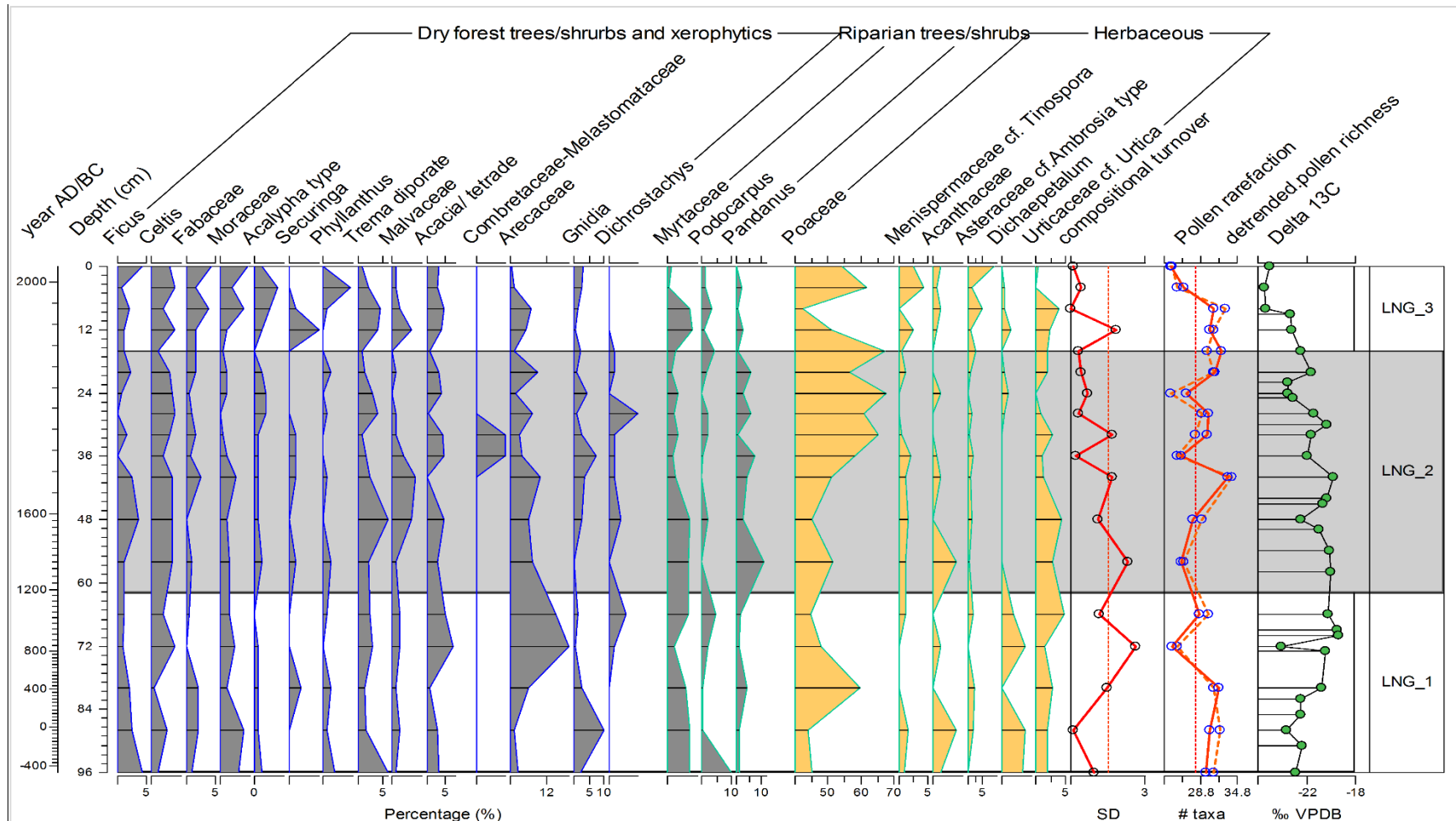


Figure 5.12: Pollen diagram of pollen taxa with proportions higher than 2% grouped with their associated ecosystem and physiognomy. Dry forest trees and shrubs are shown in grey and xerophytic taxa of the dry forest in light brown. Riparian trees and shrubs are indicated in blue while herbaceous taxa are in orange. Measure of diversity such as DCA axis 1 indicating compositional turnover and pollen richness evaluated through rarefaction analysis and detrended pollen richness are represented by red lines. The associated $\delta^{13}\text{C}$ content of the sediments is shown in green marker. The secondary y-axis representing the age of the core is not linear due to different sediment accumulation rate of the sediment.

➤ Variation of aquatic taxa at Lake Longiza in the last 2400 years

Pollen of aquatic plants was counted separately from terrestrial total pollen sum, but its proportion was calculated based on the total pollen sum (TPS). An increase in the abundance of aquatic taxa relative to terrestrial is recorded in the LNG core over the last 2400 years reaching 48% of proportion from TPS at the upper zone of the core (Figure 5.13). The recorded aquatic taxa were mainly *Typha* (Typhaceae) and Cyperaceae with some invasive/weed taxa (i.e. introduced/non-native taxa) such as the case of Pontederiaceae, *Ludwigia* (Onagraceae) and *Polygonium*. The period from 450 BC to AD 1250 (LNG_1) was marked by a generally low abundance of aquatic plants with a mean abundance of $8.7 \pm 4.4\%$ and maximum proportions of 15%. Cyperaceae (6.9 ± 4.1) contributed mostly to this proportion of aquatics which peaks around AD 420 of 13.6%. All the other aquatic taxa remained relatively low during this period. Aquatics increased to $10.4 \pm 3.6\%$ in LNG_2 from AD 1250 to 1985 despite the decrease and variable rate of Cyperaceae ($6.3 \pm 2.6\%$). This increasing abundance of aquatic plants was marked by the emerging presence and increase in *Typha* which recorded its highest value 11.2% around AD 1660. This period was also marked by the first appearance of Pontederiaceae in the record. The next period LNG_3 (AD 1985-2010) was marked by an increasing and highest value of aquatics recorded during the period covered by the LNG core ($29.3 \pm 19.6\%$). This high rate is associated with a massive increase in *Typha* surrounding the wetland reaching its highest value of 46% at AD 2000. The appearance of other aquatic taxa such as *Polygonium*, Onagraceae type (cf. *Ludwigia*) is recorded during this period. Cyperaceae, on the other hand, remained relatively low ($4.2 \pm 2.1\%$).

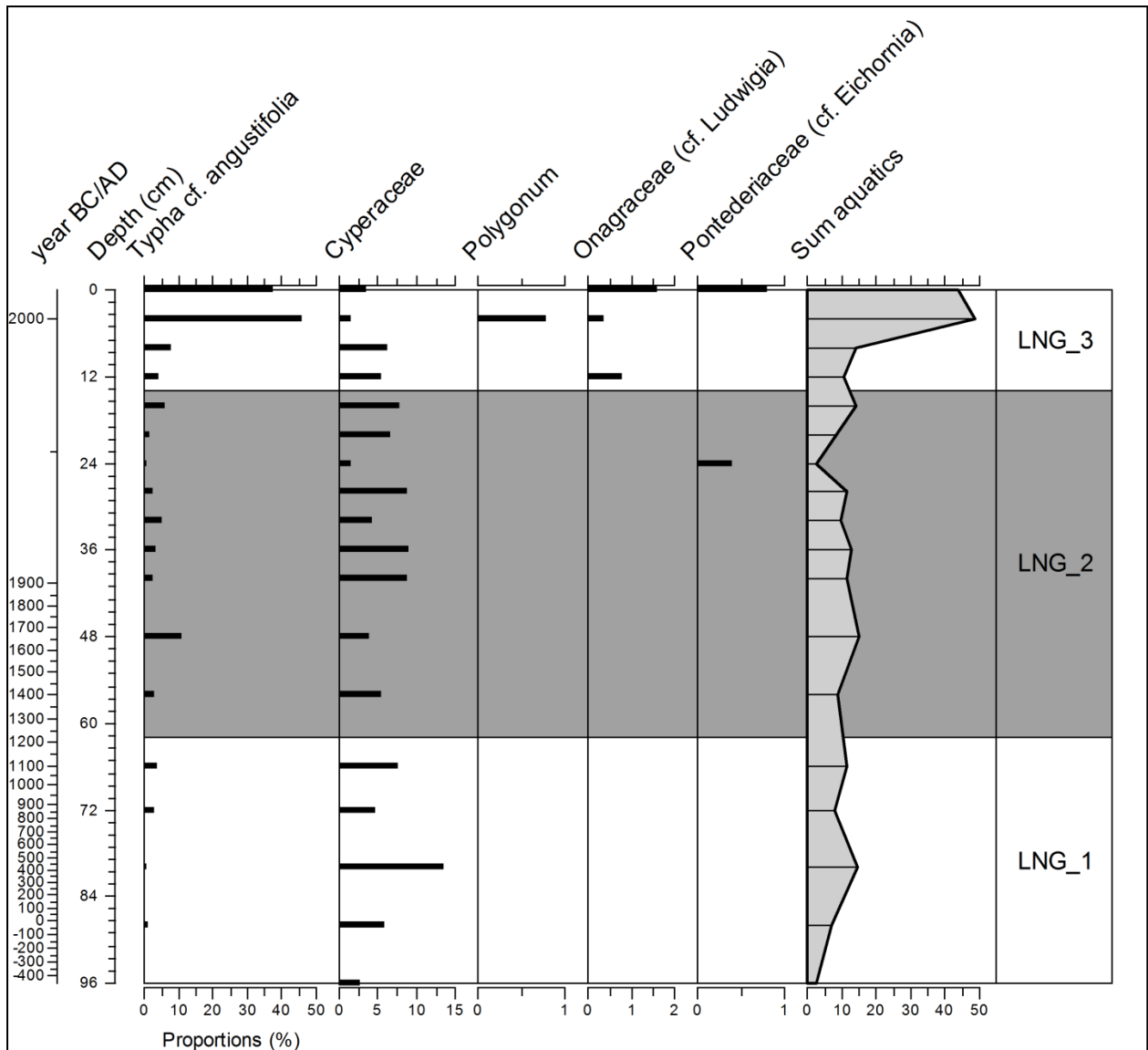


Figure 5.13: Proportions of the aquatic taxa recorded in the LNG core from the northern site in southwestern Madagascar over the last 2400 years. The secondary y-axis representing the age of the core is not linear due to different sediment accumulation rate of the sediment.

5.2.1.4. Fire history at Lake Longiza in the northern site in the last 2400 years

A total of 13,911.9 cm² of microcharcoal and 2752 particles of macrocharcoal with a mean of 632.3 ± 563.2 cm².cm⁻³ and 119.6 ± 111.5 particles.cm⁻³ respectively were counted. The highest value of microcharcoal is recorded around AD 1960 of approximately 1910.8 cm².cm⁻³ and the lowest was recorded at 450 BC with 22.5 cm².cm⁻³. In contrast, the highest value of macrocharcoal was recorded around AD 1600 with 364 particles.cm⁻³ and the lowest around AD 1400 of 8 particles.cm⁻³. The abundance of macrocharcoal and microcharcoal is not correlated ($r=0.2$, $p = 0.36$) indicating that charcoal breakdown was minimal during pretreatment process and they originated from different sources. This supports the assumption

that their influx would infer as sub-regional and local fire respectively (Carcaillet *et al.*, 2001; Gillson, 2002).

Charcoal concentration and charcoal accumulation for the core LNG are shown in Figure 5.14. LNG_1 from 450 BC to AD 1250 had very low charcoal influx with less than 2 particles. yr⁻¹ of macrocharcoal and a mean of 3.2±2.1 cm².yr⁻¹ of microcharcoal. LNG_2 from AD 1250 to 1985 is marked by an increase in charcoal influx and abundance. At the beginning of LNG_2, there were consecutive very small peaks of influx of 10.7 cm².yr⁻¹ and 1.6 particles. yr⁻¹ around AD 1400 and AD 1600 respectively for microcharcoal and macrocharcoal. This was followed by two large peaks of charcoal around AD 1950 and AD 1955 that happened simultaneously for microcharcoal and macrocharcoal. The last period from AD 1985 to 2010 (LNG_3) presented the highest charcoal around the lake with a mean of 251.6±145.7 cm².yr⁻¹ for microcharcoal and 39.2±30 particles. yr⁻¹ for macrocharcoal.

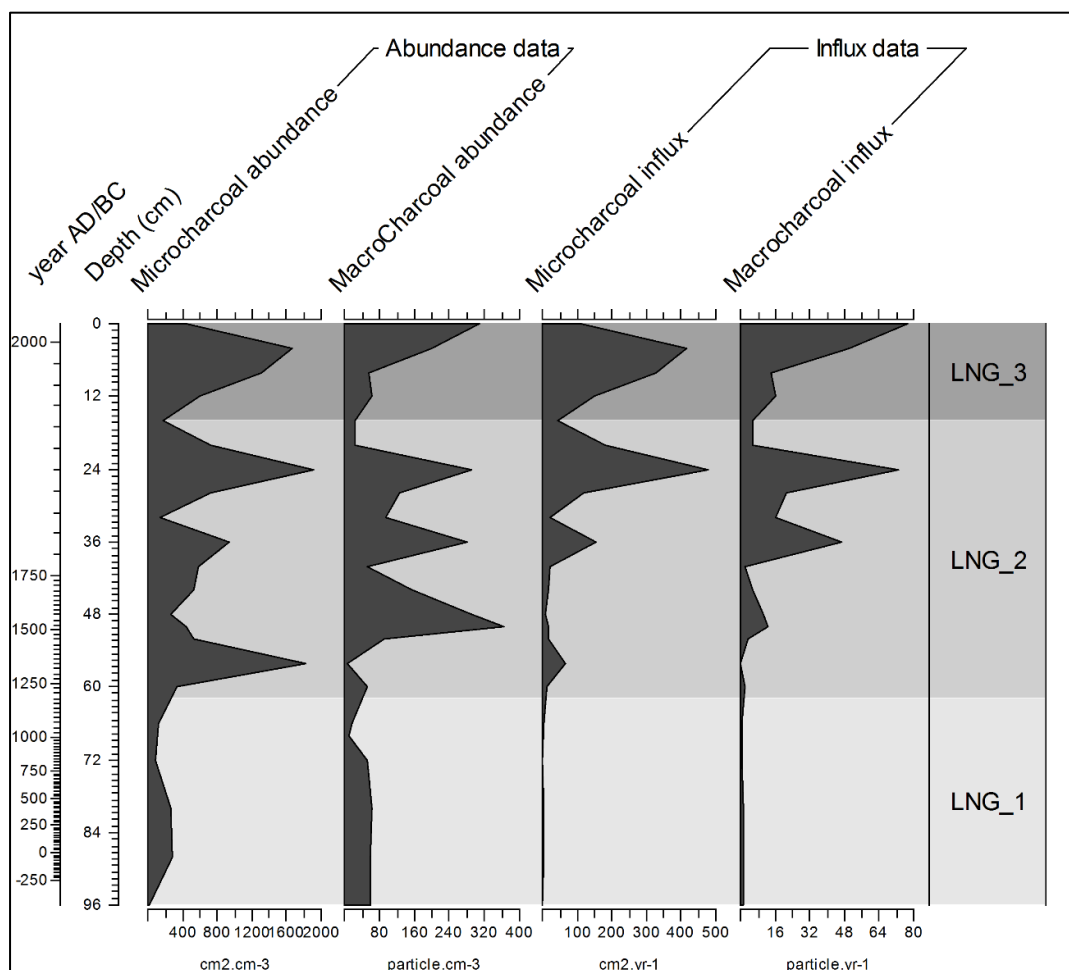


Figure 5.14: Diagram of the charcoal recorded in the LNG core from the northern site in southwestern Madagascar including the concentration of microcharcoal and macrocharcoal and influx data. The secondary y-axis representing the age of the core is not linear due to different sediment accumulation rate of the sediment.

5.2.1.5. Longiza multidimensional representation and regression analysis of pollen and charcoal data

The two-dimensional representation of taxa with abundance >5% shows no distinct partitioning of taxa over the last 2400 years (Figure 5.15). There is however distinction of taxa associated negatively or positively with microcharcoal and macrocharcoal regression line within the NMDS model. Taxa such as *Gnidia*, Asteraceae and Poaceae are located at the negative value of NMDS1 with microcharcoal and macrocharcoal as opposed to taxa such as *Podocarpus*, *Acacia*, and Malvaceae which are positively associated.

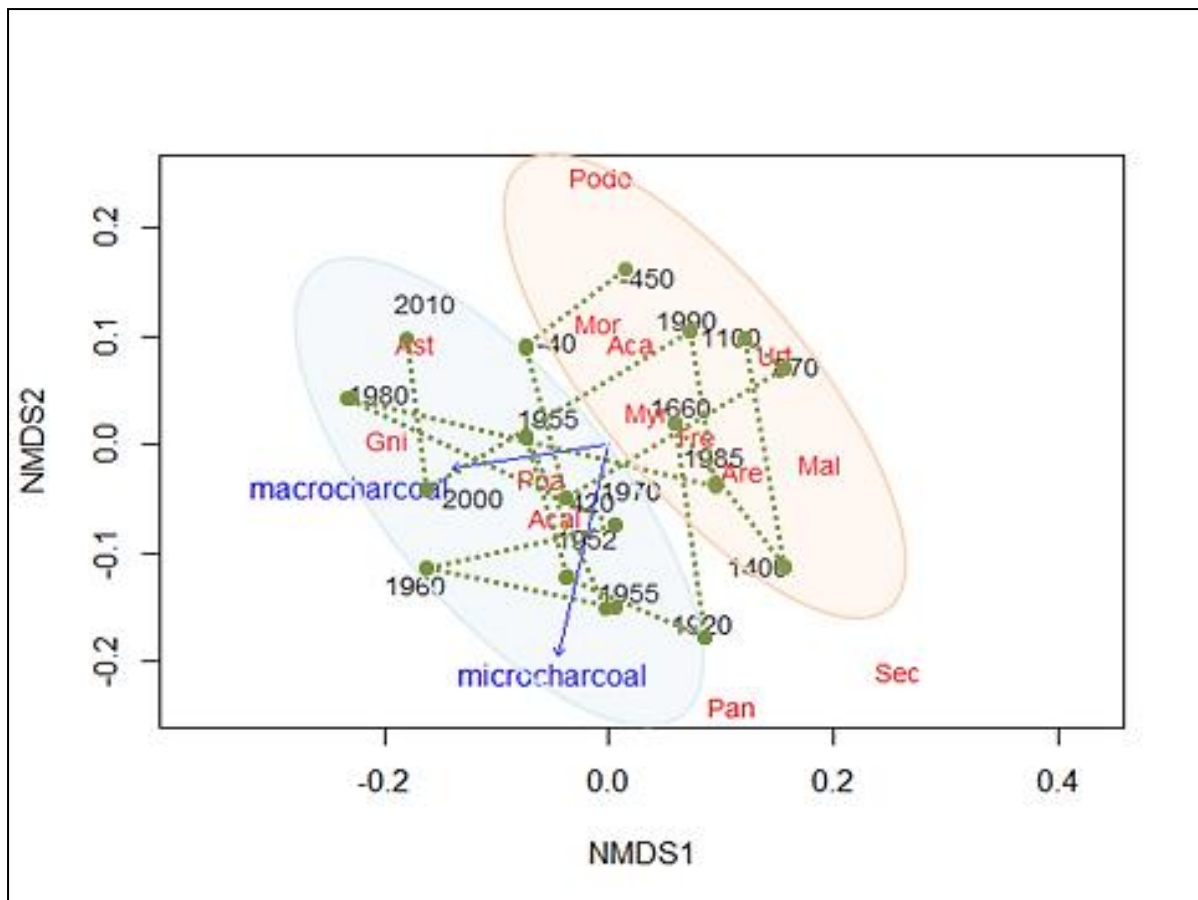


Figure 5.15: Two-dimensional representation of taxa with relative abundance higher than 5% of total pollen sum. Blue arrows indicate the regression of macrocharcoal and microcharcoal influx. Red text represents taxa, Podo: *Podocarpus*, Mor: Moraceae, Aca: *Acacia*, Myr: Myrtaceae, Tre: *Trema*, Are: *Arecaceae*, Mal: Malvaceae, Urt: Urticaceae, Pan: *Pandanus*, Ast: Asteraceae, Gni: *Gnidia*, Poa: Poaceae, Aca1: *Acalypha*, and Sec: *Securinega*. Pink oval marks tree taxa while blue oval indicate herbaceous/ pioneer taxa

Pollen rarefaction, relative abundance of dry forest taxa separately for xerophytic taxa and riverine taxa, are plotted as a function of charcoal influx in Figure 5.16. Taxa richness of the LNG core showed a non-linear response to fire, with taxa richness decreasing when charcoal influx is above 30 particles. yr⁻¹ and 660 cm².yr⁻¹ respectively for macrocharcoal and

microcharcoal. In addition, very low variation in taxa richness is explained by microcharcoal influx increase. The dry forest components (trees and shrubs and xerophytics) demonstrate different responses to fire increase. With increasing macrocharcoal influx, there is a decrease in dry forest trees and shrubs until the value of about 100 particles. yr⁻¹ is recorded after which the abundance of these trees starts to increase especially fire-adapted taxa such as *Gnidia*. In contrast, for xerophytic taxa, there was an increase in these taxa until a value of 100 particle. yr⁻¹ after which their abundance decreases. The dry forest taxa (xerophytic, trees and shrubs) remained stable until very high charcoal influx at about 660 cm².yr⁻¹ is recorded, then their abundance decreases. Riparian taxa however, decreased with an increase in charcoal over time, especially when charcoal influx reaches ca. 100 particles. yr⁻¹ and 660 cm².yr⁻¹ for macrocharcoal and microcharcoal respectively.

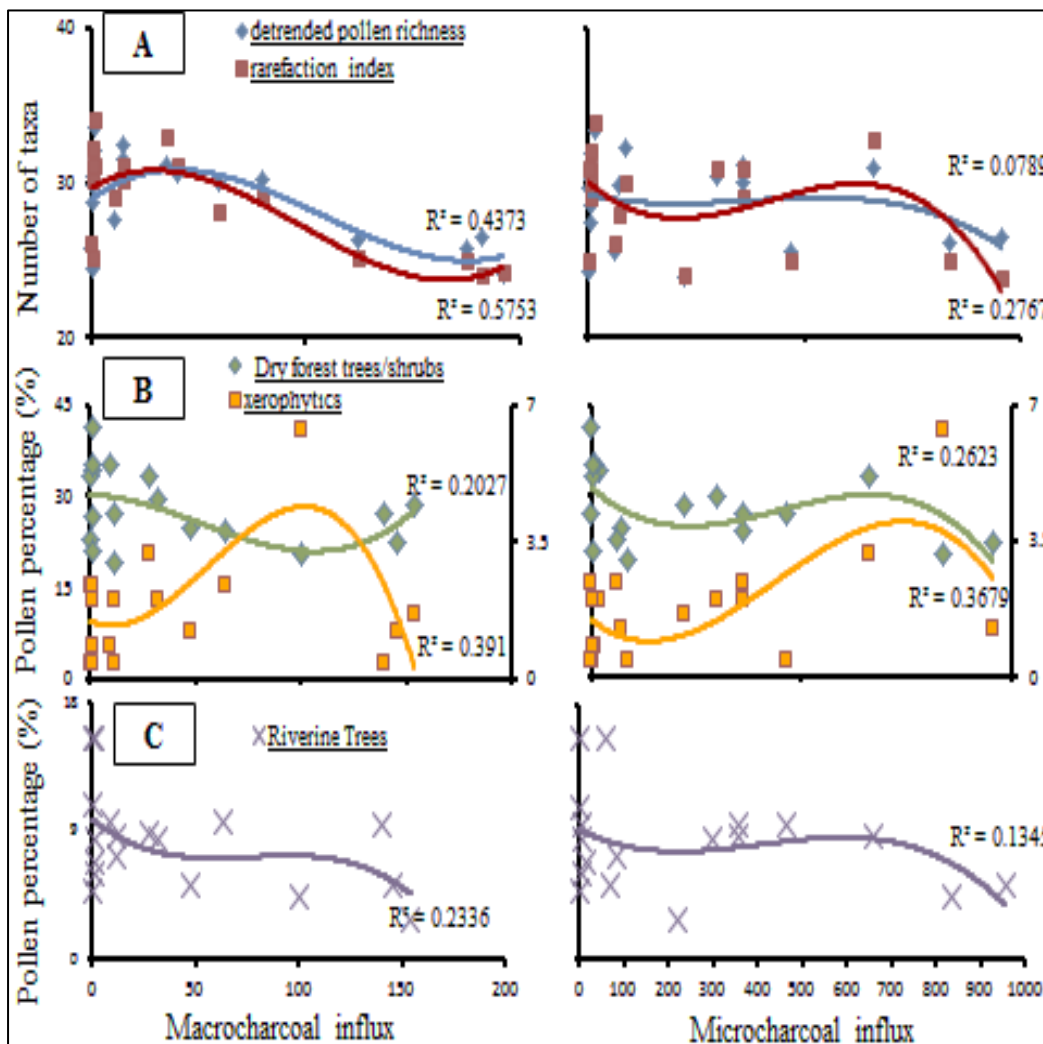


Figure 5.16: Response of taxa richness and pollen assemblage (y-axis) from the LNG core in the northern site to charcoal influx (x-axis). The influx of macrocharcoal is expressed in particles. yr⁻¹ and microcharcoal in cm².yr⁻¹. (A) Measure of diversity through pollen rarefaction and detrended pollen richness that include pollen evenness. (B) Abundance of dry

forest vegetation including xerophytic and all other trees and shrubs. (C) Abundance of riverine trees.

5.2.1.6. Longiza summary of pollen, isotope and charcoal data

The results of the 96 cm clay-rich core from Longiza Lake suggested changes in the vegetation and fire history around the wetland over the last 2400 years. The count of aquatic plant pollen suggested the presence of aquatic ecosystem components over time. Despite the decreasing concentration of pollen throughout the depth of the core, the relative abundance of the pollen count suggested the continuous presence of taxa associated with dry forest and riparian forest along three main zones identified from the pollen assemblage (Figure 5.17).

Around 2400 years ago (450 BC) to AD 1250, dry forest with a mosaic of *Podocarpus*-Myrtaceae riparian forest were identified. This was shown by a dominance of dry forest trees, a moderate rate of riverine trees and herbaceous taxa, and a variable $\delta^{13}\text{C}$ value of the sediment. A more negative $\delta^{13}\text{C}$ value is recorded at the beginning of the zone but became more positive with the increase in grass taxa around AD 420 and a short recovery of forest around AD 870. This short recovery coincides with a compositional turnover of about 2.63 SD after which overall taxa richness decreased. All of these changes occurred during a period with very low charcoal. The period from AD 1250 to AD 1985 showed a decrease in dry forest, riverine and herbaceous taxa over time in contrast to grass taxa. Similarly, charcoal was low at the beginning of this period but started to peak around AD 1400 for microcharcoal and AD 1600 for macrocharcoal and simultaneously since AD 1920. During this period there was an enrichment of $\delta^{13}\text{C}$ at the beginning but became depleted from AD 1950 towards the end around AD 1985. This period presented species poor vegetation except around AD 1922 and from AD 1955 up to the upper limit of the zone.

The third zone from AD 1985 to 2010 can be described as a mosaic of degraded dry forest xerophytics and marshland dominated with dry adapted, grass, herbaceous taxa, and aquatic taxa around the lake. A slight increase in dry forest taxa compared to the previous period was recorded which is mostly associated with the high rate of its xerophytic trees. In addition, there is an increase in herbaceous taxa especially pioneer taxa, such as Asteraceae. Aquatic taxa were abundant during this period which coincides with a gradual depletion in $\delta^{13}\text{C}$ value of the sediment. Taxa richness was high at the beginning but decreased gradually since the turnover around AD 1985. Similarly, charcoal records were low at the beginning but increased and peaked at the present period. The analysis of the relationship between charcoal records (macrocharcoal and microcharcoal) showed that the community showed a non-linear

response until a very high charcoal influx leading to an increase in fire-adapted taxa in the dry forest ecosystem, decrease in the abundance of riparian ecosystem and the richness of the overall community.

Overall, the mosaic vegetation recorded around Lake Longiza was dynamic in the last 2400 years becoming more open, degraded and drier over time. A significant increase in grass around AD 1920 coincided with the onset of increased microcharcoal and macrocharcoal indicating increased fire at local and regional scales. In the last 20 years, however, the vegetation has become species poor and is mostly dominated by xerophytic and ruderal taxa. Moreover, the establishment of marshland is recorded around the lake with a high abundance of aquatic taxa especially *Typha* at the near present period.

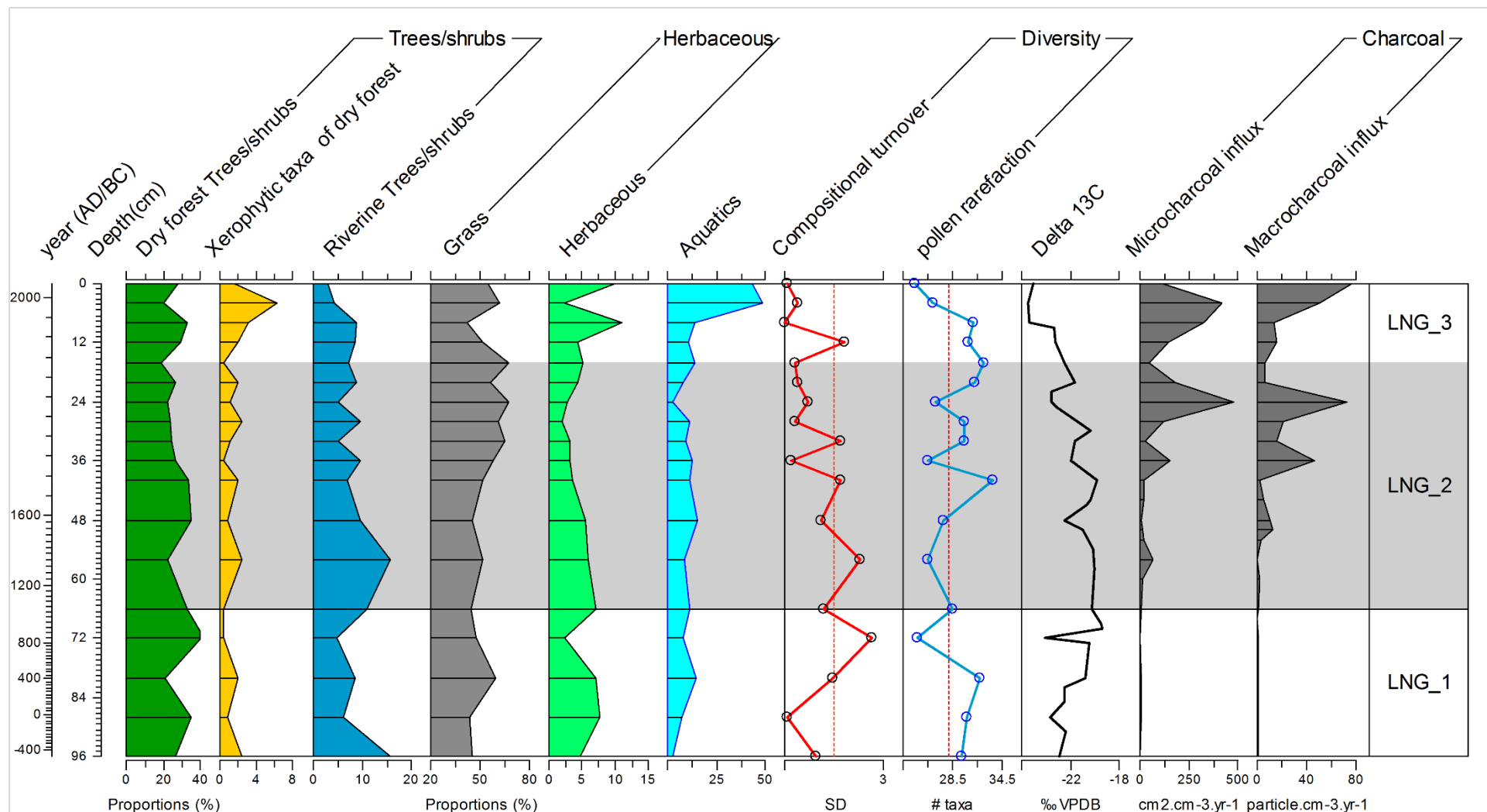


Figure 5.17: Summary diagram of the sediment core from Lake Longiza in the northern site with the major physiognomy and ecosystems identified in the pollen record. DCA axis 1 and pollen rarefaction (pollen richness and evenness) indicate the change of diversity over time. The secondary y-axis representing the age of the core is not linear due to different sediment accumulation rate of the sediment.

5.2.2. Lake Tsizavatsy (TSZ core) in the southern site

5.2.2.1. Tsizavatsy age model

Four radiocarbon dates were run on this core to establish the age depth model shown in Figure 5.18. The basal date at 43 cm depth yield an uncalibrated age of 640 ± 30 BP followed by three other dates respectively at 35 cm, 29 cm and 24 cm. The dates associated with these depths are 680 ± 40 BP, 640 ± 62 BP and 106 ± 28 BP respectively. The details of calibration and probability associated with these dates are provided in Table 5.7. The linear interpolation of the calibrated dates was based on best probability density for the upper section of the core while maximum intercepts were assigned for the lower section of the core. The age model suggested the presence of a hiatus at about 24 cm dividing the core in two parts with a 500-year gap. The section of the core from 0 to 24 cm represented the period from AD 2010 to 1910 and the section from 25 to 47 cm represented the period from AD 1420 to 1300. Each of these sections had a sediment accumulation rates of 2.5 mm. yr^{-1} at the top section of the core and 2 mm. yr^{-1} for the bottom section from 25 cm to 47 cm.

Table 5.7: Radiocarbon age of the TSZ core from the southern site with the uncalibrated and the calibrated calendar year (AD) and BP provided.

Depth (cm)	Sample code	Lab ID	Uncalibrated radiocarbon dates (years BP)	$\delta^{13}\text{C}$ (‰)	95% Calibrated radiocarbon (Cal years BP)	Probability (%)	95% calibrated calendar (Cal years AD)	Probability (%)
24-25	TSZ 24	QUB	106 ± 28			95	1804-1935	67.4
29-30	TSZ 29	IT-C-1739	640 ± 62	-19.8	572-544	68.3	1378-1406	68.3
35-36	TSZ 35	IT-C-1608	680 ± 40	-20.0	661-554	94.5	1289- 1396	94.5
43-44	TSZ 43	BET A	640 ± 30	-18.2	649-585	94.4	1301--1365	94.4

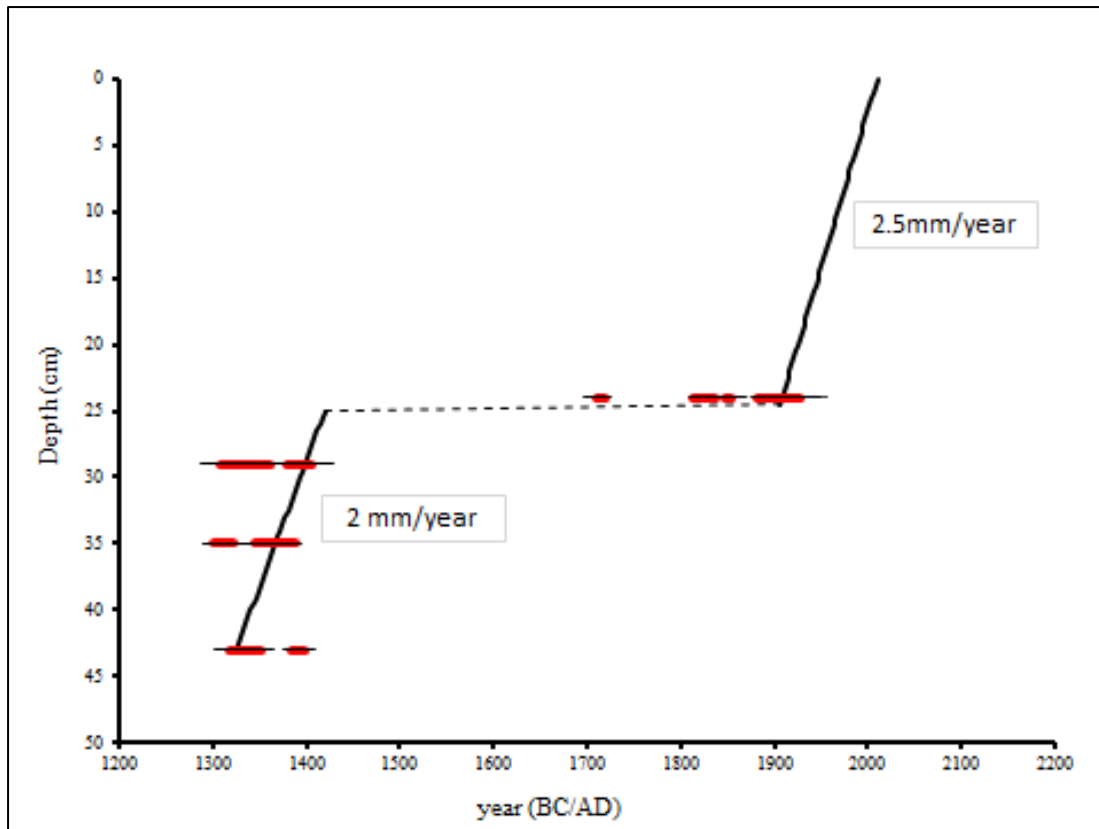


Figure 5.18: Age depth model of TSZ core from the southern site. Red horizontal lines indicate the 1-sigma calibration intervals for the radiocarbon dates done at the depth indicated in the y-axis. Dotted lines indicate the 500-year hiatus period from AD 1420 to 1910.

5.2.2.2. Tsizavatsy sediment description

The 47 cm core from a small Lake Tsizavatsy (TSZ core) in the southern site is subdivided into three (3) stratigraphic units denoted as TSZ_strat 1 to TSZ_strat 3, each differing in composition, texture, and colour (Table 5.8, Figure 5.19). The core is composed of clay *As* (*Argilla steatodes*), fine sand or *Ga* (*Grana arenosa*), coarse sand or *Ge* (*Grana minora*) and organic lake mud or *Ld* (*Limus detrituosus*). From unit TSZ-1 to unit TSZ-3, there is a reduction of the size of the grana components from coarse sand to complete clay sediment. No apparent organic materials are visible for this sediment. The colour of the sediments remains dark along the depth with a variation of grey and brown.

The temporal trends of organic and inorganic carbon (TOC and TIC respectively) recorded in this core is similar. Higher inorganic carbon with a mean of 6% against 4% for organic carbon is recorded along the core (Figure 5.19). TSZ_strat 1 contains the lowest carbon content, but from 26 cm (4% and 5.4% respectively for TOC and TIC), it increases gradually until the top of the core at TSZ_strat 3 (5% and 7% respectively for TOC and TIC).

Table 5.8: Troels-Smith description of TSZ core from the southern site in southwestern Madagascar

Depth (cm)	Unit	Troels-Smith	Description	Munsell color code	Color
16-0	TSZ_strat 3	As3 Ld1	Clayey and not very humified deposits	2.5Y 3//1 or 5Y 3//1	Very dark grey
28-17	TSZ_strat 2	As2 Ga1 Ld1	Clayey and fine sand deposits, few organic materials	10YR 4//4	dark yellowish brown
47-29	TSZ_strat 1	As2 Ge1 Ld1	Clayey and coarse sand deposits, low humicity	5Y 3//2	Dark olive gray

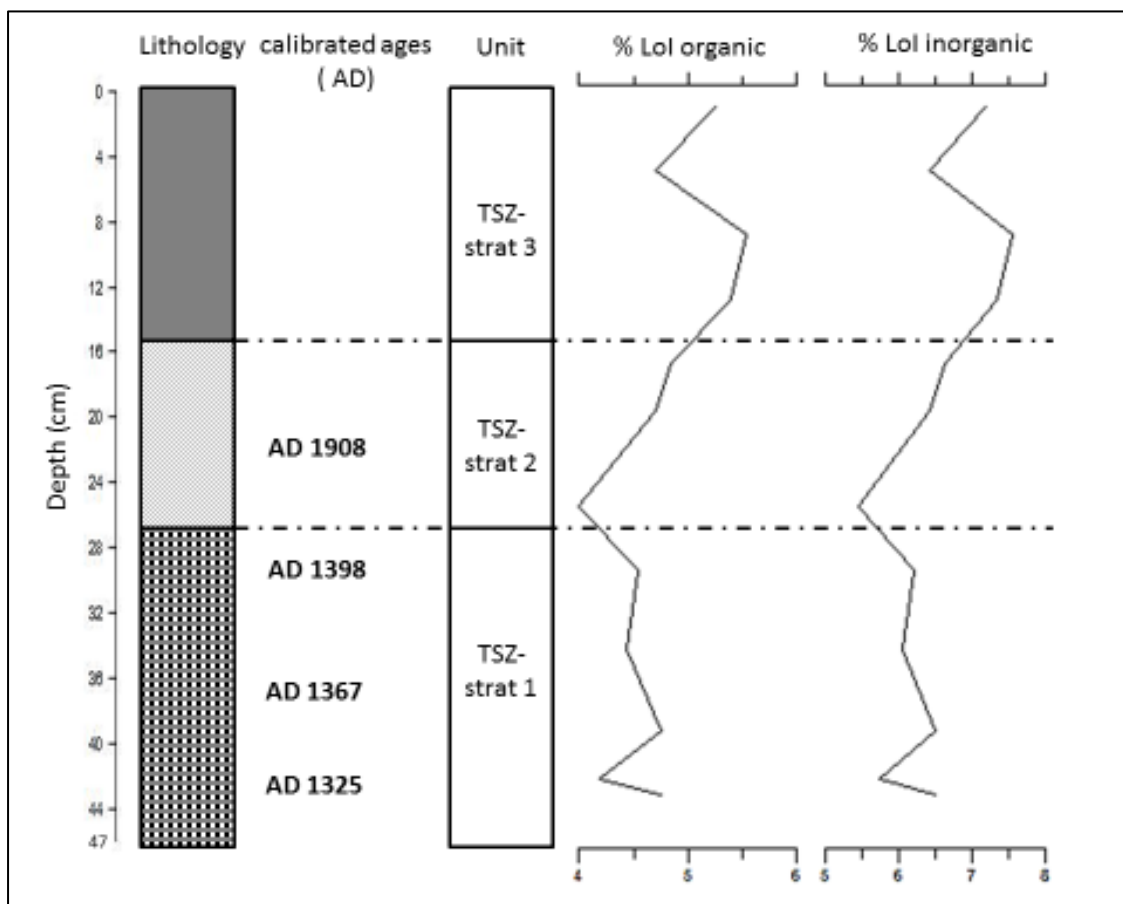


Figure 5.19: Lithology, calibrated ages and description of TSZ core from the southern site. Loss on Ignition of the sediment shows the organic and inorganic carbon content of the core.

5.2.2.3. Tsizavatsy pollen analysis of terrestrial and aquatic plants

The vegetation dynamics of the pollen record in the TSZ core from the southern site was described prior to and after the hiatus from AD 1420 to 1910. The first period (TSZ_1) covered samples from AD 1300 to 1420. The second period includes samples from AD 1910 to 2010. Figure 5.20 shows the pollen diagram of taxa with relative abundance higher than 2% as well as aquatic taxa which were not part of the TPS. The changes in abundance in the physiognomy of the identified taxa provide information about the dynamics of the wooded savanna around Lake Tsizavatsy in the southern site.

TSZ_1 from AD 1300 to 1420: Palm-*Pandanus* wooded savanna

This period is characterised as Palm-*Pandanus* wooded savanna, marked by a high abundance of Poaceae and Arecaceae as well as tree taxa such as *Acacia* and *Pandanus*. The abundance of Poaceae during this period reached a mean of $60.2 \pm 4.4\%$ of the TPS. This was associated with high relative abundance of Arecaceae $4.9 \pm 2\%$ and *Acacia* $2.5 \pm 1.6\%$ relative abundance. *Pandanus* reached a maximum of 5.1% around AD 1330 but decreased in relative abundance until around AD 1420. Other tree taxa such as *Celtis*, *Gnidia*, and *Trema* were abundant during this period with a mean value of $2.5 \pm 3.1\%$, $2.4 \pm 1\%$, and $3.6 \pm 1.5\%$ respectively. Some taxa were relatively abundant at the beginning of this period but decreased over time. This was the case for Asteraceae, with abundance of about 2.4% around AD 1300 but decreased over time until the top of this period (0%). All other herbaceous (Urticaceae and Amaranthaceae type 1) and arboreal (Phyllanthaceae, Myrtaceae, Malvaceae and Moraceae) taxa were present in traces during this period. The mean abundance of aquatic taxa was approximately 10% during this period and was mostly composed of Cyperaceae.

TSZ_2 from AD 1910 to 2010: Palm-xerophytic degraded wooded savanna

This period is marked by a highly variable abundance of grass pollen with a minimum value of 45% at AD 1940 and a maximum value of 71% at the top of the record around AD 2000. The mean value of grass over time is $58.1 \pm 10\%$. The dominant herbaceous taxa were Asteraceae (mean $3.5 \pm 3.5\%$) which reaches its highest value around AD 2010 (9.6%). All other herbaceous taxa such as Amaranthaceae type 2 and Apocynaceae remained relatively low during this period. Despite the high abundance of Arecaceae in the period mentioned above, there was an increase in its relative abundance from AD 1910 to 2010 (mean $7.3 \pm 5.3\%$) but with variation over time. The minimum value of Arecaceae was recorded around AD 2000 (1.6%) while the maximum value is recorded at AD 1940 (11.6%). Some

taxa such *Celtis* and *Gnidia* (mean $2.6 \pm 0.8\%$) also increased in abundance during this period with a mean value of $3.4 \pm 3.2\%$. Some other trees, considered as dry adapted taxa such as *Securinega* (mean $2.4 \pm 1.8\%$), peak during this period with a maximum value recorded at AD 1990 (4.4%). *Acacia* which was previously abundant, decreased in abundance to the current period from 2.5% to 1.5%. *Trema* was also recorded in trace amounts during this period. The abundance of aquatic taxa during this period remained similar to those recorded from AD 1300 to 1200 (10%) but with an increase in the abundance of *Myriophyllum* and *Colocasia* and a reduction in the abundance of Cyperaceae.

➤ **Tsizavatsy pollen rarefaction, detrended pollen richness and compositional turnover**

During the two periods covered by the core from AD 1300 to 1420 and AD 1910 to 2010, the most important compositional change was recorded around AD 1360 (2.65 SD) and around AD 1920 (2.6 SD) as well as at the near present time around AD 2000 (1.98 SD). These periods of compositional turnovers were not reflected in the taxa richness except around AD 1920 where the moderate richness became very low (Figure 5.20). During the first period from AD 1300 to 1420, taxa such as *Pandanus* and *Acacia* were abundant at the beginning but decrease throughout the period. After the turnover around AD 1920 in the second period, taxa such as Asteraceae, *Gnidia* and *Securinega* dominated and the taxa richness remains stable until the near present period around AD 2010.

➤ **Tsizavatsy sediment $\delta^{13}\text{C}$**

The carbon stable isotope value ($\delta^{13}\text{C}$) recorded in the TSZ core in the southern site decreased over time (Figure 5.20). The $\delta^{13}\text{C}$ at TSZ recorded a mean value of $-19.3 \pm 1.3\text{‰}$ with a range of 4.2‰. The minimum value -22.1‰ is recorded at the top of the core (AD 2010) while the maximum value of -17.9‰ is recorded around AD 1420. During the two different periods of vegetation change, TSZ_1 is marked by more positive isotope values around the lake with a mean isotope value of $-18.3 \pm 0.4\text{‰}$. From AD 1910 to 2010 in TSZ_2, there was a decrease in the isotope value with a mean of $-20.2 \pm 1.2\text{‰}$.

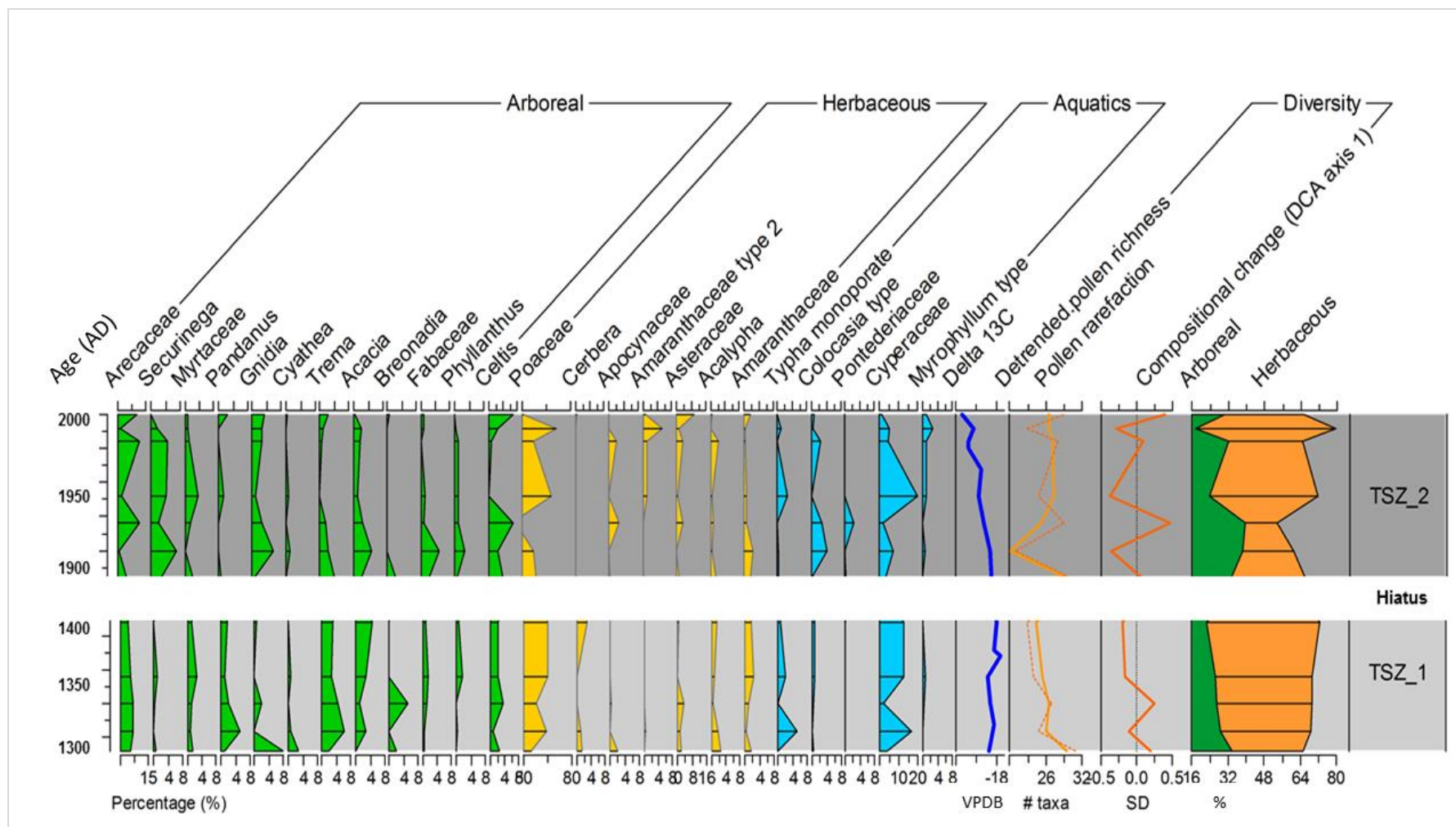


Figure 5.20: Diagram representing the relative abundance of terrestrial taxa higher than 2% and total abundance of arboreal (green), herbaceous (yellow) and the associated $\delta^{13}\text{C}$ (blue line) of the TSZ core from the southern site. The abundance of aquatic taxa which was not included in the total pollen sum is represented in blue. Diversity represented by pollen rarefaction and detrended pollen richness and DCA axis 1 for the compositional turnover are shown in yellow and orange lines.

5.2.2.4. Fire history at Lake Tszavatsy in the southern site (AD 1300-1420 and AD 1910-2010)

The analysis of microcharcoal and macrocharcoal from the southern site at Lake Tszavatsy allowed reconstruction of fire history of the area for two time periods including from AD 1300 to 1420 and from AD 1910 to 2010. For macrocharcoal, a total abundance of 1228 particles.cm⁻³ was recorded with the lowest value recorded at AD 1420 with 28 particles.cm⁻³. Macrocharcoal abundance remained relatively low during the first period AD 1300 to 1420. For the microcharcoal, total abundance of charcoal recorded for this site is 3719 cm².cm⁻³ and lowest charcoal abundance was recorded at the bottom of the core AD 1300 for microcharcoal with the value of approximately 51 cm².cm⁻³. Correlation between microcharcoal and macrocharcoal abundance were not significant ($r=0.02$, $p=0.92$). There was no variation in the pattern of charcoal abundance and influx during these periods due to relatively similar accumulation rates of sediments. Therefore, only the influx diagram is represented in Figure 5.21.

Between the two periods identified from the age model, the influx of charcoal differs. TSZ_1 corresponded with the period from AD 1300 to AD 1420 is marked by a very dynamic fire regime. The lowest charcoal abundance was recorded at AD 1300 after which the charcoal influx increased and reached the highest recorded fire at AD 1360 of about 107.7 cm².yr⁻¹ of microcharcoal though macrocharcoal remained relatively low (16.8 particles. yr⁻¹). Low charcoal influx was recorded at the end of the period around AD 1380 to 1420 reaching as low as 33.47 cm².yr⁻¹ for microcharcoal and 8 particles. yr⁻¹ for macrocharcoal. The second period TSZ_2 covered the period from AD 1910 to AD 2010 (up to present time) had more stable charcoal influx with a mean of 52.2±16 cm².yr⁻¹ and 26.8 ±2.2 particles. yr⁻¹ for microcharcoal and macrocharcoal respectively. During this period, macrocharcoal is high while microcharcoal remains relatively low compared to the previous period.

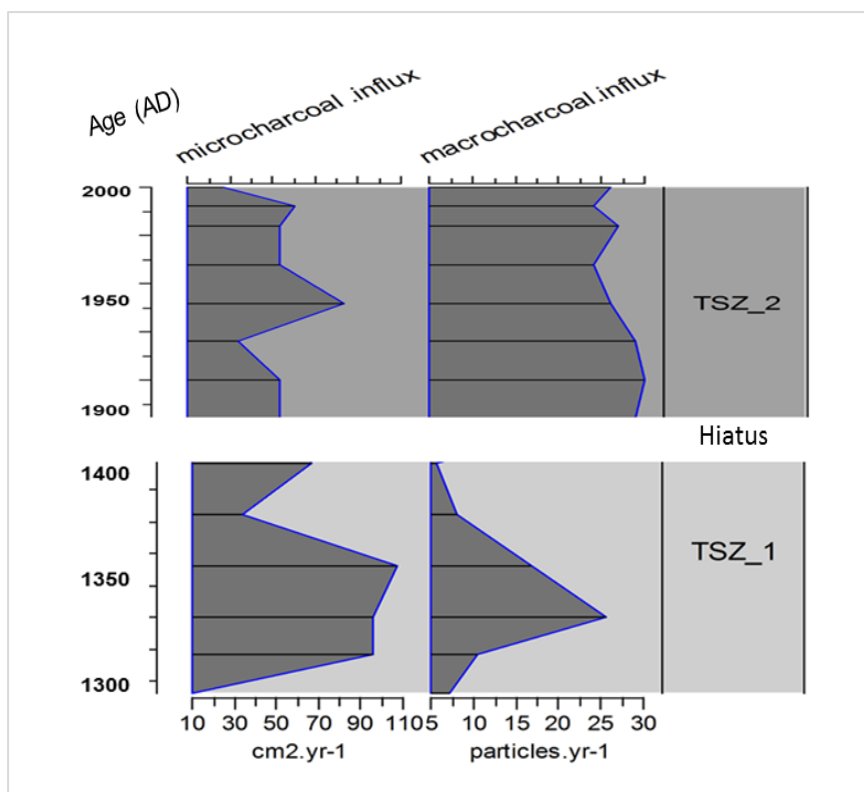


Figure 5.21: Microcharcoal influx ($\text{cm}^{-2}.\text{yr}^{-1}$) and macrocharcoal influx ($\text{particles}.\text{yr}^{-1}$) of the core TSZ from the southern site following the two periods prior and after the hiatus.

5.2.2.5. Tsizavatsy Multidimensional representation and regression analysis of pollen and charcoal data in the southern site

The two-dimensional representation of abundant taxa (>5%) and charcoal influx were obtained with a stress value of 0.11. It shows that there is temporal partitioning of the pollen and charcoal influx separating the two periods prior to and after the hiatus as shown in the Figure 5.22. The period from AD 1300 to 1420 is correlated with the influx of microcharcoal influx while the period from AD 1910 to 2010 is associated with the influx of macrocharcoal.

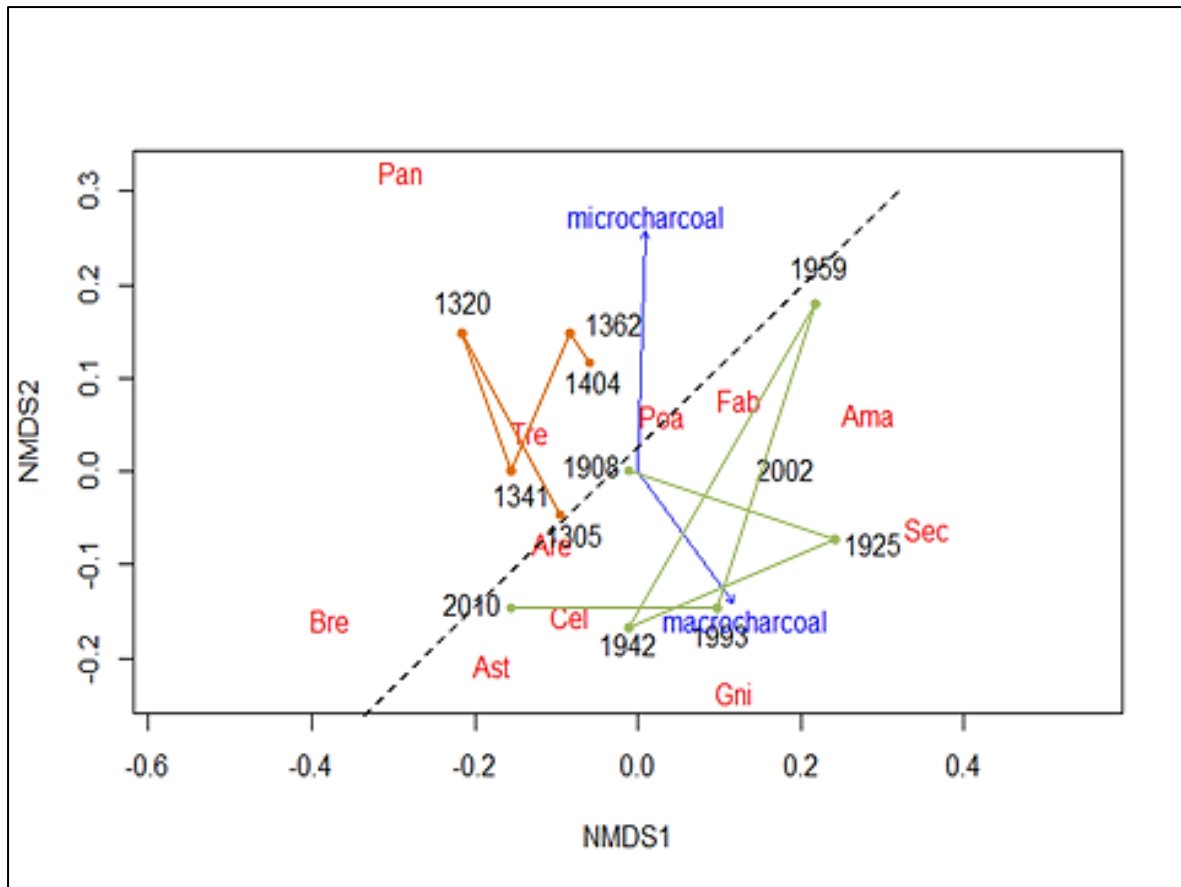


Figure 5.22: Two-dimensional representation of pollen with relative abundance higher than 5% and charcoal influx of the TSZ core in the southern site during the two periods covered by the core. The two periods are grouped separately within the NMDS axis. The period from AD 1300 to 1420 is indicated in orange while the period from AD 1910 to 2010 is shown in green. Red labels indicate taxa: Pan: *Pandanus*, Bre: *Breonadia*; Tre: *Trema*, Poa: Poaceae, Are: Arecaceae, Ast: Asteraceae, Cel: *Celtis*, Fab: Fabaceae, Ama: Amaranthaceae, Sec: *Securinega*, Gni: *Gnidia*.

5.2.2.6. Tsizavatsy Summary of pollen, isotope and charcoal data

The 47 cm clay-rich sediment core TSZ from the southern site presented three stratigraphic units and was dated to about 700 years. The age model revealed the presence of a hiatus around 24-25 cm corresponding to a period from AD 1420 to 1910. Two sections of the core; TSZ_1, from the period AD 1300-1420 and TSZ_2, from AD 1910-2010, were used to describe the vegetation change as summarised in Figure 5.23. The first period from AD 1300 to 1420 is marked by an abundance of grass and trees associated with low xerophytic taxa coinciding with a more positive $\delta^{13}\text{C}$ ($-18.3 \pm 0.4\%$) value in the sediment. This period is marked by one compositional change around AD 1360 leading to a slight increase in taxa richness and was associated in the two multidimensional NMDS representation by influx of microcharcoal. The second period from AD 1910 to 2010 is marked by a continuous decrease in $\delta^{13}\text{C}$ ($-20.2 \pm 1.2\%$) which coincides with the gradual increase in the abundance of

xerophytic taxa, herbaceous taxa, and tree taxa at the top of the core despite the high abundance of Poaceae. The most important turnover during this period occurred from AD 1910 to 1940 marked by an increase in the abundance of pioneer and xerophytic taxa. The abundance of taxa during this period was associated with the multidimensional analysis to macrocharcoal influx.

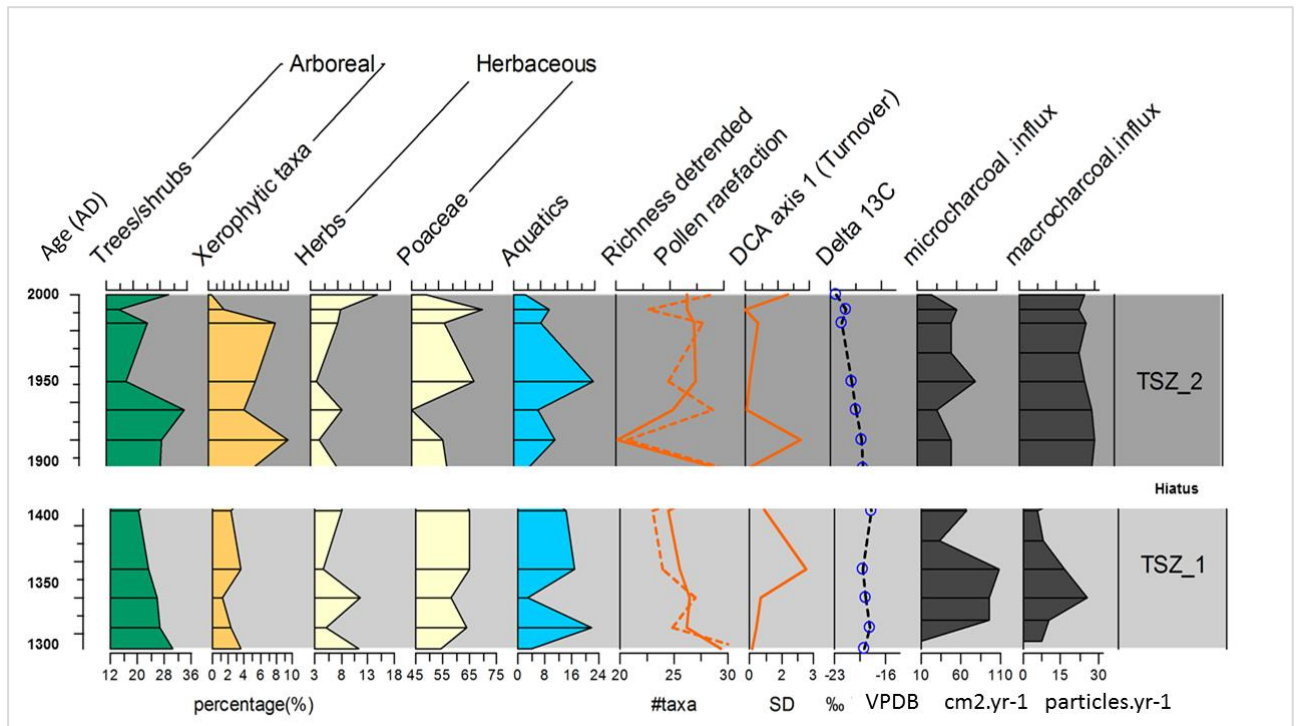


Figure 5.23: Summary pollen diagram of the physiognomy of taxa present in the core TSZ from the southern site in southwestern Madagascar, representing the two periods prior and after the hiatus. The white blank indicates the hiatus period from AD 1420 to 1910.

6. CHAPTER SIX: DISCUSSION

In this chapter, the results described in Chapter 5 are discussed and interpreted. The chapter highlights the main findings and responds to the various objectives stated in the introduction (see Chapter 1: Introduction). The first section focuses on the rainfall reconstruction through the isotope analysis. It starts by describing the isotope record and interpretation as a rainfall proxy. It then discusses the importance of such records and extends the time span of the record back 1700 years through its comparison with the western regional records. This allows for the analysis of the drivers of change in vegetation back to that period. The second part of the discussion focuses on the vegetation dynamics in the two lakes investigated, and how they have responded to rainfall variability and fire over time. The next section highlights when major changes in the southwest ecosystems happened and what the main drivers of such changes were. Finally, the analysis and interpretation of microcharcoal and macrocharcoal with historical human land-use are used to infer to the history of human subsistence and anthropogenic interactions in and around the study area. Understanding the socio-ecological process and context in these ecosystems provide a guideline towards forming conservation strategies.

6.1. Rainfall reconstruction of the southwest Madagascar during the late Holocene

6.1.1. $\delta^{13}\text{C}$ in baobab rings as rainfall proxy

The isotopic composition of baobab trees (*A. grandidieri* and *A. za*) collected in southwest Madagascar (see Figure 4.1) shows C_3 -like photosynthetic pathway with a mean value of -25.5‰ . This value corresponds to the suggested value for succulent species in more mesic areas (Szarek and Troughton, 1976) which have the ability to adapt and survive during dry conditions (Baum *et al.*, 1998; Chapotin *et al.*, 2006). The value is similar to that recorded for the African mainland baobab (*A. digitata*) which was used as a rainfall proxy for the summer rainfall region in South Africa (Woodborne *et al.*, 2015; 2016). When the individual trees analysed in this research are compared with each other, trees in the southern site (GTR and TSP) were enriched in $\delta^{13}\text{C}$ with a higher variance and standard deviation compared to those from the northern site (DFL and DFS). This shows that these trees from the southern site are responding to more arid conditions and have higher ecological plasticity (Hall *et al.*, 2009) although they do belong to different species; *A. grandidieri* for GTR and *A.za* for TSP. Such plasticity allows the trees to survive in a wider range of climate variability especially during

dry periods. It also indicates that the rainfall in the southern site is more variable compared to the northern site. Such conclusions were also drawn in the analysis of a short-term instrumental record showing more seasonal variability recorded in the south of Madagascar compared to the record from Morondava which is the northern site in the present study (Randriamahefasoa, 2013).

There was a negative correlation between the stable carbon isotope records of the trees and the instrumental rainfall record from Morondava and Toliara for all the trees, except TSP. The significant negative relationship recorded for DFL when compared with the annualised record at Morondava station from 1960-2008 was expected as this tree was located 13 km away from the rainfall station (see Figure 4.1). Once the distance between the location of both trees and instrumental record increased, different approaches had to be applied. For example, the 21-year biweight mean record of the isotope for DFS and GTR provided a significant negative correlation when compared with the rainfall record from Toliara for the period 1960-2008. This was not true of tree TSP as its negative correlation value was not significant when compared with instrumental records from Toliara. This tree was particularly problematic as the measure of correlation with its nearest rainfall station located 20 km further inland did not produce the anticipated negative correlation. Considering the east-west gradient of rainfall in Madagascar, stations located more inland in the east, record different rainfall than those near the coast in the western region (Vallet-Coulomb *et al.*, 2006; Jury, 2016). The low correlation between these datasets could be explained by the localized climate for each micro-habitat in which the trees were living, and the non-climate signals that are recorded within the isotope data. Nevertheless, the negative correlation indicates an inverse relationship between both measured local rainfall and $\delta^{13}\text{C}$ which meets the theoretical expectations (McCarroll and Loader, 2004).

When the wet (dry) periods from the isotope record in the 20th century was compared with historical records of extreme events such as droughts and cyclones, most of the extreme events that have heavily impacted the region were reflected in the isotopic records. The regional isotope record of the 20th century has changed on a decadal scale and is dominated by dry years with intermittent wet years. The beginning of the century is marked by a dry period from AD 1901 to 1950 followed by a brief wet period from AD 1950 to AD 1976, and then dry conditions until AD 2000. Within the reported extreme events, (Fenn and Rebara, 2003; Middleton and Beinart, 2005; Elmqvist *et al.*, 2007; Randriamahefasoa, 2013; Von Heland and Folke, 2014; Jury, 2016; Gaspard *et al.*, 2018), a drought which started around 1930

(Middleton and Beinart, 2005), and a drought from 1941-1942 called “many bones” (Von Heland and Folke, 2014) were reflected in the isotope record. Also reflected were dry periods recorded in the 1980s called “belt of iron” (Von Heland and Folke, 2014) which peaked at the beginning of the 1990s. The drought in the 1980s particularly impacted the population in the area as in the previous 30 years the region experienced wet conditions. The current dry period is marked by a tendency towards a wet period in the past 20 years as suggested by previous research from analysis of the instrumental record (Tadross *et al.*, 2008). Similarly, cyclones in 1953, 2004 and 2010 that caused severe damage to the southwest region are reflected in the isotope data during wet periods (Nash *et al.*, 2015). This confirms that strong cyclones bring rainfall to the region (Waeber *et al.*, 2015). In contrast, cyclone events that happened at the beginning of the 20th century were focused in the north up to Morondava along the western region (Nash *et al.*, 2015) and did not affect the rainfall in the southwest region. The results of these comparisons support the strong consistency of the age model within the trees and confirms the use of the isotope data as a rainfall proxy.

6.1.2. Local, sub-regional and regional records comparison

The sub-regional southwest Madagascar rainfall record reflects a quasi-annual, multi-decadal and centennial variability of rainfall over the last 700 years. The maximum variability within the $\delta^{13}\text{C}$ is recorded in the quasi-annual to decadal scale (Figure 5.6) where the mean range for all the trees is about 4‰ compared to the multi-decadal to centennial scale of only 1.5‰ (Figure 5.6A). Such variability might be associated with the localised weather conditions that each tree is experiencing and its response to its specific environmental variables. This indicates that the fluctuation in rainfall is more pronounced at an annual to a decadal scale than at a centennial scale across the southwest region as recorded for the last 700 years. Such variability is probably the results of the seasonal variation of rainfall where an increase in the lengths of dry spells has occurred in dry areas in the western region from 1961 to 2005 (Tadross *et al.*, 2008).

Comparing the northern and southern sites allows comparison of rainfall variability at a local scale. The variation is shown by the range between the maximum and minimum $\delta^{13}\text{C}$ indicating a more pronounced dry or wet period. This is higher for the southern site compared to the northern site with a range of 1.9‰ and 1.2‰ respectively. The reduced variability in the northern site is most likely related to the more regular occurrence of cyclone activities recorded in this area (Nash *et al.*, 2015). This is combined with its position close to the southern

distribution of the Intertropical Convergence Zone (ITCZ) at 20° South in Madagascar, that guarantees more advected moisture compared to the south of the island. However, the multi-decadal to centennial analysis of rainfall shows a decrease in the duration of wet periods and more prolonged dry periods in the northern site over time, even though more pronounced trends are recorded in the southern site (0.001‰ per year, $p < 0.05$). Nevertheless, in the near present period, there is a tendency towards wetter conditions in the southwest record which supports the projection of wetter condition in the area by 2050 (Tadross *et al.*, 2008).

At a sub-regional scale (combining all four tree records to represent southwest Madagascar), the 700-year proxy rainfall record is in agreement with the increasing aridification trends in the last millennium as suggested from pollen analysis in the southwest region (Burney, 1993; Burns *et al.*, 2016; Virah-Sawmy *et al.*, 2016). The centennial variability of the rainfall is marked by pronounced and prolonged dry periods covering 50 years or more and reduced wet periods over time. Similar patterns have also been observed in northwest Madagascar since AD 1700. The comparison between the tree ring $\delta^{13}\text{C}$ record from the southwest (this study) and the speleothem $\delta^{18}\text{O}$ record from the northwest Madagascar (Scroxton *et al.*, 2017) indicate shifts in rainfall patterns around AD 1700 across the western region. It is considered that the movement of the Intertropical Convergence Zone (ITCZ) has a significant impact on rainfall variability in Madagascar (Haug *et al.*, 2001; Liu *et al.*, 2003; Verschuren *et al.*, 2000; Schneider *et al.*, 2014). A change in the position of the ITCZ might result in a shift in sub-regional rainfall patterns. This was probably the case during the supposedly southward shift of the position of ITCZ recorded at the beginning of the Little Ice Age (Lechleitner *et al.*, 2017; Putnam and Broecker, 2017) which could have brought rainfall to the southwest.

Prior to the Little Ice Age, similar rainfall patterns were most probably experienced across the western region which then shifted at around AD 1300 resulting in the opposite pattern of rainfall between northwestern and southwestern Madagascar from AD 1300 to 1700 as recorded in this study. Therefore, during this period, dry conditions were recorded in the northwest while a wet period was recorded in the southwest. After about AD 1700, similar trends of rainfall were evident in both records. This change in the rainfall pattern along the western region of Madagascar might be related to the suggested stronger global climate forcing (known as the Maunder Minimum) that happened around mid-17th century (Scroxton *et al.*, 2017). The effect of global climate forcing has reduced the effect of localized drivers of rainfall from the ITCZ (for the northwest) (Jury and Huang, 2004; Tadross *et al.*, 2008) and moisture

from the ITCZ, temperate tropical troughs and sea surface temperature (for the southwest) (Woodborne, personal communication 2018, July; PAGES 2k Consortium, 2013). This has become a common rainfall pattern across the western region in the last 300 years.

The identified shift in the position of the ITCZ suggests a corresponding shift in the rainfall pattern across the western region. As such, prior to AD 1300, the rainfall in the southwest probably followed the 500-year wet and dry cycle recorded in the northwest (Scropton *et al.*, 2017). From AD 300 to 500, there was a dry period in the region which was then followed by a wet period from AD 500 to 1000. After this period, a dry period returned until AD 1200 when the shift in the opposite rainfall pattern started. From AD 1300, the record from the southwest suggests the following rainfall patterns: AD 1300 to 1400 marked the wettest period in the record, followed by a decreasing but still wet period until AD 1600. AD 1600 to 1800 represents the driest period, peaking around AD 1700. Subsequently there was a relatively wet period of about 50 years and another 100-year dry period. The last period from AD 1985-2000 encompassed a relatively wet period.

On a more global comparison, the records from southwest Madagascar (this research) suggests a very wet period around AD 1300 which then dried drastically in the first half of the Little Ice Age with the driest period recorded around AD 1700. This dry period coincides with the widespread decrease of temperatures considered as the maximum of Little Ice Age (Tyson *et al.*, 2001). During the Little Ice Age, dry periods were recorded around East Africa (Russell and Johnson, 2007; Tierney *et al.*, 2013) and southern Africa (Huffman, 2004; Chevalier and Chase, 2015; Huffman and Woodborne, 2016; Woodborne *et al.*, 2016). This indicates that the equatorial West Indian Ocean which brings moisture to Madagascar and East Africa (Scropton *et al.*, 2017) was stronger than their respective atmospheric forcing. The dry period around AD 1630 to 1790 coincides with the dry period recorded for the summer rainfall region in South Africa (Woodborne *et al.*, 2015; 2016), which could be explained by common drivers of rainfall (Woodborne, personal communication 2018, July). Southwest Madagascar is more prone to and impacted by changes of global and localized climate forcing which should be investigated further. Nevertheless, this record showed the trends towards lower rainfall, and more frequent extreme events such as drought as identified through short-term analysis of the instrumental record (Waeber *et al.*, 2015).

6.1.3. Summary of rainfall reconstruction

This section presented the results of the $\delta^{13}\text{C}$ analysis of baobab rings as a proxy for the rainfall in southwestern Madagascar. It was shown that the rainfall in the region has decreased over the past 700 years. In addition, a tendency of increasing variability at the centennial scale has been recorded over this period. This variability is marked by the reduction in the duration of wet periods over time. The local records (both northern and southern sites) showed a reduction in the duration of wet periods over time and an increase in the duration of dry periods for the northern site while a higher rate of decreasing trend of rainfall is recorded for the southern site over the last 700 years.

Palaeoclimate research in Madagascar is limited and most regions do not have high-resolution climate reconstructions. The north-south and east west rainfall gradients (see: Chapter 2: Literature review) cannot be investigated because there are so few palaeoclimate records. Only the 1700-year $\delta^{18}\text{O}$ record of speleothems from the northwest region (Brook *et al.*, 1999; Burns *et al.*, 2016; Scroxton *et al.*, 2017; Voarintsoa *et al.*, 2017), the 300-year spectral luminescence of corals from the northeast region (Grove *et al.*, 2013), and this new 700-year isotope record of baobabs from the southwest, present high resolution reconstructions for the island. Along the western region, the comparison of the new record in the southwest with $\delta^{18}\text{O}$ of speleothem in the northwest showed that there was a shift in the rainfall pattern after the global forcing in the mid-17th century (PAGES 2k Consortium, 2013; Scroxton *et al.*, 2017). Prior to AD 1700, an anti-phase period was recorded where patterns of rainfall towards dry periods in the northwest sub-region corresponded with wet periods in the southwest and inversely. After AD 1700, however, an in-phase relationship was recorded with patterns of wet (dry) phases in the northwest coinciding with wet (dry) periods in the southwest. This shift in phase was related to the maximum of the Little Ice Age around AD 1700 which coincides with dry periods in east Africa and southern Africa.

This research has provided the first rainfall reconstruction from the isotopic composition of tree rings for the southwest sub-region of western Madagascar with high spatial and temporal resolution at decadal to centennial-scale over the last 700 years. The analysis conducted here was used to understand rainfall patterns across the western region where tropical dry forests occur. It also provides information of rainfall changes and drivers which then allowed inference of the rainfall patterns of the southwest relative to the duration of the record available from the northwest (about 1700 years) (Scroxton *et al.*, 2017). Such information provides opportunities

to evaluate the impacts of human land-use or land use change (reflected in the charcoal, pollen, and isotope analysis in sediments) and rainfall variability on the vegetation (obtained through pollen and isotope analysis) in the region during the late Holocene which is the goal of this thesis.

6.2. Vegetation dynamics at Lake Longiza (northern site) and Lake Tsizavatsy (southern site)

6.2.1. Lake Longiza, vegetation dynamics over the last 2400 years

The 2400-year pollen record of the sediment cores at Lake Longiza (northern site), presented taxa associated with dry forest and riparian forest ecosystems, and herbaceous taxa including grass. The dry ecosystem is characterised in the pollen record by taxa such as Fabaceae, Malvaceae, Moraceae, Arecaceae, *Celtis* (Cannabaceae) and a few xerophytic taxa such as *Securinega* (Phyllanthaceae), *Phyllanthus* (Phyllanthaceae), and *Croton* (Euphorbiaceae). These taxa are only found today in pockets of dry forest along western Madagascar from the north in Cape d'Ambre to the Mangoky River in the south (Humbert and Cours Darne, 1965; Abraham *et al.*, 1996; Baum *et al.*, 1998). The riparian ecosystem in the pollen record is characterised by evergreen trees such as *Podocarpus* (Podocarpaceae), *Pandanus* (Pandanaeae) and Myrtaceae. *Podocarpus* spp. are mostly abundant in mountainous areas, however some species occur in dry forest along streams and are dependent on a permanent water supply (Gray, 1953; Farjon, 2010). Myrtaceae and *Pandanus* (*cf. P. xerophyta*) also occupy humid or riparian environments on a calcareous substrate (Snow, 2008; 2010; Virah-Sawmy *et al.*, 2016). The herbaceous layers of the community in the pollen record are dominated by Poaceae, Asteraceae, Urticaceae, and Acanthaceae. Mosaic vegetation is inferred, when both dry and riparian forest species elements are observed in the pollen record alongside herbaceous taxa, indicating patches of more open vegetation. This indeed reflects the biologically and physically heterogeneous nature of the modern landscape in southwest Madagascar (Cornet and Guillaumet, 1976; Du Puy and Moat, 1996; WWF, 2001; Grubb, 2003; Moat and Smith, 2007; Callmander *et al.*, 2013).

The variation of the stable carbon isotope values of the bulk sediments also indicated change in the structure of the vegetation. Values between -34‰ to -22‰ are inferred by the abundance of C₃ plants including trees, shrubs, forbs and herbs while values between -17‰ to -9‰ are interpreted as a dominance of C₄ plants mostly grass (Ehleringer and Rundel, 1988; McCarroll and Loader, 2004). The carbon isotope variation of either more positive or more negative

values towards these values in sediment cores suggest opening up of the ecosystem over time (loss of tree cover) and is compared with the changes in the pollen data. In the LNG core, these ecosystems (dry forest and riparian forest) has varied in abundance during the three significant periods of vegetation change: from 450 BC to AD 1250, AD 1250 to 1985 and AD 1985 to 2010.

6.2.1.1. Vegetation dynamics from 450 BC to AD 1250

During the period 450 BC to AD 1250, the evidence from the pollen record and carbon isotope record from LNG core suggest an impact of climate and human activities around AD 420 and AD 980 respectively. Overall, the vegetation around Lake Longiza was dominated by riparian and dry forest trees with an abundance of taxa such as *Podocarpus* in the riparian forest ecosystem at the beginning of the record around 450 BC. Dry forest trees and shrubs were also abundant but xerophytic taxa such as *Securinega*, *Croton*, *Phyllanthus*, *Uapaca* were low except around AD 420 where most of them were simultaneously present. These xerophytic taxa establish more during dry periods and are currently a major component of the dry forest in southwest Madagascar (Sussman and Rakotozafy, 1994; Grubb, 2003). Such taxa are known to have increased in the past due to prolonged and increasing dry periods (Burney, 1993; Burns *et al.*, 2016; Virah-Sawmy *et al.*, 2016). Although evidence from other sites in southwest Madagascar suggest expansion of xerophilous thickets and contraction of woodland vegetation in the late Holocene coinciding with the drying trend of the climate since the mid-Holocene (Burney, 1993; Clarke *et al.*, 2006; Burns *et al.*, 2016; Virah-Sawmy *et al.*, 2016), the present data however did not show high incidence of xerophytic taxa during this period (450 BC to AD 1250) except around AD 420.

The increase in xerophytic taxa and decrease in dry forest trees around AD 420 was associated with an increase in the abundance of Poaceae at this time period, also confirmed by the less negative bulk sediment $\delta^{13}\text{C}$ values. For instance, a dominance of C_3 plants was recorded at the beginning of this period ($\delta^{13}\text{C}=-22.9\text{‰}$ around 450 BC) but gradually shifted into increased abundance of C_4 plants as grass increased ($\delta^{13}\text{C}=-20.7\text{‰}$) around AD 420. This change in vegetation with high grass abundance and low arboreal taxa was also recorded in the Fiherenana-Manombo complex, a site located further south of the study area around AD 350 (Virah-Sawmy *et al.*, 2016). For Lake Longiza, the increase in xerophytic taxa and grass, and decrease in trees suggest that climate was having an effect on vegetation structure. This is confirmed by the rainfall record analysis which suggests that the southwest region experienced

dry conditions from AD 300 to 500 similar to the northwest and thus, as recorded in the pollen record, a gradual increase of both xerophytic and grass taxa. Very low to no charcoal was recorded during that period despite archaeological evidence of human presence and activities (Burney, 1987b; Perez *et al.*, 2005; Burney *et al.*, 2004; Dewar *et al.*, 2013; Anderson *et al.*, 2018; Douglass *et al.*, 2018).

After the xerophytic taxa and grass peak associated with a change in the structure of the community, the vegetation around Lake Longiza remained C₄ dominated for over 300 years (AD 420 to 790) despite the slow recovery of dry forest trees in the pollen record. Around AD 870, the isotopic data at Lake Longiza suggests a short recovery of C₃ plants coinciding with a peak in trees and shrubs such as *Acacia*, *Ficus*, and *Arecaceae* in the pollen record. This recovery of C₃ plants was similarly observed in the dry forest in the northwest region around AD 795 (1155 cal years BP) and AD 870 (1080 cal years BP) (Burns *et al.*, 2016; Voarintsoa *et al.*, 2017). In these studies, the recovery in the northwest vegetation was attributed to monsoonal rainfall and the relative position of the Intertropical Convergence Zone (ITCZ) (Voarintsoa *et al.*, 2017) during a wet period from AD 500 to 1000 (Scropton *et al.*, 2017). The similar rainfall pattern recorded for both regions suggests that this was also the case for the southwest vegetation recovery.

A rapid shift to an abundance of C₄ plants combined with a decrease in taxa richness was recorded in the pollen of the LNG core around AD 980. This rapid decrease in the abundance of C₃ plants reflects more open vegetation after a wet period from AD 500 to 1000. Opening of ecosystems were also recorded in other regions across Madagascar around the same period and were associated with human activities. From Andolonomy, south of the study sites, floral extinctions were recorded from AD 350 to 1250 (1600-700 cal years BP), simultaneously with a charcoal peak that was interpreted as the presence of agropastoralism using fire (Virah-Sawmy *et al.*, 2016). In the northwest, gradual change in vegetation from AD 870 to 1130 was suggested to be associated with shifting cultivation (Voarintsoa *et al.*, 2017) and in the east, it is suggested that a massive forest extraction and clearing expansion occurred around AD 700 to 1100 (Agarwal *et al.*, 2005). Despite the low charcoal influx in the record from the LNG core, the change in vegetation structure with the reduction in trees during a wet period implies human activities occurring around Lake Longiza probably associated with the expansion of pastoralism in the southwest. Additional data on herbivory activities from this site from dung

fungal spores would provide robust evidence of human presence and activities in the area during this period (Baker *et al.*, 2013)

6.2.1.2. Vegetation dynamics from AD 1250 to 1985

During the period AD 1250 to 1985, the pollen and isotope record of the LNG core suggest a substantial decrease in dry forest, riparian trees and an increase in grass over time, which is probably associated with an increase in human activities. Such tree loss is possibly associated with the local and regional expansion of pastoralism, as suggested by the onset of charcoal peaks in the sediment around AD 1400 and AD 1600. The pollen record also showed a decrease in the abundance of trees during a 300-year wet period in the southwest region from AD 1300 to 1600 (see: Chapter 5.1.4). This period also marked the increasing trends in *Gnidia* occurrence after the regional fire event inferred from microcharcoal influx around AD 1400, taxa known for its ability to resprout through underground rootstock after fire events (Rogers, 2009). But even as fire incidence declined after AD 1600, as suggested by the microcharcoal data, the abundance of *Gnidia* continued to increase gradually with the recovery of most of the dry forest trees until AD 1920.

The increase in fire events around AD 1920 suggests a burnt landscape probably associated with human activities which led to the high prevalence of Poaceae reaching its maximum abundance around AD 1980. In contrast, dry forest taxa and riparian trees along with the taxa richness of the overall landscape decreased indicating a more open, species poor landscape. Pioneer taxa such as Asteraceae started to increase gradually indicating an increase in degradation during this period. This is also reflected in the carbon isotope value of the sediment, which displayed a more C₄-dominated vegetation, all during the succession of the wettest and the driest period in the southwestern rainfall record (see Chapter 5.1.4).

6.2.1.3. Vegetation dynamics from AD 1985 to 2010

Since AD 1985, there was a decrease in the abundance of riparian trees over time, associated with an increase in herbaceous taxa and high charcoal influx. During this period, the ecosystem was dominated by Myrtaceae, which is abundant in degraded vegetation in Madagascar today (Koechlin *et al.*, 1974). Forest clearing and burning practices may have been responsible for the decline and degradation of the riverine ecosystem as recorded along the Mangoky River (Vallet-Coulomb *et al.*, 2006). This ecosystem is impacted especially by the increase in agricultural practices inferred from ethnological studies and such areas with access to water and

alluvial soils are favoured for agriculture (Smith *et al.*, 1997; Scales, 2011; Raharimalala *et al.*, 2010). These facts suggest the reduction and the degradation of the riparian forest probably associated with human activities through agricultural activities (Vallet-Coulomb *et al.*, 2006). Despite the recent wettings recorded in the rainfall record, drying of some rivers were recorded since 1960, probably because of the long-term decreasing trends of rainfall (Scales, 2012) and increase in irrigation scheme that are fed by groundwater as seen through satellite images from Google Earth. Such drying combined with population increase (Sussman *et al.*, 1994) require the need for new agricultural lands, which are often acquired through shifting cultivation (locally called *hatsake*). The *hatsake* consists of cutting down trees and burning the biomass (Waeber *et al.*, 2015) to transform the ash as nutrients for the soil (Scales, 2012) and can be practiced on poor soils (Casse *et al.*, 2004; Waeber *et al.*, 2015). This explains the high rate of charcoal influx and decrease in trees recorded during this period. After a few years of cultivation, the land is abandoned as “Monka” which allows the establishment of new taxa and recovery of the soil (Bloesch, 1999; Raharimalala *et al.*, 2010). This would explain the abundance of pioneer taxa such as Asteraceae (cf. *Ambrosia*) reaching its maximum at the near present period. The increase in agricultural practices as well explains the increase in Poaceae and probably Fabaceae in the pollen record as crops such as rice, maize, and butter beans are the most cultivated on these land (Scales, 2012).

Xerophytic taxa also became abundant during this period possibly as a response of the ecosystem to the increasing dry periods and the shortening duration of wet periods associated with the anthropogenic warming of the 20th century (Thomas *et al.*, 2004; Scroxton *et al.*, 2017). Prior to this period, there was a 150-year dry period recorded from AD 1650 to 1800, where a slight increase in dry adapted taxa occurred. The next wet period was around AD 1800 to 1850, about a shorter 50-year period compared to previously wet periods which were a minimum of 100 years. An abundance of xerophytic taxa such as *Securinega* were then recorded coinciding with a dry period around AD 1850 to 1950, with a high abundance of xerophytics in the last period from AD 1985 to 2010. Simultaneous with the increase in agricultural practices, the pronounced and prolonged dry conditions in the region led to a dramatic increase in pollen from xerophytic taxa. Human land-use, probably an increase in agricultural practices, and shifting cultivation and climate, through drying, reduced the tree abundance, and increased grasses and xerophytics. This indicates an influence of both factors on the structure and composition of the community over time.

Since 1990, there has been an increasing abundance of *Typha cf angustifolia* reaching a maximum value at the near present period. This taxon generally establishes itself in disturbed, unstable wetlands (Grace and Wetzel 1981). This taxon tolerates a broad range of climates and is known to be one of the most productive groups of plants reported, regenerating through vegetative and sexual reproduction (Apfelbaum, 1985; Grace and Harisson, 1986). These taxa have a C₃ photosynthetic pathway, which explain the very low isotope value (-25‰) recorded at the near present period in the sediment record despite the decrease in trees. During the period from AD 1985 to 2010, the landscape appeared to be heavily impacted by human land-use and climate change. It became degraded, open and drier with concentrated activities within the lake based on the evidence of high pioneer species and C₃ plants abundance. Forest clearing and burning most likely reduced the components of riverine ecosystem and dry forest trees while climate change has promoted the xerophytic component of the dry forest.

In summary, climate variability and human activities simultaneously or consecutively affected the ecosystem around Lake Longiza during the late Holocene (Figure 6.1). Prior AD 1250, low rainfall (the long dry period recorded until AD 500) triggered a shift in the abundance of grass and xerophytic vegetation around AD 420 leading to a relatively C₄ dominated landscape. This change was simultaneously experienced in the southwest region as recorded in other published pollen records further south (Virah-Sawmy *et al.*, 2016). Followed by a wet period of about 500 years, dry forest trees recovered slowly, and the landscape became dominated by C₃ plants around AD 870, a recovery that was also recorded in a vegetation analysis in the northwest (Voarintsoa *et al.*, 2017). A rapid transition into a more open landscape initiated, most probably, by humans was recorded around AD 980. This opening was seen through the high prevalence of Poaceae, low prevalence of dry forest and riverine ecosystems, but during the AD 1920 transformation of the landscape, charcoal peaks became high indicating a burnt landscape which almost certainly the result of human activities. This suggests that the human practice of shifting cultivation has impacted the natural vegetation. Climate change on the other hand might have favoured the increase of xerophytic taxa of the dry forest ecosystem during the last 2400 years. Little is known about the mechanism that has maintained the mosaic vegetation around Lake Longiza over the last 2000 years and the response of the associated ecosystems to increasing fire activities and climate change, which requires further investigation.

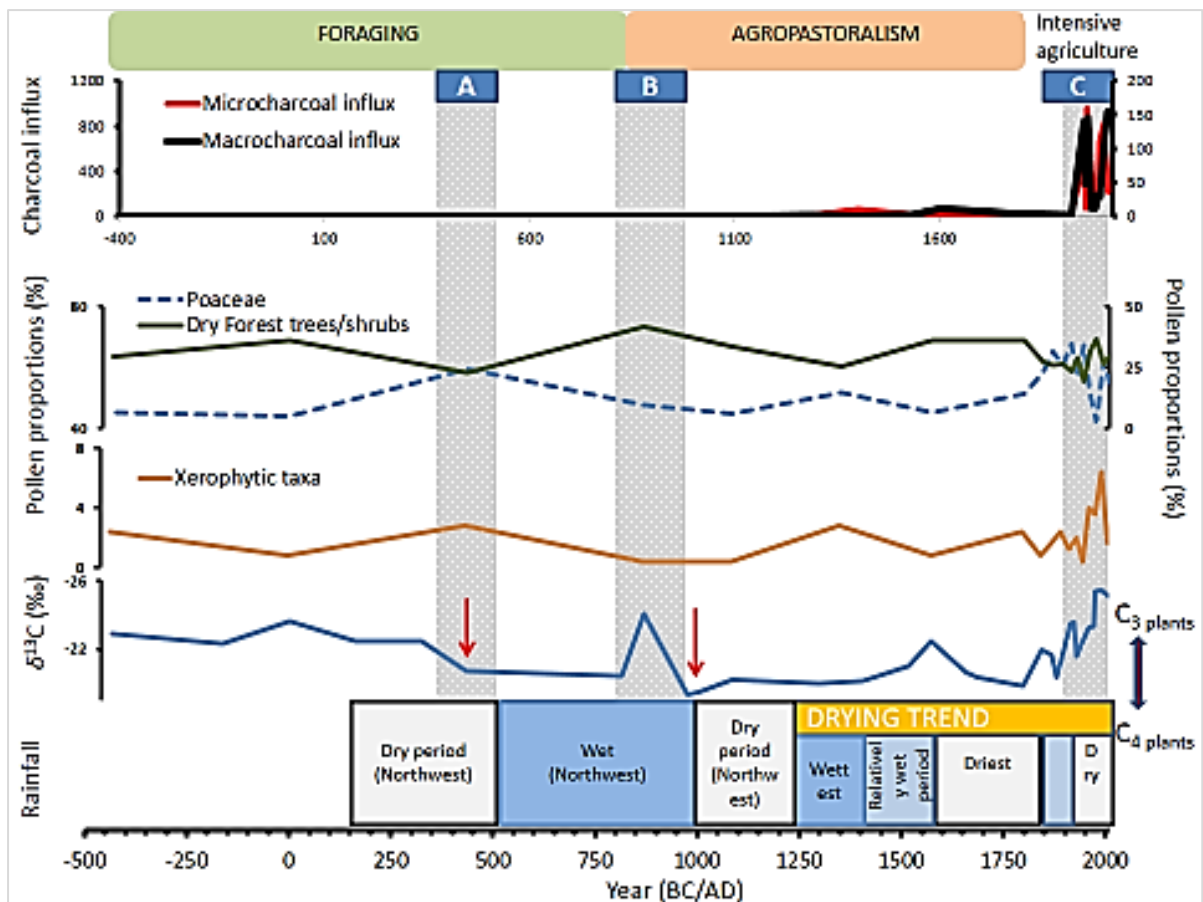


Figure 6.1: Major changes of the mosaic dry forest ecosystem around Lake Longiza, from the LNG record (grey dashed boxes). Box A indicates the gradual decrease of C₃ plants towards more open vegetation. Box B shows the short recovery of the vegetation followed by a rapid shift into a C₄ dominated landscape. Box C represents the massive changes recorded in the last 40 years. Red arrows show the direction of the vegetation change. Human subsistence with potential impact on the landscape are represented at the top.

6.2.1.4. Ecological response of the mosaic vegetation in the tropical dry forests at Lake Longiza to fire regime and rainfall variability

The reconstruction of the vegetation at Lake Longiza shows consecutive or simultaneous interactions between climate and anthropogenic disturbances over the last 2400 years. Despite the influence of these drivers, taxa associated with dry forest and riparian forest were present throughout the whole period, suggesting the presence of mosaic vegetation in the area. It is important to evaluate the mechanism that maintained the abundance of taxa that composed the mosaic and the diversity of the ecosystem. Also, what is the response of each group of taxa representing the mosaic ecosystem and diversity to an increasing fire regime, most probably associated with human land use and drying climate?

The record shows that there was internal reorganization of the ecosystem during the last 2400 years that would have maintained the presence of mosaic ecosystem over time (Müller *et al.*, 2016). This internal reorganisation is demonstrated through the decrease in certain taxa while others became abundant. With an increase in disturbances, changes in the abundance of dominant taxa and introductions of new taxa were recorded, yet most of the taxa remained present over time. The persistence of such a landscape is explained by the wide range of resources and microclimate refugia that they provide facilitating the presence of a diverse array of species (Watt, 1947; Kindvall, 1996; Oliver *et al.*, 2015). In addition, in tropical dry forests, many species have the ability to re-sprout and / or have long seed persistence such as *Gnidia*, which dominates the record from Lake Longiza (Elmqvist *et al.*, 2007; Bongers *et al.*, 2009). Some taxa also have wind dispersed seeds such as some genus belonging to Fabaceae and Bignoniaceae Family which enable them to invade wetter zones and might contribute to landscape scale stability through patch dynamics (Bongers *et al.*, 2009; Becknell *et al.*, 2012). An abundance of fire resistant taxa such as Arecaceae are also recorded in this ecosystem (represented by *Medemia cf. nobilis*, *Hyphaene*) (Koechlin *et al.*, 1974; Matsumoto and Burney, 1994; Tropicos Madagascar, 2009). The resources provided by different habitats within the mosaic landscape, and the ability of some of these taxa to resist or recover after disturbance provided a resilience to fire regime and climatic variability of the tropical dry forests around Lake Longiza over time.

In terms of taxa richness, the mosaic community demonstrated no response to rainfall variation which suggests that the historical range of rainfall variability during the period of study (2400 years) was within the tolerance of all vegetation types present (Figure 6.2). This was not the case for the diversity of the community response to fire regime most likely associated with human activities. The richness of the community demonstrated a non-linear response to the fire regime, as during low fire periods, taxa richness remained high. However, when the influx of macrocharcoal indicating local fire, increased above 50 particles. yr⁻¹, taxa richness declined (see: Figure 5.16). In addition to fire, regional expansion of pastoralism recorded around AD 800 to 1000, AD 1400 to 1600 and the shift of subsistence to agriculture around AD 1900 reduced the taxa richness (Figure 6.2). Land-use change has been previously confirmed to reduce community composition and richness (Scott *et al.*, 2006), but the response is not linear and higher richness can be found at intermediate levels of disturbance, because of the landscape heterogeneity, which is suggested to be important for biodiversity (Gil Romera *et al.*, 2010; Gillson, 2015). This has been demonstrated to be valuable in tropical dry forests (Bongers *et al.*, 2009) and further research is still needed to understand the baseline value of fire that allows

the maximum diversity in the case of a mosaic ecosystem in the tropical dry forests in Madagascar.

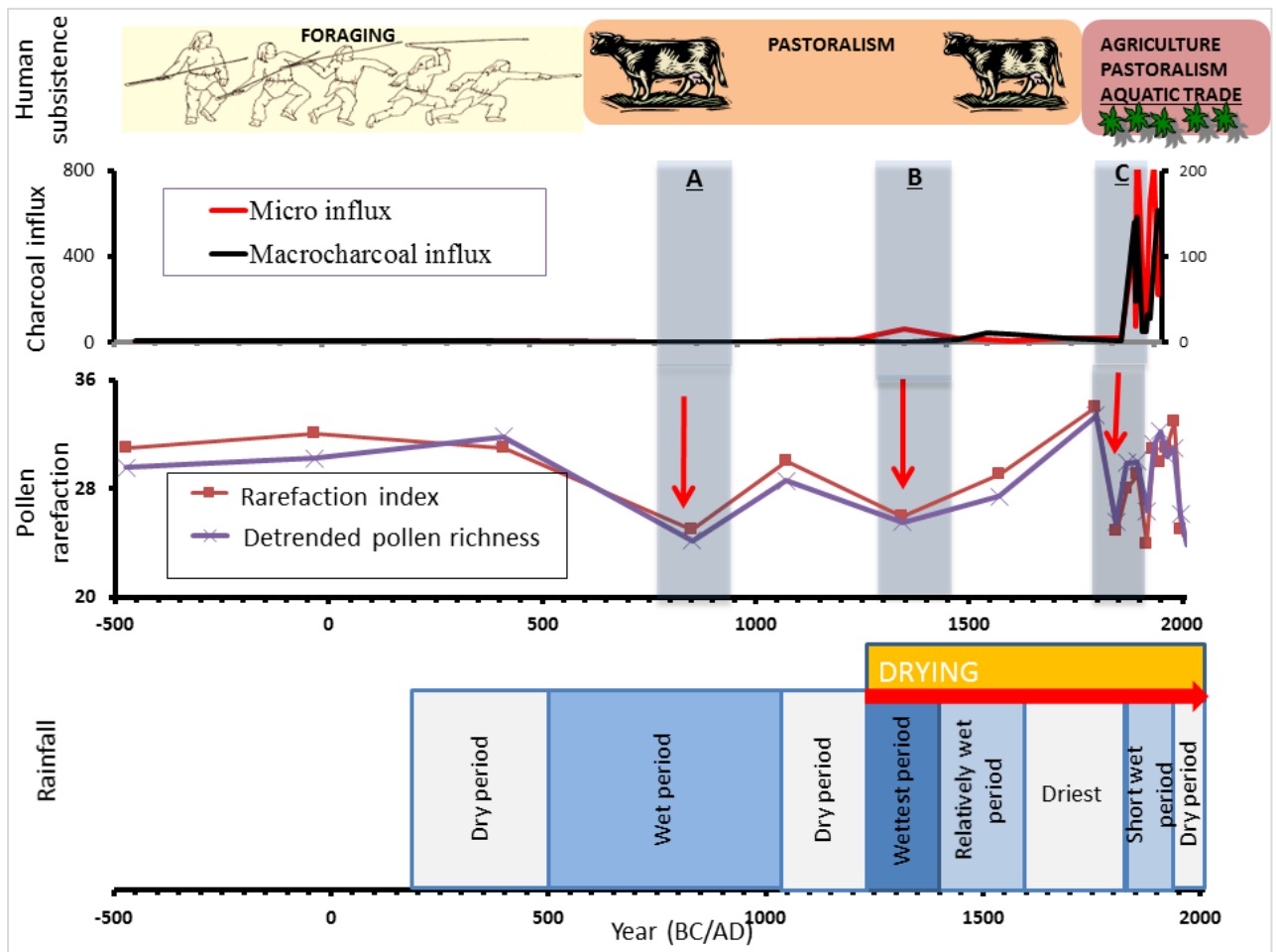


Figure 6.2: Landscape diversity response to rainfall variability, fire events and human subsistence over the last 2400 years. The top graph represents the human subsistence strategy. Charcoal influx provides the change in fire regimes where microcharcoal is expressed by $\text{cm}^2 \cdot \text{yr}^{-1}$ and macrocharcoal expressed as $\text{particles} \cdot \text{yr}^{-1}$. Pollen rarefaction indicates the pollen richness and detrended pollen richness (taxa richness and evenness). Dark grey indicates a major shift in land-use in the southwest where A and B indicate regional expansion of pastoralism while C indicates the beginning of agricultural practices. Red arrows show the decrease in taxa richness during land-use change. Combined rainfall records for the northwest prior to AD 1300 (Scroxton *et al.*, 2017) and AD 1300 to 2010 from southwest Madagascar (this study) are at the bottom, where grey and blue indicate dry and wet periods respectively.

Despite the recorded presence of the mosaic vegetation over time, each group of taxa that represented dry forest and riparian forest in the pollen record have responded differently to regional and local fire events (inferred respectively from microcharcoal and macrocharcoal records) and drying conditions. The dry forest taxa abundance in the pollen record showed a

non-linear response to fire until its influx became very high until there were long periods of aridity. For the trees and shrubs in the dry forest ecosystem, no response is recorded in their abundance with low charcoal influx. When fire increases to a moderate influx of less than 100 particles. yr⁻¹ and 660 $\mu\text{m}^2\cdot\text{yr}^{-1}$ respectively for macrocharcoal and microcharcoal, trees abundance reduces. This effect is more pronounced with increased microcharcoal influx representing regional fire events than with macrocharcoal with local fire events. At a very high charcoal influx, above the previously mentioned value, fire-adapted taxa such as *Gnidia*, and *Arecaceae* (Koechlin *et al.*, 1974; Rogers, 2009) increased the impact on the overall abundance of trees within the dry forest group in the pollen record. In addition, a high influx of charcoal is linked to the opening of vegetation indicated by increased grass abundance and an increase of pioneer taxa. On the other hand, the abundance of xerophytic taxa responded linearly to the decrease in rainfall regime until dry periods became more pronounced and prolonged and the duration of the following wet period was too short to allow a full recovery of evergreen trees. If prolonged and pronounced dry periods favour abundance of xerophytics, their abundance was restricted and decreased when a high influx of charcoal was recorded. As such, the dry forest ecosystem represented by the dry forest tree group in the pollen record shows resilience to low and moderate fire regimes during wetter conditions, but an increase in dryness would impact negatively on dry forest and lead to the abundance of xerophytic taxa. A further increase in fire regime would lead to the replacement of these xerophytics by fire resistant and pioneer taxa.

The riparian ecosystem represented in the pollen record by taxa such as *Podocarpus*, *Myrtaceae* and *Pandanus* responded negatively to the increase of fire activities (see Figure 5.16) which was probably associated with forest clearance. This is demonstrated in the changes in abundance and composition from *Podocarpus*-*Myrtaceae* dominance (2400 years ago to AD 1250) to *Pandanus*-*Myrtaceae* dominance (AD 1250 to 1985). Recently (from AD 1985), the ecosystem is mostly dominated by *Myrtaceae*, which is abundant in degraded vegetation in Madagascar today (Koechlin *et al.*, 1974). The riparian ecosystems are often considered as refugia for species with specific requirements as it is in the case of *Podocarpus* and *Pandanus*, which requires permanent water flows (Gray, 1953; Farjon, 2010; Virah-Sawmy *et al.*, 2016). These riparian ecosystems also contain diverse faunal communities and are habitats for local and regional plant endemics (Gardner *et al.*, 2009; Virah-Sawmy *et al.*, 2016).

The abundance of the riparian taxa in the pollen record responded negatively during increases in the microcharcoal and macrocharcoal influx indicating regional and local fire events (Figure

5.16.). Though only 20% of the variation in the data is explained by fire incidences, another factor that might lead to the decrease of taxa in this ecosystem is land-use through selective logging for woody charcoal production or clearing for agricultural purposes (Fauroux, 2001; Gardner and Davies, 2014; Randriamalala *et al.*, 2016). Areas with water access are more prone to clearing as they are preferred areas for agriculturalists for their alluvium fertile soil (Du Puy and Moat, 1996). Thus, species occupying such ecosystems would become increasingly rare and, susceptible to disappearance with an increasing intensity of land-use. These riparian ecosystems would most likely be replaced by agricultural land. Therefore, a continued increase in the exploitation of riparian forest in the form of forest clearing and shifting cultivation might lead to loss of biodiversity. Riparian species also have higher sensitivity to climate change and, in the case of a decreasing trend of rainfall would be vulnerable.

Despite the response of the taxa recorded in the mosaic of dry forest and riparian ecosystem around Lake Longiza to fire and climate disturbance, all mosaic elements remained present suggesting that no ecological threshold was exceeded during the past 2400 years. This means that there was no shift of state of the community to a new alternative stable state but rather an internal reorganization of the ecosystem with changes in the relative abundance of vegetation types and pioneer species (Müller *et al.*, 2016). With an increase in future anthropogenic and climatic disturbance, such a landscape could reach its ecological threshold and move to an alternative stable state (Folke *et al.*, 2004). With increasing fire pressure and clearing, the dry forest ecosystem might shift into degraded savanna (Bloech, 1999; Folke *et al.*, 2004) while the riparian ecosystem will probably become agricultural land, a change which could become irreversible if no refugia of riparian forest remain. Intensification of human land-use also diminishes the ability of some specialist taxa such as *Terminalia* spp. (very under-represented in the pollen record of the LNG core) to adapt to climate warming and rainfall variability, which could lead to an overall loss of heterogeneity and resilience (Aguirre *et al.*, 2017). Continuous dry periods and decreasing soil fertility, might lead to a shift of the dry forest ecosystem into spiny thicket forest, mostly dominated by xerophytic taxa, as it is currently further south (Koechlin *et al.*, 1974).

6.2.2. Lake Tsizavatsy, vegetation change AD 1300 to 1420 and AD 1910 to 2010

The basal age of the TSZ core from Lake Tsizavatsy in the southern site of the study area was AD 1301, but a hiatus of about 500 years was recorded from AD 1420 to 1910. This hiatus is

probably because of sediment scouring from the floodwaters of the Mangoky River which is considered as a main regional aquifer in the area (Vallet-Coulomb *et al.*, 2006) and is located less than 5 km south from Lake Tsizavatsy (see Chapter 4, Figure 4.3B). Similar regional flooding could have impacted surrounding lakes such as in the case of Lake Ihotry located 25 km from the river during the late Holocene at about 3300-2000 cal years BP (Vallet-Coulomb *et al.*, 2006). This flooding was probably pronounced after the wettest period recorded in the region around AD 1400 which could have mobilised sediment, leading to a hiatus in the record, and might have occurred more frequently until the beginning of the 20th century. With the drying trend of rainfall and the recorded drying of several lakes in the southwest including Lake Ihotry (Vallet-Coulomb *et al.*, 2006; Scales, 2012; see Chapter 6.1), the river extent and the lake level probably lowered, reducing flooding and the removal of sediment since AD 1910 at Lake Tsizavatsy. The periods prior to and after the hiatus contained information on vegetation dynamics in the southern site.

The pollen record of the TSZ core showed an abundance of Poaceae (mostly higher than 60%) in both time periods. A few trees that are common along the southwestern region today such as *Acacia* and *Celtis* were in the pollen record in addition to xerophytic taxa such as *Croton*, and *Securinega* (Koechlin *et al.*, 1974). Taxa that are fire-adapted and tolerate permanent and temporary flooding such as *Arecaceae* (*Medemia cf. nobilis*) were also present (Koechlin *et al.*, 1974; Vallet-Coulomb *et al.*, 2006). The abundance and presence of these taxa suggest a savanna woodland ecosystem around the lake in the two time periods presented here, as it is present in the coastal bushland of the southwest Madagascar today (Humber and Cour Darne, 1965; Lowry *et al.*, 1997). Savanna woodland exists within tropical dry forest areas (Miles *et al.*, 2006; Sanchez_Azoifeifa *et al.*, 2005; Pennington *et al.*, 2006; Portillo-Quintero *et al.*, 2014) and occupy 80% of the western region of Madagascar (Koechlin *et al.*, 1974). The pollen record of the TSZ core from the small Lake of Tsizavatsy (see Chapter 4) informs local vegetation dynamics from AD 1300 to 1420, the first period, and from AD 1910 to 2010, the second period.

6.2.2.1. Before the hiatus: between AD 1300 to 1420

This period is marked by the presence of C₄-dominated vegetation as indicated by the $\delta^{13}\text{C}$ value of the bulk sediments which corresponds with the abundance of Poaceae in the pollen record. However, there is also a decreasing trend of tree components including xerophytic taxa from the beginning, around AD 1300, until the end, AD 1420 of this period. A decrease in tree

cover was also recorded in the pollen record of a core collected at the Lake Ihotry around AD 1300 (650 cal years BP) (Vallet-Coulomb *et al.*, 2006). This coincides with increasing charcoal influx and high abundance of pioneer taxa such as Asteraceae and a decrease in taxa richness especially around AD 1320-1340. This decrease in trees, low taxa richness, high abundance of pioneer species and high charcoal rate happened during the wettest period in southwest Madagascar (See Chapter 5.1.4). This suggests a non-climate related change to the vegetation, possibly because of human activities most likely through the expansion of pastoralism since pastoralism has been recorded in the region since AD 600 (Anderson *et al.*, 2018).

6.2.2.2. Period from AD 1910 to 2010

After the hiatus at about AD 1910 to 2010, there was massive increase in xerophytic taxa that remained high throughout this period. This suggests that the long dry and short wet phases that precede this period have impacted on the xerophytic taxa component of the ecosystem. In parallel, from AD 1910 to 1950 there was a higher prevalence of arboreal taxa mostly dominated by Arecaceae coinciding with lower prevalence of Poaceae but with very low species richness in the ecosystem around Lake Tsizavatsy. The abundance of such taxa (Arecaceae) is explained by their ability to tolerate various conditions, (Koechlin *et al.*, 1974; Vallet-Coulomb *et al.*, 2006) that the ecosystem might have experienced during the hiatus period (relatively wet period from AD 1400-1600, very dry period from AD 1600-1850, and relatively wet period from AD 1850-1900). Since AD 1950, there has been a decrease in the tree component of this ecosystem including Arecaceae coinciding with an increase in Poaceae and pioneer taxa such as Asteraceae at the near present period. These vegetation changes occurred during a period with constant macrocharcoal influx. This constant macrocharcoal influx most likely indicates human activities through the seasonal shifting cultivation practiced by the current occupant forager communities of the area (Stiles, 1998), a subsistence strategy that was practiced by these communities at least in the last century as suggested by the charcoal data. The decrease in tree cover despite a stable charcoal influx suggests activities with little use of fire such as selective logging practiced, probably by other ethnicities such as Masikoro that closely interact with the Mikea communities (Stiles, 1998). These other ethnicities live outside the forest and probably collect wood for charcoal production or construction which gradually reduces the tree abundance. This is seen in the reduction of *Acacia*, Fabaceae, Myrtaceae which composed the tree component in the TSZ pollen record (Figure 5.20).

The two periods covered by the TSZ core collected in the southern site of the study area show an increase in ecosystem degradation and drying over time as inferred from the abundance of arboreal, grass, pioneer and xerophytic taxa. The decrease in trees and increase in pioneers and grass at around AD 1300 and AD 1950 could be because of human activities while the increase in dry adapted taxa in the last century suggests a decreasing rainfall in the last 700 years. The evidence indicates a long-term impact of declining rainfall on the savanna woodland. In the future, if continuing dry periods associated with an increase in the abundance of xerophytic taxa, in conjunction with human exploitation of the tree component of such ecosystem, is most likely going to increase the rate of grass abundance resulting in a permanent opening in the area.

6.2.3. Evolution of human subsistence across the study areas in southwest Madagascar

To explore the shift in human subsistence across the study areas, charcoal evidence from palaeoecological investigations from the two sites (northern and southern) were interpreted alongside the historical record of human land-use and climatic variability particularly the practice of agropastoralism and specifically forest clearing through *hatsake* (Virah-Sawmy *et al.*, 2016). It has been proposed that sudden peaks of charcoal in sediments can be interpreted as a past human land-use proxy and probably infer a shift in human subsistence (Burney, 1987b; Dewar *et al.*, 2013; Virah-Sawmy *et al.*, 2016) especially in an area where natural fire is less frequent (Koechlin *et al.*, 1974). It is thought that 95% of fire in the southwest Madagascar is currently anthropogenic despite its semi-arid climate conditions (Bloech, 1999; Waeber *et al.*, 2015). This is because many species in the ecosystem have xerophytic characteristics and do not burn easily, unless cut down first. A high charcoal record in the present study would therefore indicate a burnt landscape probably because of human activities.

Little to no fire activities as reflected through fire influx were recorded in the sediment core LNG from the northern site from 450 BC to AD 1400 (ca. 2400-550 BP) (Figure 6.3). This, indicates that during this period, there was no evidence of subsistence associated with the use of fire or natural burning of the vegetation in response to rainfall variability. Archaeological evidence of human presence and activities is highly debated and various methods and dating quality relating to cut marks on bones (Perez *et al.*, 2005; Burney *et al.*, 2004; Hansford *et al.*, 2018), occupations in coastal rock shelters (Douglass *et al.*, 2018) and pollen and bone analysis (Anderson *et al.*, 2018) have estimated human colonisation to range from 10 000 cal years BP to 1350 cal years BP. The evidence therefore suggests that at Lake Longiza, if people were

present, then they were mainly foragers prior to and during that period. In fact, forager communities, known as the Mikea people, still exist in the western forest at present, even though agriculture and cattle are thought to have been introduced 1200 cal years BP (750 AD) (Burney, 1987b; Blench, 2008; Beaujard, 2012). If the charcoal result is overlapped with rainfall analysis (see: Chapter 5.1.4), the results indicate that from 450 BC to AD 1300, a succession of wet and dry periods associated with very low to no charcoal influx were recorded in the region. This indicates that rainfall apparently did not lead to a change in human subsistence from foraging to pastoralism around Lake Longiza, though changes in the vegetation were recorded in the pollen record (see Chapter 6.2.1).

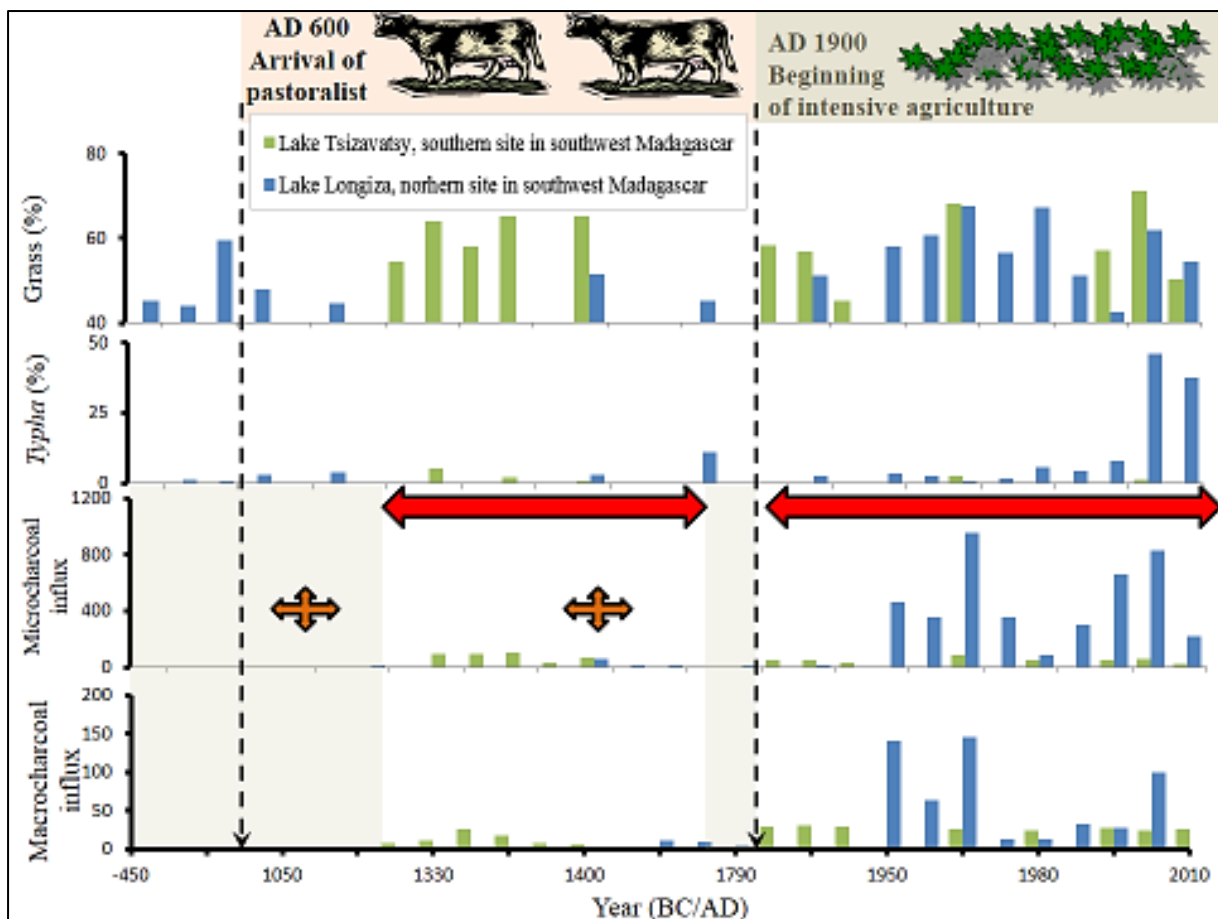


Figure 6.3: Pollen (grass and *Typha*) and charcoal evidence from LNG and TSZ cores in southwest Madagascar over the last 2400 years. Blue shows records from Lake Longiza in the northern site (core LNG) while green indicates records from Lake Tszavatsy in the southern site (core TSZ). Grey boxes indicate periods with very low to no charcoal while red arrows show periods with increasing fire events at both a regional and local scale. Orange crosses indicate charcoal peaks at Andolonomy in the southwest (Virah-Sawmy *et al.*, 2016) while bars represent records of the present research. Charcoal influx is expressed in particles. yr⁻¹ for macrocharcoal and cm².yr⁻¹ for microcharcoal. Note the increase in Poaceae percentage

coinciding with the increase in fire events at the near present period around AD 2000 for the northern site

The onset of microcharcoal peaks occurred around AD 1400 and AD 1300 respectively for Lake Longiza and Lake Tsizavatsy. Such increases happened during the wettest period (AD 1300-1450) in the rainfall record of the southwest over the last 700 years (see: Chapter 5.1.4). These increases in charcoal influx could be associated with increased biomass due to wetter conditions, which probably encouraged the expansion of pastoralism activities across the region. It is important to note that pastoralism was already present in the island since AD 600 (Anderson *et al.*, 2018). The results suggest that pastoralism, did not reach Lake Longiza until 800 years later (Figure 6.3). Pastoralism and agriculture might not have been practiced in the area surrounding Lake Tsizavatsy which may explain the persistence of the only forager community in Madagascar there, the Mikea people, until today. The evidence of human activities in combination with the wet period recorded in the southwest, and the presence of these small peaks of microcharcoal influx suggests regional expansion of pastoralism (though possibly not in the immediate vicinity of Lake Tsizavatsy). These microcharcoal peaks were followed by an increase in macrocharcoal influx in the vicinity of Lake Longiza in the northern site, at around AD 1600 which coincides with a record of fire from further south at Andolonomy at around AD 1500 (Virah-Sawmy *et al.*, 2016), suggesting movements of pastoralism in the west. The data suggest the presence of pastoralists settling during a wet period and are consistent with the expansion of agropastoralism activities across the southwest region from AD 1000 to 1600 but probably not around Lake Tsizavatsy.

After the macrocharcoal peak around AD 1600 at Lake Longiza, there was very low evidence of fire in the charcoal record of the core LNG in the northern site until AD 1920. The dry conditions in the region from AD 1600-1750 might have led people to migrate to wetter regions. Also, the lack of evidence for fire during this long dry period suggests that dry conditions alone do not trigger fire incidences (see: Chapter 5.1.4). A possible explanation is that people started to settle in the region during the wettest period (AD 1300-1600) but moved when the lake became too dry at around AD 1700 in search of wetter areas. They probably practiced zebu transhumance, a traditional agropastoralism in southwest Madagascar where cattle herders move their cattle long distances from settlements during certain periods of the year when water and food become scarce (Kaufmann and Tsirahamba, 2006; Von Heland and Folke, 2014; Feldt and Schlecht, 2016; Hänke and Barkmann, 2017).

Since AD 1920, there has been a continuous increase in fire with consecutive peaks of microcharcoal and macrocharcoal around AD 1952, AD 1960, and AD 2000 at Lake Longiza in the northern site. These changes in fire influx suggest agricultural expansion in the region which was favoured by national policies and international trade (Fauroux, 2001). This period marks the shift of subsistence from extensive pastoralism to agriculture dominated mostly by shifting cultivation recorded in the last 100 years in the northern site (Fauroux, 2001; Waeber *et al.*, 2015). For instance, various agricultural booms of crops such as rice (1900, 1940), maize (1930-1940), and butter beans (1920) were recorded in the region (Fauroux, 2001; Scales, 2011). This change is reflected in the pollen record with a sudden increase of Poaceae reaching approximately 67% of total pollen sum. In addition, disturbance indicator taxa such as *Polygonium* and *Ludwigia*, found in frequently flooded habitats, were recorded from AD 1960 onwards. This shift of subsistence into extensive agriculture probably increased the need for new arable land and would explain the increasing rate of fire in the last century in the vicinity of Lake Longiza due to forest clearance and preparation of the land for crop cultivation. Currently, Lake Longiza is surrounded by patches of rice field with degraded forest and savanna woodland (see: Chapter 4). The sediment in the core LNG in the northern site was clayey and dark in colour like that recorded in Kirindy forest, a protected area in the northern part of the study area (Felber, 1984; Ehrensperger *et al.*, 2013). The sediment also contains debris of ligneous and herbaceous fragments and has elevated organic and inorganic carbon content which is one indicator of higher soil fertility (Razafimbelo *et al.*, 2010). Alluvium soils along riparian areas provide fertile soils that favour agricultural practices (Du Puy and Moat, 1996). This area is known to receive more rainfall and is less subject to drought than the southern part of the study area (see Chapter 3). The availability of fertile soils and water explains the shift of subsistence by the occupants of the northern site from foraging and pastoralism to being more exclusively agricultural as corresponding with the high charcoal influx in the LNG core.

The core from the southern site (TSZ), with its unconsolidated sand, is typical of conditions encountered around the Mikea National Park (Stiles, 1998; Seddon *et al.*, 2000; Du Puy and Moat, 1996) where the climate is drier, and the rainfall record suggests faster aridification (see Chapter 5.1.4). This area is currently occupied by foragers and recent social studies suggest that they alternate between hunting and gathering and slash and burn agriculture of maize and cassava during the rainy season from December to March (Stiles, 1991; 1998). This practice explains the slight increase in charcoal in the TSZ core since AD 1910 while it remained

relatively low and stable in the last hundred years. The steady and stable rate of charcoal influx probably indicates the beginning of seasonal agricultural practice by these forager communities. With the low water availability, and low soil fertility, mostly composed of sand as confirmed in the lithology of TSZ core, these communities did not adopt radical shift in their subsistence, as occurred elsewhere in the region. Such conditions might also not have attracted other ethnicities to practice extensive agriculture even though the Masikoro and Antandroy ethnicities have been recorded practicing cattle grazing in the area (Stiles, 1998; Fauroux, 2001).

In addition to subsistence agriculture that involves fire, pollen results from Lake Longiza at the northern site showed a large increase of *Typha cf. angustifolia* (Typhaceae) within the lake ecosystem from AD 1990. Despite its invasive characteristics, it is suggested that it has various benefits including being used for food, livestock and craftwork, and it is currently exploited in the region and elsewhere (Grace and Harisson, 1985; Lebigre, 1997; Báez-Lizarazo *et al.*, 2018). It has been also identified as a key contributor to fodder biomass sources in the southwest (Ratovomanana *et al.*, 2013). This suggests the presence and the possibility of alternative subsistence practices through the trade of aquatic plants which has probably occurred at least since 1990s and the adaptation of traditional pastoral activities based on the exploitation of aquatic ecosystems.

To summarise, the charcoal and pollen records from the two lakes investigated here provide information on human subsistence in the region during the last 2400 years. The northern site initially occupied by foragers experienced the beginning of an expansion of pastoralism across the region around AD 1400. Extensive pastoralism was practiced until AD 1920, a period with a drastic increase in fire which suggested a shift to extensive agricultural activities probably because of high soil fertility and water availability in the northern site. Since the 1990s, possible alternative subsistence activity through the exploitation of invasive aquatic taxa such as *Typha* were likely practiced in the northern site as it is today in addition to pastoralism and agriculture. These shifts in subsistence did not, however, affect the southern site most probably due to infertile soil and water scarcity. Its occupants remained foragers until present day but included seasonal practice of agriculture (Stiles, 1991; 1998), which is explained in this study by the low and stable charcoal influx since AD 1910.

7. CHAPTER SEVEN: SYNTHESIS AND CONCLUSION

The influence of climate variability and human land-use in Madagascar is poorly understood due to the scarcity of palaeoecological records, especially in the tropical dry forests along the western region. There are few palaeoecological records along the western region for vegetation and climate (see Chapter 2). With the presence of the north-south rainfall gradient in Madagascar, the southern parts of the western regions receive less rainfall and experiences a more variable climate which perhaps affected ecosystems and livelihood strategies differentially. Similarly, both regions are occupied by different ethnicities that differ in their practices and subsistence strategies. This research has aimed to understand how and when land-use change, and rainfall variability impacted the landscape in the southwest region during the late Holocene, using dendroclimatological and palaeoecological approaches. New records of rainfall, vegetation and fire history were generated in this research in an area where there was previously none. Local and regional rainfall records of the last 700 years were generated through isotope analysis of four baobab trees (*Adansonia* spp.). The regional record was then compared with the available high-resolution climate records from Anjohibe Cave in the northwest where tropical dry forests also occur. Past vegetation and fire were reconstructed through pollen, carbon isotopes, and charcoal from two radiocarbon dated sediment cores from two lakes. The northern site, Lake Longiza, is currently surrounded by mosaic woodlands of degraded dry forest, large areas of cultivated land and a riparian ecosystem along the river Morondava. This area has higher soil fertility (Du Puy and Moat, 1996) and higher mean annual rainfall (Sorg and Rohner, 1996; Stiles, 1998; Randriamahefasoa, 2013). The southern site represented by Lake Tsizavatsy, is in an area of savanna woodland with lower soil fertility and more arid climatic conditions than the northern site. Results were interpreted in terms of the interacting effects of changing land-use and climate. To respond to the aims established earlier, three main hypotheses have been tested:

- Hypothesis 1: Southwest Madagascar has experienced a rapid decrease in rainfall in the last 700 years.
- Hypothesis 2: Biodiversity and taxa richness of the tropical dry forests in southwest Madagascar would decrease in response to a drying climate and an increasing fire regime over time.

- Hypothesis 3: The introduction and practice of pastoralism and agriculture in human subsistence led to an increase in fire influx over time but is directly dependent on soil fertility.

The main findings of this research are detailed in Chapters 5 and 6 with the results of rainfall reconstruction, vegetation and fire records. The discussion provides an interpretation of regional rainfall of the last 1700 years and the vegetation dynamics and fire events in the two sites. These chapters also discuss the variation in human subsistence within the study area and the impact of each factor including human land-use and rainfall variability on the tropical dry forests of sub-arid southwest Madagascar during the late Holocene.

7.1. Hypothesis 1: Rainfall of southwest Madagascar in the last 1700 years has been declining

The isotopic composition of four baobabs coupled with AMS radiocarbon dating provided a high-resolution proxy record of rainfall for the past 700 years (from AD 1300 up to present) for the southwest region, interpretable at decadal, multidecadal or centennial scales. In accordance with published palaeoecological investigations from the southwest, results found here suggest a decreasing trend of rainfall over time indicating a drying in the region with a higher variability at a century scale. Within the study area, this drying is more pronounced in the southern rather than the northern site. Over the long-term, durations of wet periods have decreased while those of dry periods have increased. At the beginning of the Little Ice Age, there was southward displacement of the Intertropical Convergence Zone (ITCZ) (Lechleitner *et al.*, 2017; Putnam and Broecker, 2017). This displacement would have led to a change in the rainfall pattern between the northwest and the southwest regions of Madagascar, from following in phases pattern of wet and dry periods to a dipole (antiphase) of rainfall as recorded from AD 1300 to 1700. Since AD 1700, similar patterns of rainfall have been experienced across the western region (southwest and northwest), a shift that is explained by the global climate forcing during the 17th century (Scroxton *et al.*, 2017). From these analyses, the results suggest that the rainfall in the southwest was variable in the last 1700 years, with a succession of wet and dry periods like to the northwest sub-region prior to the Little Ice Age. Patterns of rainfall then shifted until AD 1700 with a wet period in the northwest corresponding to a dry period in the southwest. Since AD 1700, an in-phase pattern of wet and dry periods was observed between both regions up to the present time.

The combined analysis of the four baobab records and the comparison with the oxygen isotope of the speleothem in the northwest provided the rainfall record for the southwest during the last 1700 years. From AD 300 to 500 the southwest region experienced a dry period, followed by wet period until AD 1000. Then a dry period was recorded from AD 1000 to 1250, after which, a very wet period was recorded in the southwest. The period from AD 1300 to 1400 represents the wettest period in the record followed by a decreasing but still wet period until AD 1600. The period from AD 1600 to 1800 represents the driest period peaking around AD 1700. A relatively wet period of about 50 years followed and then another dry period of 100-years. The last period from AD 1985 to 2000 was comparatively wet. Further investigation is needed, however, to evaluate the drivers of these rainfall patterns at a regional and sub-regional scale. Such variability of rainfall in the southwest region at decadal to centennial scales has impacted the tropical dry forest ecosystems of the region and accentuated or inhibited human land-use which will be detailed in the next section.

7.2. Hypothesis 2: Biodiversity is affected by both drying climate and human-induced fire during the late Holocene

The interaction between climate and human impact as drivers of ecosystem change remains a topic of debate in Madagascar. The evidence gathered through this study partly agrees with the synergy hypothesis (Burney, 2003; Burney *et al.*, 2004) and the aridification hypothesis (Virah-Sawmy *et al.*, 2010) to explain environmental change in the tropical dry forests in southwest Madagascar during the late Holocene. Records from two lakes in southwest Madagascar, suggest that both human and climate influences have, together or independently, impacted the tropical dry forest ecosystems in the southwest during the late Holocene. In the northern site, the pollen record at Lake Longiza shows that low rainfall (a long dry period recorded until AD 500) triggered a shift of abundance in grass and xerophytic taxa at around AD 420 leading to a more C₄ dominated landscape. This opening of the ecosystem was simultaneously experienced in the southwest region as recorded in another published pollen record in the spiny thickets at Andolonomy further south of the study area (Virah-Sawmy *et al.*, 2016). After a wet period of about 500 years, dry forest trees recovered slowly, and the landscape became dominated by C₃ plants at around AD 870, a recovery that was also recorded in vegetation analyses in the northwest tropical dry forests area (Voarintsoa *et al.*, 2017). This suggest that at least until AD 900, the tropical dry forests in western Madagascar was responding solely to the variation in rainfall.

A rapid transition into a more open landscape probably initiated by humans was recorded at Lake Longiza (northern site) at around AD 980, similar to that recorded for the northwest region of Madagascar (Voarintsoa *et al.*, 2017). This opening was demonstrated through the high prevalence of Poaceae in the pollen record, low prevalence of dry forest and riparian taxa, a decrease in C₃ plants in the sediment isotope record and an increase in charcoal peaks. A similar gradual change in the structure of the ecosystem was also recorded in the savanna woodland at Lake Tsizavatsy in the southern site of the present study and for a pollen record at Lake Ihotry around AD 1300 (Vallet-Coulomb *et al.*, 2006). These openings of ecosystems happened in one site after a long and wet period and in the other during a wet period in the southwest suggesting a non-climate related driver, most likely that of human activities such as the expansion of pastoralism which favours enhanced grass biomass.

Since AD 1900, the landscape appears to have been heavily impacted by human land-use and climate change given the high abundance of grass, pioneer species and xerophytic taxa and changes in the C₃ plant abundance in the sediments. The mosaic vegetation of dry and riparian forest recorded in the LNG core from the northern site demonstrated a high abundance of Poaceae and pioneer taxa associated with a high influx in charcoal, which corresponds to the increase in agricultural practices at the beginning of the 20th century. This was because of the, more fertile, alluvial soils in this area with higher carbon content and higher water availability, which favours agricultural practice. Such practice explains the current state of the ecosystem which is surrounded by patches of rice fields with degraded forest and savanna woodland (see Chapter 3). In the southern site which has less fertile soils and a more arid climate with a higher rate of decreasing rainfall (see Chapter 5.1.4), the ecosystem was more impacted by desiccation. Here, the savanna woodland ecosystem showed a high abundance of xerophytic taxa in the pollen record since AD 1910 in comparison with the northern site core where it only increased in abundance from AD 1985. The influence of humans on the ecosystems in the southern site manifest in declines of trees since AD 1950 probably related to selective logging practiced by non-forager ethnicities living outside the Mikea forest (Stiles, 1998). In summary, the evidence from this study suggests that the current vegetation across time and the study area is differentially human-impacted. The vegetation is more open, having been converted for agro-pastoral activities around AD 1400 and then intensive agriculture from AD 1900 at the northern site while more pronounced aridification effect was recorded in the southern site, which is less intensively used by humans.

7.3. Hypothesis 3: Shift in subsistence strategies to pastoralism and agriculture has increased human-induced fire and was directly dependent on soil fertility across the southwest Madagascar

The results from this study demonstrate the presence of different subsistence strategies occurring simultaneously but not homogeneously across the southwest region. The region was thought to be initially occupied by forager communities until AD 600 (Anderson *et al.*, 2018). However, a change to extensive agriculture was recorded in the northern site while foraging was maintained by the Mikea people (the only hunter-gatherer communities in Madagascar today) in the southern site. In the northern site, around Lake Longiza, the charcoal data from this study suggests that there was a shift in human subsistence from foraging into pastoralism around AD 1400, despite the recorded presence of this activity in the region since AD 600, some 800 years previously (Anderson *et al.*, 2018). From AD 1900 there was a change in crop cultivation which was related to an increase in Poaceae pollen and charcoal influx, alongside presence of pollen of pioneer taxa, indicating disturbance most likely because of extensive agriculture due very likely to the agricultural booms around that period (Scales, 2012; Waeber *et al.*, 2015). A shift in human subsistence from extensive pastoralism to extensive agriculture probably was possible because of the fertile soil and water availability in the region, similar to most areas with tropical dry forests (Portillo-Quintero *et al.*, 2015). Since AD 1990, there is also a recorded exploitation of aquatic taxa especially *Typha cf. angustifolia* confirmed by oral investigations of human activities in the region (Gardner *et al.*, 2016) and the high abundance of such taxa in the pollen record.

In contrast, the charcoal prevalence in the southern site from Lake Tsizavatsy remained low during the two periods covered by the core. From AD 1300 to 1400, there was an increase in microcharcoal associated with the expansion of pastoralism across the region which decreased in the second period around AD 1910 to 2010. However, a slight increase but stable macrocharcoal influx was recorded in this second period (AD 1910 to 2010) and may be explained by the seasonal practice of slash and burn of agriculture around the lake. This suggests that the Mikea communities around Lake Tsizavatsy, the only foragers currently present in Madagascar, practiced their foraging activities while adopting seasonal practices of agriculture. The harsh conditions of soil and water scarcity in the southern site may explain its lesser use by to agropastoralist who did not extend their practice there. This research presented here is the first interpretation of palaeoecological analysis in terms of subsistence shift within two sites in the southwest Madagascar.

7.4. Future scenarios and conservation strategies adapted to the tropical dry forests in southwest Madagascar

At Lake Longiza in the northern site, the mosaic vegetation was dynamic during the late Holocene but displayed resilience to anthropogenic and climatic disturbance as indicated by the heterogeneity of the landscape. It might be expected that large scale anthropogenic activities related to the expansion of pastoralism, and extensive agriculture would significantly impact on the richness of the landscape over time. Taxa richness remained stable until charcoal influx became very high at the beginning of the agricultural expansion. After approximately 100 years, however, there has been an increase in taxa richness following the period of intense fire activity indicating a recovery of the biodiversity. This suggests that even if forest extent decreased over time, and was negatively impacted by fire, the remaining forest patches have acted as refugia and seed sources, allowing forest expansion when conditions became more favourable. Based on the abundance of the indicator taxa associated to the different ecosystems, the biodiversity of the landscape is determined by patch dynamics associated with the physical and biotic heterogeneity of the landscape. This leads to resilience over time without a regime shift to an irreversibly deforested landscape. However, recent industrial agriculture or mining projects (which are now becoming abundant in the area) as well as further extension of agricultural land would lead to a massive decrease of landscape richness.

Of the dry forest and riparian ecosystems that compose the mosaic vegetation in the LNG record, the dry forest ecosystem showed resilience to fire disturbance until it increasingly favoured the development of fire-adapted taxa. This indicates that there was a non-linear response to fire. Similarly, dry forest trees were reduced during a dry period and were replaced by xerophytic taxa, especially during long dry periods followed by short wet periods. With increasing fire events, the abundance of xerophytics was reduced. In the future, with continued increases in fire and disturbance, we may predict a certain limit of fire threshold that would prevent successful regeneration of dry forest evergreen and xerophytic species. A calibration study of past and current charcoal influx in the region like those conducted in various regions globally (Duffin *et al.*, 2008; Gillson and Ekblom, 2009; Adolf *et al.*, 2018), could be needed to help managers reduce fire to within the historical range of its variability. A more quantitative understanding of the level of response to fire could inform the design of fire management that preserves the resilience of the ecosystem and provides the best opportunity for a recovery of the dry forest. It is essential to reduce the clearing of the forest which is one of the major factors impacting directly on the abundance of trees in this ecosystem, and therefore on its resilience

and adaptive capacity. The riparian forest declined over time in response to human land-use and fire activities, suggesting either more intensive land-use of this vegetation type, or that it has lower resilience. This ecosystem is vulnerable in the face of increasing human population and aridification. The riparian ecosystem should be considered a conservation priority and it is essential to include it within protected area schemes to act as refugia for species with very specific requirements. Such strategies applied to each ecosystem within the mosaic would favour the heterogeneity of the landscape and thus participate in restoring biodiversity of tropical dry forests of the southwest Madagascar.

The Lake Longiza ecosystem also showed significant changes in its aquatic taxa component through the massive increase in invasive taxa *Typha* cf. *angustifolia* since the 1990s. This coincides with the appearance and presence of disturbance indicator taxa such as Onagraceae cf. *Ludwigia*. Such changes might indicate a shift in the state of the lake ecosystem which should be investigated further. However, considering the characteristics of *Typha* as a fast reproducer with an ability to survive under a broad range of climates and its benefits (see below), this taxon could be exploited to develop potential sustainable alternative livelihoods for the population to reduce their dependency on forests. This taxon is used in Madagascar and elsewhere for food, handcrafts, and construction. The development of such alternative livelihoods could benefit both conservation of the landscape and its associated ecosystems (dry forest, riparian forest, lake ecosystem) by reducing the propagation of such taxa within the landscape. It might also provide more sustainable livelihoods to rural households in the region.

At the southern site, Lake Tsizavatsy, the vegetation has changed from a palm-*Pandanus* wooded savanna (AD 1300-1420) into a degraded palm-xerophytic savanna (AD 1910-2010) as evidenced by the increase of pioneer and xerophytic taxa during the two periods covered by the core. There was also a reduction of trees possibly indicating a loss of functional species (Oliver *et al.*, 2015) such as *Acacia* and *Arecaceae* within the savanna woodland. Conservation efforts targeting this ecosystem should be based on reducing the pressure on these functional tree species. These losses might lead to a decrease in the resilience of the ecosystem due to anthropogenic and climatic variability. Restoration of the abundance of these species within the ecosystem might be preferable, as in the long-term a possibility of a regime shift to grassland or bush xerophytic ecosystems might occur if no action is taken. Such action would avoid an ecosystem shift and thus reduce the loss of ecosystem services as indicated in the Figure 7.1. This strategy of conserving functional taxa is cost effective compared to the establishment of new protected areas in a site where human land use is within the landscape. It is important to

inform human communities about the importance of these species and provide support in terms of materials for replanting or maintaining the abundance of such taxa in the landscape.

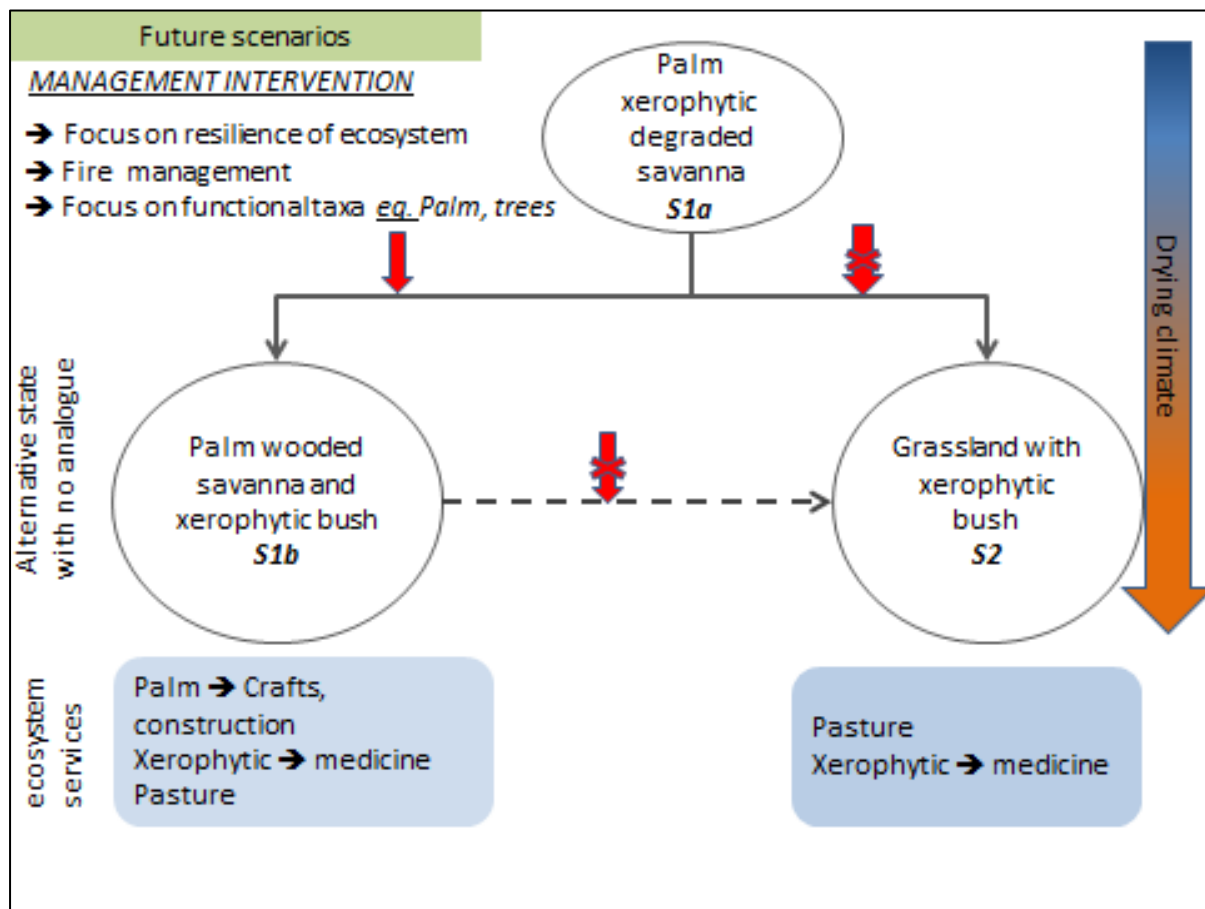


Figure 7.1: Future scenarios of vegetation change and ecosystem services with and without management interventions as indicated by red arrows. It shows the direction of the ecosystem state response to increasing disturbance and provides insight into the potential of an ecosystem shift. The ecosystem services provided by both scenarios are indicated in blue.

Despite the increase in rainfall in the last 20 years, the continuous decreasing trends of rainfall at centennial scales as recorded in the present research might affect human subsistence across southwest Madagascar. Given this scenario, agropastoralists communities will have difficulties in the southwest region. They might increase the practice of slash and burn even on infertile soils and reduce the time of abandonment of the “Monka” to conduct agriculture. This will result in the permanent loss of soil fertility when combined with natural hazards (Gay-des-Combes *et al.*, 2017) and will have higher impact on the biodiversity of the region. These agriculturalists might also conduct activities that are forest dependent, during dry periods, as a safety net. Activities such as woody charcoal production are already conducted today in the southwestern region (Raoliarivelo *et al.*, 2010; Gardner and Davies, 2014; Randriamalala *et al.*, 2016). Such activities will permanently impact the structure of the vegetation and in the long

term might lead to a regime shift of the ecosystem state to irreversibly degraded grassland. The Mikea communities, who are foragers, will be less affected by such desiccation as they are used to the harsh conditions with low water availability and have adapted their subsistence strategies to variable rainfall. They might be impacted by the reduction of available food resources within their forest due to pressure from agropastoralism practices or the adaptability of these resources to the changing climate. Conservation management of these areas occupied by these forager communities in the form of protected areas would provide sustainable subsistence strategies for these communities. Such management would reduce pressure from clearance and selective logging on ecosystem resources and allow natural regeneration of species that provides ecosystem services for such communities.

7.5. Significance of the study and research opportunities

This thesis made a significant contribution by generating palaeorecords for climate and vegetation in southwestern Madagascar, a region previously without such record. It established interpretations of biodiversity's response to rainfall variability and human land-use, and suggested conservation priorities based on vegetation history. The newly generated rainfall record has the potential to inform further research on scenarios of climate change and its drivers at national and international scales by comparison with existing palaeoclimate datasets and climate models. Increasing the spatial coverage of high-resolution records available for Madagascar is still necessary considering the north-south and east-west rainfall gradient that is currently associated with trade winds variation, topography and cyclone genesis (Donque, 1972; Jury, 2016). Hence, proxies such as diatoms (Gasse and Van Campo, 2001; Virah-Sawmy *et al.*, 2010; Williamson *et al.*, 1998), tree rings (this research), coral reefs (Brook *et al.*, 1999; Grove *et al.*, 2013), and speleothems (Burns *et al.*, 2016; Voarintsoa *et al.*, 2017; Scropton *et al.*, 2017) could be explored, with the ultimate goal of testing climate models through hindcasting. Obtaining a national scale palaeoclimate dataset would improve the understanding of the patterns and change in the island's rainfall patterns and drivers' over time to enrich predictions and climate change scenarios at a more worldwide scale.

A more global impact of the record generated here would to compare and analyse it with other tree records available for southern Africa to better evaluate regional drivers of rainfall within the Indian Ocean and southern Africa coupled systems (Woodborne *et al.*, 2015; 2016). Using the local record obtained from tree ring data across southern Africa and the present research in Madagascar, comparison and validation of existing models or theories of rainfall drivers within

this area could be evaluated. The great temporal and spatial variability of rainfall has made the prediction on a continental scale challenging (Tadross *et al.*, 2008). For the African continent, there is limited knowledge of natural variability of rainfall which is better understood through palaeoclimate records like those generated here. This limited knowledge hampers understanding of the regional climate system dynamics, which is further blurred by downscaling methods used in climate models (Tadross *et al.*, 2008). Data such as those generated here are important for understanding the natural variability of rainfall and deviation from variability when associated with anthropogenic warming. In addition, it can assist in the better evaluation of the adaptive capacity of societies in the event of climate change at a regional scale (Adger and Vincent, 2005). Moreover, the rainfall record generated here has provided an opportunity for the evaluation of biodiversity's response to rainfall variability over time. The effects of the observed drying trend are signals of future change that can inform biodiversity monitoring, and as the basis for assessing the responses of species distribution to rainfall variability. Integrating the patterns of rainfall identified here including the drying trends over time, allows better understanding of ecosystem change and improve the certainty of predictions of the distribution of the tropical dry forests. In such cases, this ecosystem might become reduced and replaced in some areas by a xerophytic dominated vegetation as is present today in the southern spiny thickets.

This research shows that ecosystems within the tropical dry forests of Madagascar have responded differently to climate and human land use over time, and it highlights some opportunities for enhancing livelihoods while restoring or maintaining resilience of forest mosaic and savanna landscapes. The work has succeeded despite challenges in pollen preservation at the sites, as evidenced by the hiatus at one of the sites, which is one of the limiting factors of palaeoecological investigations of tropical dry forests in arid areas worldwide (Chase and Meadows, 2007; Virah-Sawmy *et al.*, 2016). Establishment of reference material (pollen, diatoms) like those conducted in mainland Africa would facilitate further research (Gosling *et al.*, 2013) and might increase palaeoecological record in these areas. Increasing the availability of a database for fire (charcoal), climate (such as tree rings, diatoms) and vegetation (pollen) data for Madagascar and the African continents would facilitate future potential research in these regions, especially through informing models that explore the link between climate, land-use and vegetation. In Madagascar's case, an establishment of national maps of palaeo data associated with climate variation within the island's different ecosystems would aid in providing an understanding in differentiating anthropogenic and climatic events

on fire and vegetation. Moreover, an attempt in interpreting human presence and activities were conducted in the present research based on charcoal data and historical records, yet additional analysis of direct indicators of human activities such as herbivore dung spores is needed. Interacting drivers of fire variability (specifically climate and land-use) across different biomes in Madagascar also need to be investigated further for better fire management policy with the increasing population and future climate change.

Palaeoecological analysis from sediment cores in semi-arid areas is also challenged by their low temporal resolutions and the uncertainties associated with radiocarbon dates. The present research benefitted from multiple radiocarbon datings conducted on the trees and sediments, but results would have been enhanced with improvements on radiocarbon dates modelling and increasing accessibility. This is important for palaeoecologists, who need to balance the need for scientific rigour with the realities of working with disturbed sediments with poorly preserved palynomorphs. The challenges relating to radiocarbon date interpretation are recognised and many studies are now focusing on facilitating its interpretation (Blaauw, 2010; Blaauw *et al.*, 2018). Yet, these models do not provide a biological or environmental explanation of the outcome but are often limited to numerous simulations rather than addressing the complex taphonomy of semi-arid regions with variable rainfall and past or existing communities of mega-herbivores. In the present research, these challenges were resolved using Clam and combined with the local knowledge of the landscape history.

7.6. Conclusion

This research has provided new palaeoecological records and additional information about environmental change and history in Madagascar over the last 2400 years. Vegetation dynamics, fire history and rainfall variability were obtained through palaeoecological and dendroclimatological approaches. This research investigated the role of human land use and rainfall variability on the various ecosystems in the tropical dry forests area of the southwest Madagascar, and how these remaining mosaics of dry forest, riparian ecosystem and savanna have responded to climate and land-use change. From the analysis conducted here, we showed that tropical dry forests are resilient to rainfall variability and human land-use through fire as no regime shift were recorded, yet the results also indicated decreasing resilience associated with a loss of functional taxa, mostly woody. An increase in human pressure led to the opening of the ecosystem and the establishment of pioneer taxa while prolonged and pronounced dry periods increased xerophytic components of the vegetation.

The northern site within the study area demonstrated a greater impact by human activities than did rainfall variability over time. Large shifts of subsistence practices such as pastoralism or agriculture have affected not only the richness of the ecosystem but also the structure of the vegetation at a scale of decades. In addition, since the northern area contains more fertile soil, it is more favoured for agricultural practices. Over longer time scales, with dry periods exceeding 200 years, the impact of climate manifested by the increase in xerophytic taxa in the pollen record from Lake Longiza was recorded, like the case of the near present period since AD 1985. The southern site shows more impact of aridification as demonstrated by the high abundance of xerophytic taxa in the pollen record from Lake Tsizavatsy since the beginning of the last century (AD 1910). Despite the slight change in subsistence strategies adopted by the forager communities in practicing seasonal slash and burn agriculture, the ecosystem demonstrated less impact by their activities. The effect of humans within this ecosystem is most likely associated with selective logging practiced by agropastoralist ethnicities, neighbours of the Mikea people.

This study has increased the scientific knowledge of Madagascar's biota and has differentiated the specific roles of the climatic and anthropogenic drivers of change. This information might also help in informing ongoing debates over the disappearance of large herbivores in Madagascar during the late Holocene. In the present research, data were used to explore better conservation approaches to help maintain biodiversity in the landscape and to propose alternative livelihoods for the rural communities in southwest Madagascar and in regions where tropical dry forests occur. Specifically, the need to conserve and restore forest will be essential in building resilience to climate change but will require the development of alternative livelihood strategies that reduce pressure on forest species in the face of a changing climate.

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APPENDIX

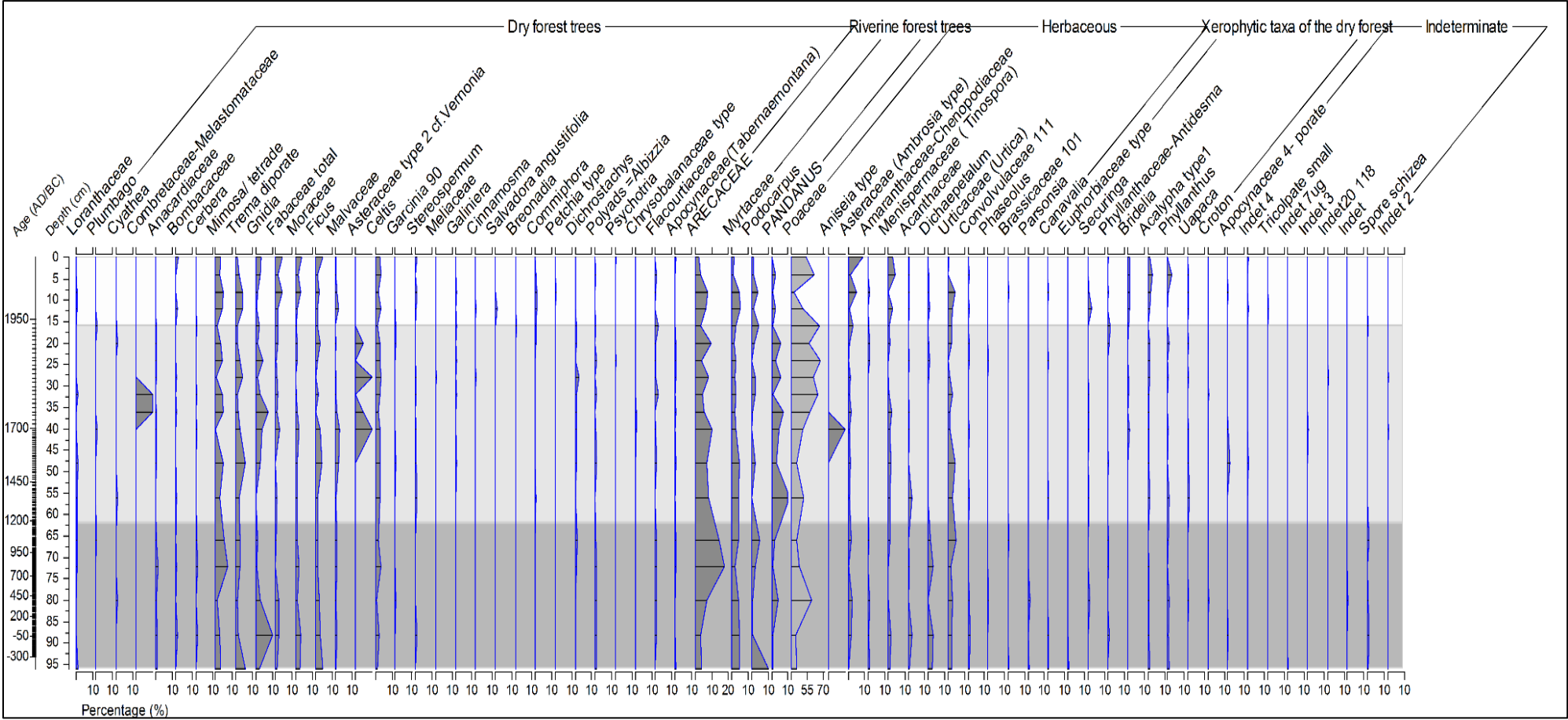
Appendix 1: Radiocarbon dates of each tree replicate from both northern and southern sites

	Sample ID	Core/ring number	Date (uncalibrated years BP)	AD Calibrated date 1sig, **2sig	Assigned year	Lab ID
Northern site	DFL	62	133.78±0.645PMC	1963	1955	IT-C-848
		121	1860.1±43.7	1743	1740	IT-C-851
		124	495.8±73.9	1610	1889	IT-C-365
		127	95.9±33.75	1880	1886	Not noted
		151	82.8±31	1868**	1862	IT-C-539
		199	127.3±38.2	1802**	1797	IT-C-1214
		250	253.6±30.2	1672	1669	IT-C-1213
		300	384.8±31.4	1548	1552	IT-C-542
		374	543.8±40.3	1409	1411	IT-C-850
		377	518.9±50.8	1409	1407	IT-C-878
		432	664±43.4	1307	1303	IT-C-145
		433	644.8±31.3	1298**	1302	IT-C-536
		DFS	40	129.09±0.481 PMC	1982	1986
	111		101.18±0.512 PMC	1956	1943	IT-C-846
	116		140.2±62.9	1949	1942	IT-C-856
	201		161.6±28.8	1835	1852	IT-C-1216
	205		349±76.2	1646	1845	IT-C-171
	251		47.4±40.4	1808**	1788	IT-C-847
	255		207.7±31.8	1804	1784	IT-C-858
	275		118.6±29.3	1806**	1760	IT-C-1215
	315		100.5±0.76 PMC	1713	1713	IT-C-624
	338		216.4±30.8	1680	1684	IT-C-541
	403	461.2±45.5	1498	1502	IT-C-860	
445	793±132.8	1389	1384	IT-C-173		

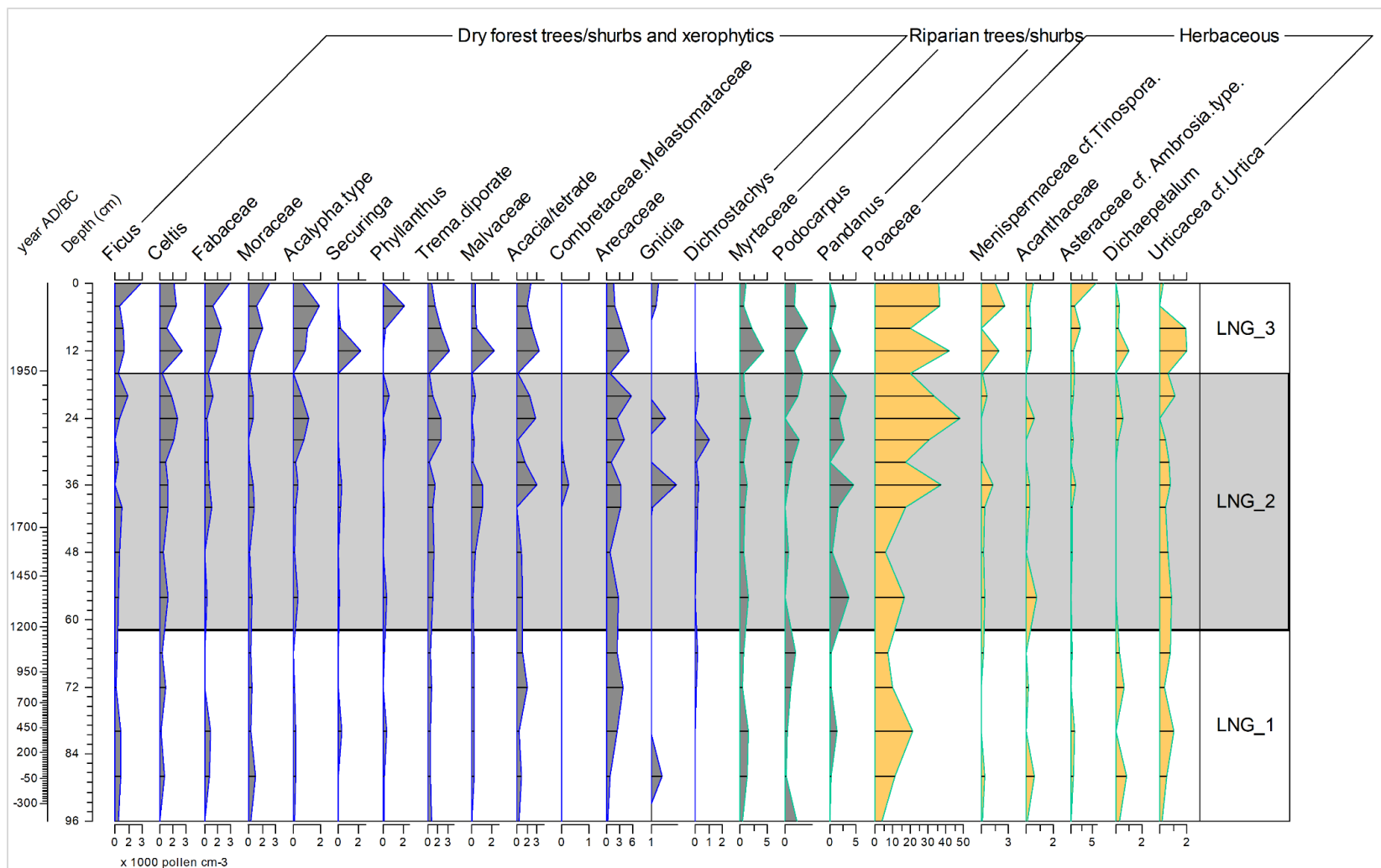
	Sample ID	Core/ring number	Date (uncalibrated years BP)	AD Calibrated date 1sig, **2sig	Assigned year	Lab ID	
Southern site	GTR	50	106.69±0.405 PMC	2005	2000	IT-C-544	
		148	148.57±0.52 PMC	1963	1951	IT-C-573	
		151	153.99±1.61 PMC	1964	1950	IT-C-367	
		183	206.5±42.8	1947	1933	IT-C-1050	
		188	99.914±0.525 PMC	1921	1932	IT-C-1072	
		219	101.27±0.615 PMC	1956	1916	IT-C-788	
		250	122.7±28.3	1866	1900	IT-C-1222	
		275	177.5±34.7	1836	1848	IT-C-1221	
		295	843±31.5	1220	1808	IT-C-575	
		299	109.7±96.9	1805	1800	IT-C-361	
		359	232±31.7	1675	1674	IT-C-540	
		403	508.2±54.9	1461	1487	IT-C-845	
		447	890.3±192	1310	1300	IT-C-668	
		TSP	26	136.98±0.438 PMC	1963	2007	IT-C-1273
			77	103.44±0.369 PMC	1956	1990	IT-C-1223
	126		100.21±0.395 PMC	1956	1973	IT-C-1219	
	159		104.81±0.611 PMC	1958	1962	IT-C-1217	
	226		102.79±0.371 PMC	1955	1940	IT-C-557	
	276		82.3±30.8	1925	1904	IT-C-1218	
	291		34.3±28	1897	1891	IT-C-574	
	298		125.8±30.9	1879	1885	IT-C-374	
	402		372.6±40.1	1496	1796	IT-C-849	
	405		287.5±28.3	1792	1793	IT-C-881	
	500		82.1±31.3	1712	1712	IT-C-558	
	512		190±44.2	1708	1701	IT-C-172	
	601		284.5±41	1544	1542	IT-C-556	
675	715.6±74.9		1326	1329	IT-C-1051		
705	252.1±31.1		1647	1246	IT-C-1058		

** indicate dates from 2 sigma-calibrated error

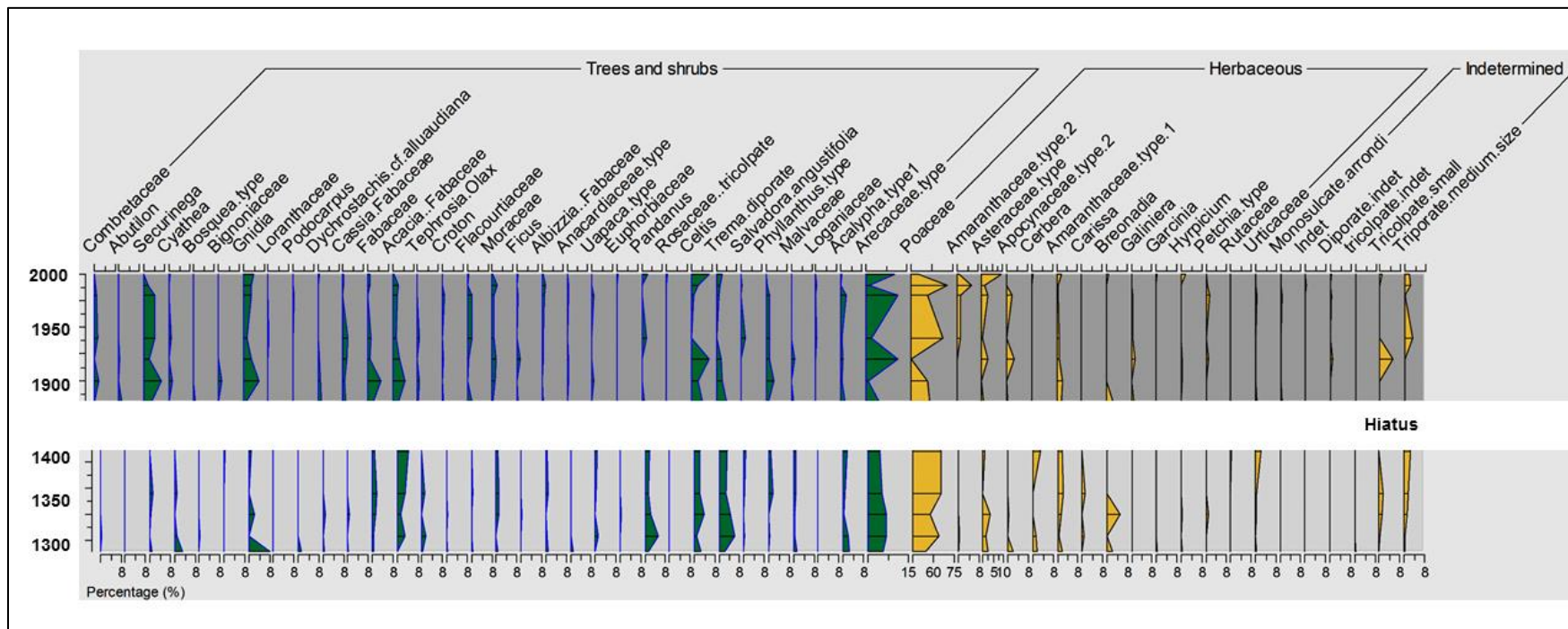
Appendix 2: Pollen diagram with relative abundance of all taxa identified and concentration of taxa with relative abundance higher than 2% in the sediment cores LNG and TSZ



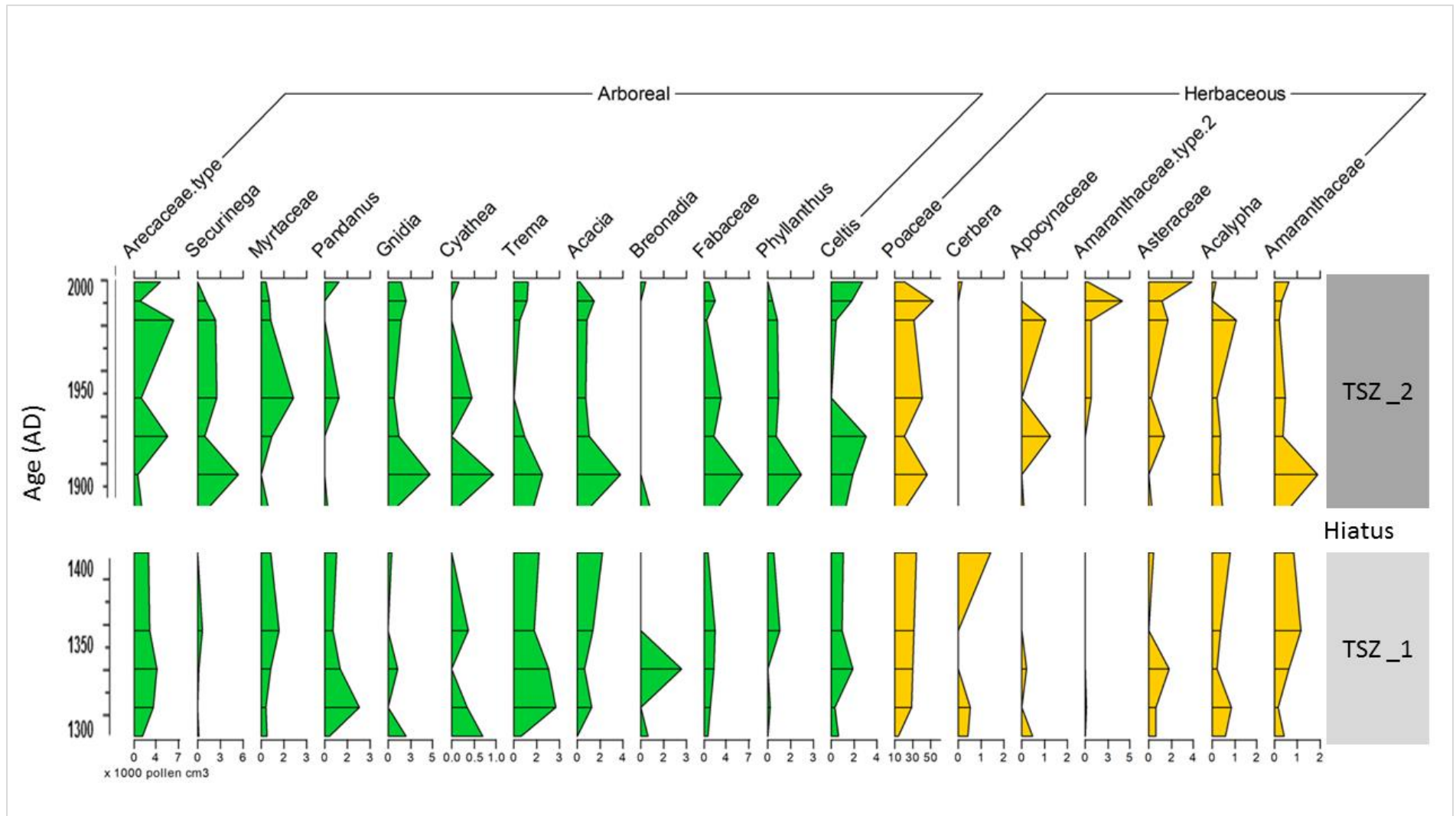
Appendix 2.1: Pollen diagram of all taxa recorded from the core LNG in the northern site from southwest Madagascar



Appendix 2.2.: Pollen concentration of LNG for the species with relative abundance higher than 2%



Appendix 2.3: All pollen type identified in the TSZ core from Lake Tszavatsy in the southern site in southwest Madagascar



Appendix 2.4: Pollen concentration of TSZ for the species with relative abundance higher than 2%

Appendix 4: Distribution of sediment and tree cores collected in southwest Madagascar during the field work in 2015



Appendix 4.1: Distribution of tree cores collected in southwest Madagascar (Google Earth, 2015)



Appendix 4.2: Sediment cores collected in southwest Madagascar (Google Earth, 2015)

