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**PALAEOECOLOGICAL EVIDENCE OF ECOSYSTEM
DYNAMICS IN SUMATRA, INDONESIA
CASE STUDIES OF TROPICAL SUBMOUNTAINS AND MANGROVES**

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“ All that I am, or hope to be, I owe to my angel mother”
Abraham Lincoln

I dedicated this work to my mother *Yustina Endang Sumarsih* – thank you for all the love, support and for believing in me through all my journey. I love you mother

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Summary

I worked on this thesis with the final aim of improving our understanding of the history and dynamics of the rich and diverse ecosystems in Sumatra, Indonesia. Using multi-proxy palaeoecological methods, I focused on the long-term vegetation and fire dynamics as well as human-landscape interaction in the highlands and mangrove ecosystems in the province of Jambi.

The mountain and mangrove ecosystems are an important component of Sumatra's landscape. These highly diverse ecosystems provide numerous ecological services as well as socio-economic function, but they are also sensitive to disturbance such as climate and human activities. I use the results of my research as a point of discussion for what are the most important drivers of ecosystem change as well as ecosystem resilience and recovery.

As part of the Pacific 'ring of fire', volcanism is one of the most important element in Sumatra and volcanic processes play an important role in the history of vegetation. A 5000 years old record from Danau Njalau in the Kerinci Seblat National Park (KSNP) provides first evidence on how much volcanism can impact the vegetation composition in the tropical mountain of Sumatra. Our palynological record show that the formation of the modern forest took several centuries after the volcanic deposition in the soil ended. The results also show no evidence for prehistoric human-landscape interactions in the area despite the close proximity to known megalith sites. The local fire reconstruction indicates that fire was rare for the last 5000 years and the phases of increased fire frequency could not be linked to either any of the vegetation phases or regional climatic changes. Our results overall suggest the effect of volcanism on the western side of Sumatra might be spatially and temporally more important than expected in shaping the composition and structure of these diverse rainforests.

A second record from the Kerinci valley, provides a better understanding of the history of human activities, another important driver of change in Sumatra. While today rice is the main subsistence crop in Indonesia, historical evidences of its cultivation are still scarce and there is no clear understanding to when rice was first introduced. The water buffalo (*Bubalus* sp.) was used in wet-rice cultivation to plough wet-rice field before the introduction of machineries. Therefore, finding evidence of the presence of swamp buffaloes can hint to important information regarding rice cultivation and its introduction in Sumatra. I used palaeoecological proxies like pollen and non-pollen palynomorphs to reconstruct the history of rice and buffaloes grazing in order to improve our understanding on when human activities intensified in Sumatra. Our results from Danau Bento are in agreement with the archaeological and linguistic records of the introduction of rice and the water buffaloes husbandry with the arrival of Austronesian migrant to Sumatra about 4000 years ago. Pollen results show an intensification of rice cultivation in the Danau Bento, at about 2500 years ago. A similar age was found in the Toba Plateau, in the north of Sumatra. Both these findings might suggest an increase in population and/or change in technology corresponding to the Bronze Age period in Sumatra. However, this phase

lasted only a couple of centuries until ca. 2100 cal yr BP. Following the decline of rice cultivation, the swamp forest never recovered and human continued to maintain the swamp as a grassland for buffalo's grazing. Overall the results indicate that men have shaped this ecosystems for thousands of years continuously.

Mangrove forests in Sumatra are widely distributed along the east coast of the island and provide important ecological services as well as socio-economic function. However, present development of mangroves is under threat due to human activities and possible effect of future sea-level rise (SLR). Our palynological record from a secondary forest in the Mendahara Ilir (MI), Jambi Province suggests that mangroves in the southeast coast of Sumatra could adapt to the changes in sea-level which have occurred in the past 2300 years. The pollen record and the sediment accretion suggests that mangroves in MI could keep up with a SLR of about 2.2 mm/yr (average), however the current estimate is above both the sediment accretion estimate and the rate of sea-level change experienced in the past 2300 years (0.68 mm/yr for the past 1000 years' transgression phase; 5 mm/yr current estimate for the last century; 7 mm/yr future estimate by 2100). Our pollen results show that even under a lower than current and projected SLR, mangroves migrated seaward (regression phase) and landward (transgression phase). If sea-level will rise at the pace predicted, mangroves will need a migratory path inland. This escape is however impeded, due to intensive human agriculture and urbanization in the coastal areas in Sumatra. With the application of palaeoecology, I could reconstruct thousands of years of vegetation history. Overall the results are important evidence of the role of human activities and volcanism in the highlands of Sumatra and the sensitivity of mangroves to future sea-level change.

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Outline of the chapters

This thesis comprises a preface which states the aims of the study in a synthetic way. The Introduction in [Chapter 1](#) is a general overview of Sumatra with a special focus on the highland and the coastal regions where this research is based. Themes of investigation highlighted in this research are presented in [Chapter 2](#). A description of the methods, the multi-proxy palaeoecological analyses and the study sites for this research are given in [Chapter 3](#). The chapters that follow are compiled using the manuscripts published in a peer-reviewed journals. The manuscripts were written based on three themes related to the main topic of investigations and are synthetically described below:

[Chapter 4 – Theme 1: Volcanism in Sumatra](#)

The effect of volcanism on submontane rainforest vegetation composition: Paleoeological evidence from Danau Njalau, Sumatra (Indonesia)

The importance of the role of volcanic processes in the vegetation history in Sumatra are investigated using palaeoecological analysis from a 5000 years sediment core in the submontane rainforest. The multi-proxy applied includes pollen and spores for vegetation and non-pollen palynomorphs (NPPs) and fire as disturbance indicators.

[Chapter 5 – Theme 2: Human History in Sumatra](#)

First palaeoecological evidence of Buffaloes husbandry and rice cultivation in the Kerinci Seblat National Park in Sumatra, Indonesia

We trace back the starting of rice cultivation and water buffaloes husbandry in the Kerinci valley using a sediment record from a swamp forest. Pollen and spores are used to reconstruct past vegetation changes around the site. Non-pollen palynomorphs (NPPs) of coprophilous fungi are used as markers for grazing activities and macro-charcoal analysis to reconstruct the local fire history.

[Chapter 6 - Theme 3: Mangroves and sea-level change](#)

Response of mangroves to late Holocene sea-level change: palaeoecological evidence from Sumatra, Indonesia

The effects of past sea level change on mangrove forest are reconstructed using palaeoecological analysis from a sediment core in Mendahara Ilir. The vegetation dynamics were reconstructed from the palynological record and compared with available sea-level data to investigate mangrove resilience to current and projected sea-level rise (SLR).

[Chapter 7](#)

In this final chapter I synthetized the main findings of the research, discuss conclusions and future possible research aspects.

PREFACE

General motivation and thesis aims

Tropical forest areas have unique ecosystems and they are acknowledged as global biodiversity hotspots (Myers et al. 2000). However, their existence and diversity are severely threatened by climate change and human activities which will affect the biodiversity and ecosystem function, as well as human community (Schüler 2012). Tropical rainforests are not all the same. In the island of Sumatra, where this research is based, several kinds of forest can be seen. This includes mountain rainforests, lowland dryland rainforest, peat-swamp rainforest and mangrove rainforest (Laumonier 1997; Whitten et al. 2000). Despite their diversity, the rainforests in Sumatra have been less studied compare to other forest in Indonesia (i.e Java and Kalimantan).

The main interest of this study is to reconstruct past vegetation dynamics and to highlight the effects of disturbance and change on these ecosystems in the long-term. I focus on two of the most sensitive and less studies forests in Sumatra: mountain rainforest and mangroves.

The principal aims of this PhD thesis are divided in 3 different themes which are explained in detail in Chapter 2. The overall aims are to:

- Provide an understanding on how much volcanism can impact the vegetation composition in the tropical mountain of Sumatra.
- Investigating the history of rice cultivation and buffalo husbandry in the Kerinci valley to improve our understanding of historical and prehistorical agriculture and human activities in Sumatra.
- Reconstructing long-term mangrove history to discuss resilience and sensitivity of these ecosystems to current and projected sea-level rise (SLR).

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CHAPTER 1: INTRODUCTION

Sumatra

Sumatra, with an area of 476,000 km² is the second largest island of the Sundaland (Sunda Region) after Borneo and the largest island in the Indonesian archipelago (Laumonier 1997). Sumatra supports an enormous biodiversity with various niches and diverse landscapes from the mountain to the lowland to coastland.

The western part of the island is dominated by mountainous areas with the Barisan Mountains, which extend for the whole length of Sumatra in a narrow belt (Barber et al. 2005). The main peaks within the Barisan range are mainly quaternary or recent volcanoes, commonly rise 2000 m above sea level with the highest peak being Mt Kerinci at 3805 m (Barber et al. 2005; Bramley et al. 2004) which comprises the Barisan range. In the eastern part, on the other hands, lowland areas are extensive and traversed by various rivers. Closer to the coastline, the dryland forests are replaced by extensive peat-swamp rainforests and a belt of mangrove forests (Laumonier 1997; Whitten et al. 2000).

Each of these ecosystems is highly diverse. The forests in Sumatra support a wide range of vegetation types with very high species diversity. It is estimated that more than 10,000 species of higher (seed) plants, can be found in Sumatra (Whitten et al. 2000). Endemism is also high. In Sumatra alone, 17 endemic genera of plants are found (Whitten et al. 2000).

Formally, the forests coverage in Sumatra can be classified based on the altitudinal changes into lowland rainforest (0-800 m), submontane rainforest (800-1400 m), montane rainforest (1400-1900 m), upper montane rainforest (1900-2500 m) and tropical subalpine forests (> 2500 m). The present montane forest covers about 8% of all Sumatra, and it is mainly located at altitude between 800 m and 1800 m. While mangrove forest dominates the east coast of the island (Laumonier 1997).

Jambi Province where this study was carried out is in the center of Sumatra, which crosses from west to east. In this province in fact, all the different forest types in Sumatra can be found and it is therefore ideal for our research aims. For this research I selected two of these ecosystems, focussing on the submontane (highlands) and mangroves (coastlands). The highland of Jambi are the settings for the Kerinci Seblat National Park, the largest national park in Sumatra and one of biodiversity hotspot in the island. While the mangroves in Jambi are widely distributed along the eastern coastlines and covered about 13 thousands ha of the province (Agency of Survey Coordination and National Mapping Republic of Indonesia 2009).

Climate of Sumatra

Central Sumatra is characterized by wet tropical climate as it lies within the Intertropical Convergence Zone (ITCZ). Rainfall seasonality is not usually marked, but a long rainy season of 9–10 months is alternated with a shorter drier season of 2 or 3 months from June to August. This seasonality is the

results of monsoon dynamics over the region where the wet northwest (NW) monsoon peaks from December to February (DJF) and the dry southeast (SE) monsoon from June to August (JJA; Kalnay et al. 1996). The mean annual rainfall in Sumatra is very variable depend on the topography and ranges from over 6000 mm per year in areas to the west of the Barisan Range, to less than 1500 mm per year in some areas of the east (Whitten et al. 2000). Inter-annual variability in rainfall pattern is controlled by the changes in the phase of El Niño-Southern Oscillation (ENSO) and particularly in western Sumatra, by the Indian Ocean Dipole (IOD; Abram et al. 2007; Saji et al. 1999; Webster et al. 1999).

The highlands of Sumatra

Sumatra is known as one of the most tectonically active region on Earth (Salisbury et al. 2012) and on its territory numerous volcanoes are found. The Global Volcanism Program lists 35 active volcanoes on the island (average spacing of 50 km), and reports eruption activity at 13 volcanoes for the past 100 years (Smithsonian Institution 2013; Salisbury et al. 2012). Due to this, the island is known as arc of volcanoes. These volcanoes are part of the Pacific Ring of Fire, which is formed due to subduction zones between the Eurasian plate and the Indo-Australian plate (Francis 1993). The volcanoes formation in Sumatra is formed by uplift of sedimentary deposits i.e those in the Barisan Range and by volcanic activity such as Mt. Kerinci, Mt. Sinabung and Mt. Singgalang (Whitten et al. 2000).

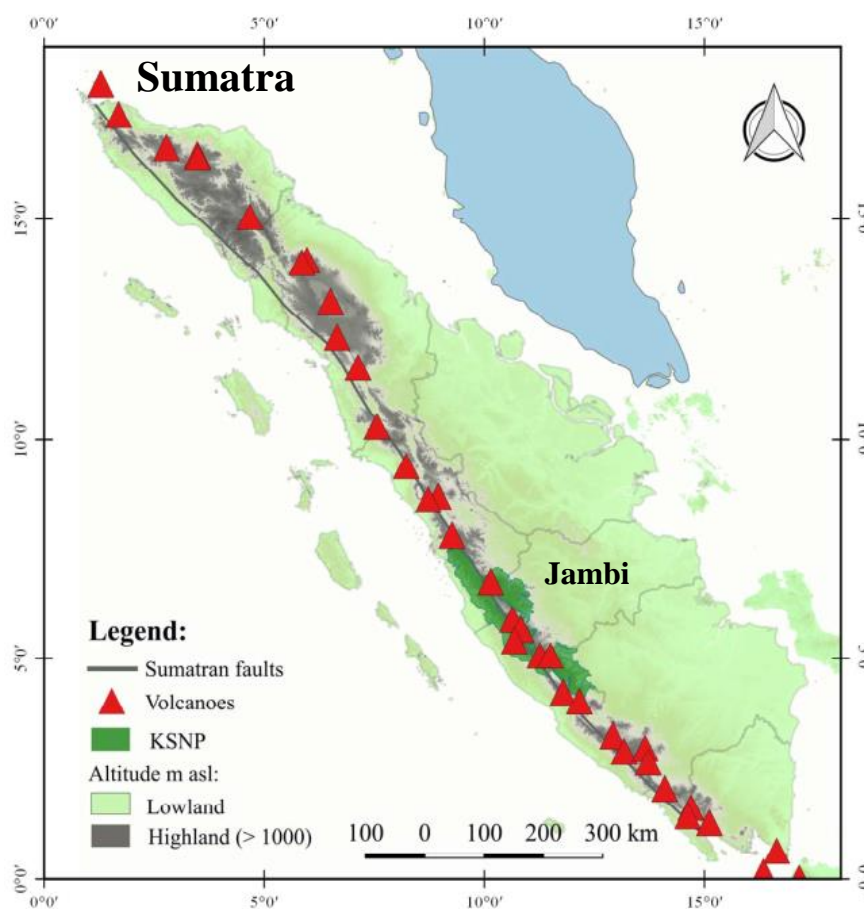


Figure 1.1 Map of the Kerinci Seblat National Parks along the active tectonic Sumatran faults. Red triangle shows active volcanoes. Data source for Digital Elevation Model (DEM): ASTER GDEM Version 2 from METI and NASA, and volcanoes from Global Volcanism Program 2013 (Volcanoes of the World, v.4.5.3. Venzke, E (Ed). Smithsonian Institution (Accessed 19 December 2016). <http://dx.doi.org/10.5479/si.GVP>

The Barisan Mountains are the main backbone of Sumatra Island and lies parallel along the whole length of the western side of the island. The Barisan Mountains are composed of an uplifted basement of Upper Palaeozoic and Mesozoic sedimentary and volcanic rocks, which finally form the currently active volcanic arc (Barber et al. 2005). The main tectonic feature of mainland Sumatra is the Sumatra Fault System (or Semangko Fault), a strike-slip dextral fault system that extends the whole length of the Sumatra. This fault runs through the Barisan Mountains and paralleled by a line of Quaternary volcanoes, mainly quiescent, but some currently active (Barber et al. 2005). The movement along this fault is associated with the oblique subduction of the Indian Plate beneath Sumatra (Curry 1989).

A significant part of the Barisan range falls in the boundaries of the Kerinci Seblat National Park (KSNP; Bramley et al. 2004; Figure 1.1). This national park located in west-central Sumatra, is the second largest protected area in Indonesia after The Lorentz National Park in Papua. The KSNP covers approximately 1.4 million hectares, spanning the provinces of Jambi, West Sumatra, Bengkulu and South Sumatra. The altitude of KSNP ranges from the lowland hill forests in Bengkulu at 200 m to the montane forests of Mount Kerinci at 3805 m, the highest point in Sumatra (Linkie et al. 2003). Its physical setting and location make KSNP as one of the richest conservation area in terms of biodiversity and the most undiminished of Sumatra's representative ecosystems (Bramley et al. 2004; Werner 2001). Well embedded in this rich and diverse protected montane rainforests, more than five active volcanoes, including the highest peak in Sumatra, Mt. Kerinci (ca. 3805 m), are found (Ohsawa et al. 1985). Mt. Kerinci is a young volcano and formed the youngest peak in a volcanic formation breaking through the Barisan range in an E–W direction (Jacobs 1958). The last major period of mountain building in the range occurred about three Mya (Whitten et al. 2000), suggesting that the still active Kerinci has a late Pliocene origin (Bramley et al. 2004).

Altitudinal zonation of the vegetation is divided into lowland (0–150 m), hills forest (150–800 m), submontane (800–1400 m), lower montane (1400–1800 m), mid montane (1800–2400 m) and upper montane and subalpine (> 2400 m) (Laumonier 1997). The lowland forest is known as ‘mixed dipterocarp rain forest’ after the dominance of this family. Further inland, the hill is dominated by Meliaceae and Sapindaceae with lesser extent of Moraceae and representation of dipterocarps. The vegetation in the submontane area is characterized by a dominance of Fagaceae, Lauraceae and Myrtaceae. These families are also well represented in the lowlands but are favoured here by the absence of dipterocarps. One of the commonest genera found in Sumatra from the Fagaceae family is *Lithocarpus*. While Lauraceae is mostly represented by the genus *Litsea*. Tree ferns are also common in lower montane forests, mostly with the genus *Cyathea* (Holtum 1977).

The level of human disturbance is higher in the valleys, where most of the original forest has been converted to rice cultivations and open grasslands. On the slopes the forest is still for the most of it primary. The main disturbance being due to agroforestry system and the local ‘garden’. The agroforestry main product is cinnamon (*Cinnamomum burmanii*) which are usually cultivated in the jungle garden system (Laumonier 1997). The agroforestry also comprises of large area of tea plantation.

The ‘garden’ refers to mono cultural estates (Laumonier 1997) for home gardening (berkebun), usually for planting annual crops and vegetables such as chilly (*Capsicum* sp.), Zea mays, egg-plant (*Solanum* sp.), and fruit such as banana (*Musa* sp.; Figure 1.2).



Figure 1.2 The ‘Garden’ of vegetables especially chilly, and spinach in the valley in the Kerinci Seblat National Park (Photo of S. Biagioni)

At higher elevation, the forest is completely protected and forest is untouched. Here the importance of epiphytes and mosses increases together with the dominant tree families like Fagaceae, Lauraceae, Myrtaceae, some Theaceae and Sapotaceae. The undergrowth is particularly rich in Myrsinaceae and Rubiaceae species. The upper montane forests consist of abundant bryophytes with a vast growth of Gleicheniaceae. In the highest subalpine level, the trees become twisted and shorter with dominant genera like *Myrsine*, *Ardisia* and *Vaccinium* (Laumonier 1997).

The coastal region

Mangrove ecosystems are widespread along the coastlines of the vast archipelago of Indonesia which for two-third is composed of water (Choong 1990). Owing to the availability of enormous coastal habitats with humid tropical climate, Indonesia has the largest mangrove area in the world (nearly 23% of the world’s mangrove with ca. 3.2 million hectares; Wilkie and Fortuna 2003; Agency of Survey Coordination and National Mapping Republic of Indonesia 2009). The Indonesian mangrove includes the highest number of species found in mangrove forests (Giri et al. 2011; Spalding et al. 2010) with about 150-200 species recorded (Soemodihardjo et al. 1993; Kusmana 1993). However, 80% of the individuals in mangrove forests belong to Rhizophoraceae (*Rhizophora* sp., *Bruguiera* sp., and *Ceriops* sp.) and 10% belong to the Avicenniaceae (*Avicennia* sp.; Vathana 1979).

Sumatra Island hold the third largest mangrove in Indonesia about 600,000 ha (Ilman 2016) which are widely distributed in the east coast of the island (Figure 1.3). In general, the mangroves are well developed at the Musi-Banyuasin delta in the South and at the Besitang delta north of Medan (North Sumatra; Laumonier 1997).

In total the Sumatran’s mangrove ecosystems are made of 157 mangrove plant species, out of the 202 total species recorded in Indonesia (Kusmana 1993). Amongst those species, only 17 trees are considered ‘true mangroves’ (Chapman 1976), or species that are limited to the mangrove habitat (Garcia et al. 2014). These species belongs to several genera (*Rhizophora*, *Bruguiera*, *Sonneratia*,

Avicennia, *Ceriops* and *Lumnitzera*; Chapman 1976) in four families (Rhizophoraceae, Sonneratiaceae, Avicenniaceae and Meliaceae; Whitten et al. 2000).

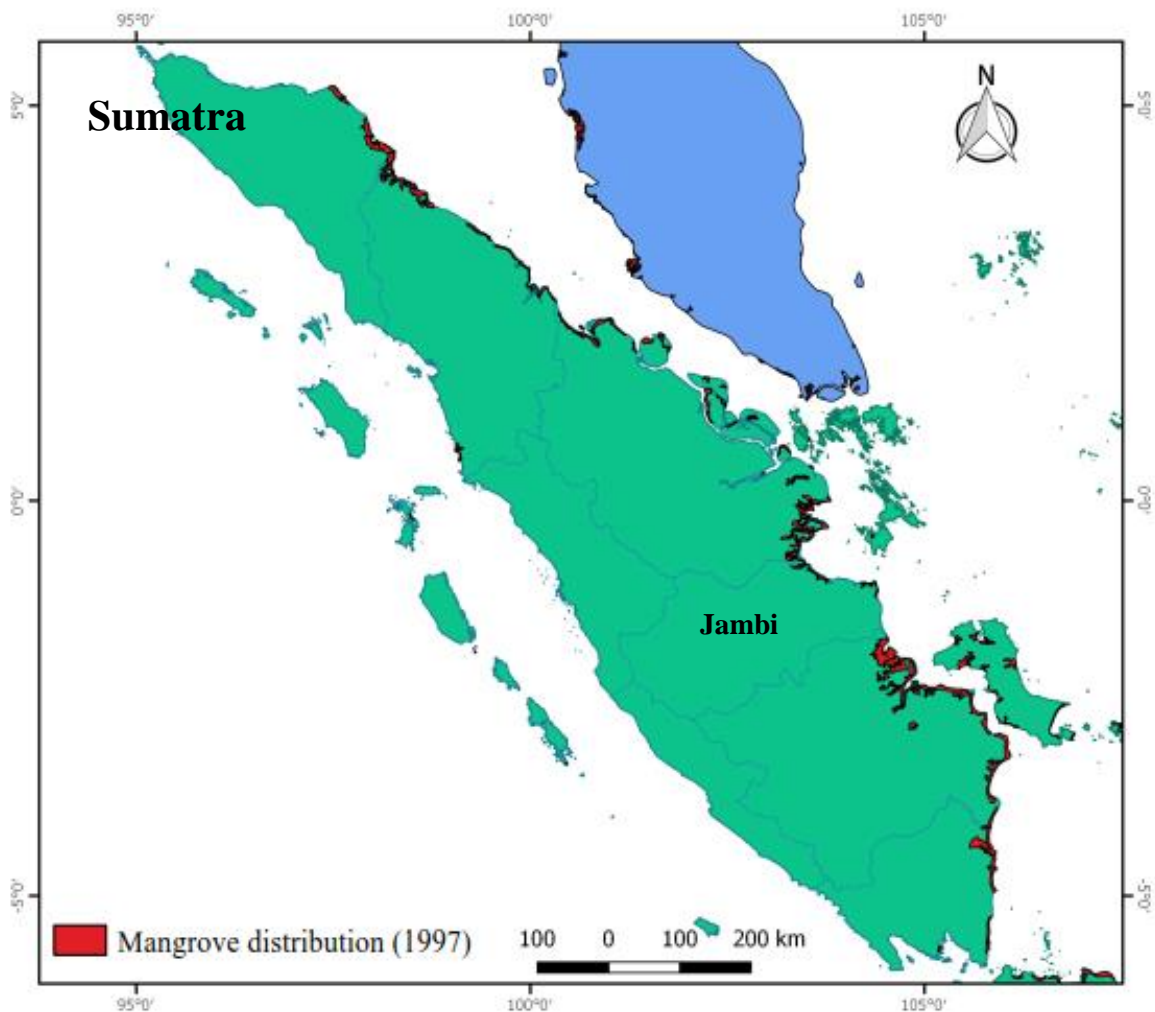


Figure 1.3. Mangrove distribution along the coastline in Sumatra Island (marked in red lines; data from Spalding et al. 2010)

Mangrove forests provide numerous benefits and ecological services such as coastal protection and buffer against sea waves, fine sediment trapping, prevent soil erosion and seawater pollution, as well as biological function by providing food and wildlife habitat for migratory bird. Mangroves also support economic well-being of the localities from its product, fisheries, etc. (Choong 1990; Gedan et al. 2011; Hashim and Catherine 2013; FAO 2007; Scavia et al. 2002; Sasekumar et al. 1992). However, despite the ecological function and the economic benefits they provide, mangroves face a huge threat in their future development.

Besides human activities, the other major concern for mangrove ecosystems is the effect that future climate change, especially sea-level rise (SLR; Krauss et al. 2014) might play on these ecosystems. Sea-level rise become a special concern for coastal land conservation and will have a tangible effect on the coastal region and small islands in Indonesia (Alongi 2015; Duke et al. 2007). This is because mangroves are sensitive to changes of frequency and duration in inundation and salinity levels that

exceeding the tolerance of a species physiological adaptation limit (Ball 1988; Friess et al. 2012). Furthermore, as many mangrove ecosystems are enable to migrate inland because of artificial blockage i.e sea wall and dikes (Krauss et al. 2014). Thus, SLR can threaten the long-term sustainability of mangrove ecosystem and its distribution in the intertidal zone (Nicholls and Cazenave 2010; Woodruff et al. 2013; McKee et al. 2007; Gilman et al. 2008; Rogers and Saintilan 2008).

As SLR can threaten mangrove ecosystems and their distribution in the coastal areas in Sumatra, long-term studies are needed to improve our understanding of mangrove ecosystem dynamics and the relation with sea-level changes and coastal development. However, in Sumatra, major studies on mangrove ecosystem have been concentrated only on the mangrove fringing in the southern part of the island (Figure 1.4; Sabar et al. 1979; Soeriaatmadja 1979; Sukardjo 1979; Sukardjo and Kartawinata 1979) and were limited to post-glacial sea-level rise and coastal development which are unrealistic scenarios in the future (i.e Yulianto et al. 2004, 2005; Ellison 2005; Engelhart et al. 2007; Soeriaatmadja 1979; Sukardjo 1979; Sukardjo and Kartawinata 1979; Horton et al. 2007; Anshari et al. 2001; Figure 1.4)

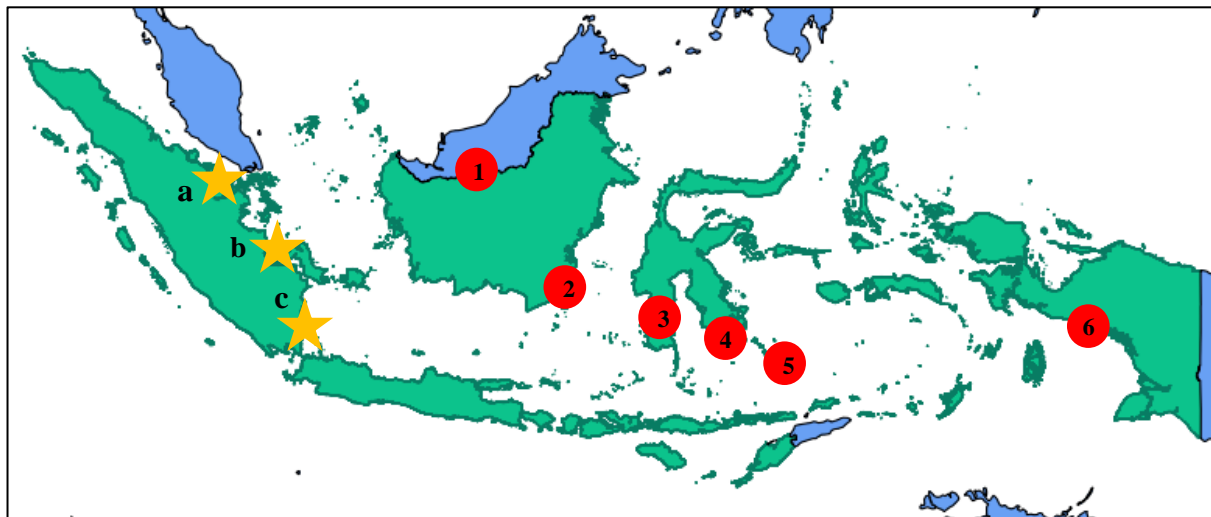


Figure 1.4. Studies on mangroves ecosystem in Sumatra. Yellow star show studies on fringing mangrove in (a) Riau (Soeriaatmadja 1979), (b) Musi River, South Sumatra (Sukardjo and Kartawinata 1979), and (c) South Lampung (Sukardjo 1979). Red dot show studies on mangrove and sea-level change in (1) Lake Sentarum, Kalimantan (Anshari et al. 2001), (2) Batu Licin, South Kalimantan (Yulianto et al. 2004, 2005), (3) Pare-pare, South Sulawesi (Yulianto et al. 2004), (4) Wakatobi Marine National Park (Engelhart et al. 2007; Horton et al. 2007), (5) Island of Buton (Engelhart et al. 2007), and (6) The Ajkwa and Tipoeka estuaries, Southern Irian Jaya (Ellison 2005)

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CHAPTER 2: THEMES OF INVESTIGATION

Theme 1: Volcanism in Sumatra

History of and present volcanic activity in Sumatra

The volcanic arc known as the 'Sunda Archipelago arc', encompass Sumatra, Java and Nusa Tenggara islands and it lies along the western border of the Sunda shelf (Laumonier 1997). In Sumatra, volcanic activity apparently occurred continuously since the Cenozoic (Bellon et al. 2004). The tertiary volcanic episodes in Sumatra during the Late Eocene-Early Miocene can be divided into two phases based on the lengthy episode of volcanism: (1) Late Eocene-mid-Late Oligocene volcanism in Southern Sumatra, and (2) Late Oligocene-Early Miocene volcanic arc in western Sumatra within the present Barisan Mountains (Barber et al. 2005). Afterward, there may have been a period of reduced activity in the Late Miocene (Crow 2005). The volcanoes of the Quaternary period (the last million years) are located in the mountainous areas and are usually associated with faults (Whitten et al. 2000). The Quaternary

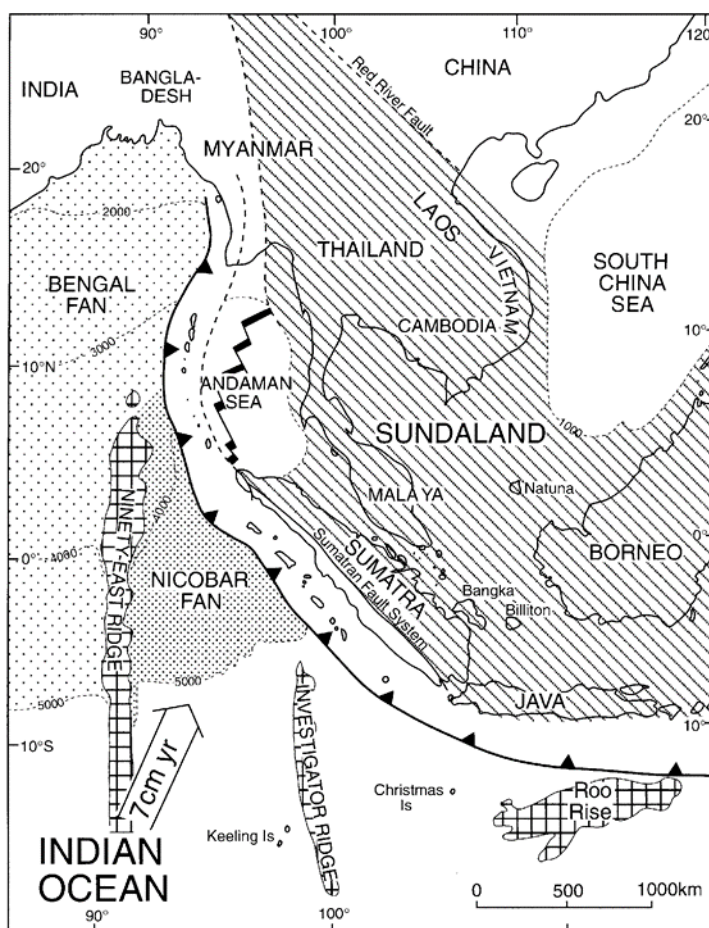


Figure 2.1 The tectonic setting of Sumatra show the subduction of the floor of the Indian Ocean beneath the southwestern margin of the Sundaland Craton. The toothed line marks the deformation front of the Sumatran subduction system; transform faults and spreading centres are shown in the Andaman Sea (from Curry et al. 1979)

volcanism is mainly characterized by intermediate-composition volcanism from stratovolcanoes of the frontal arc and by large silicic tuffs from caldera systems (Gasparon 2005). The present-day tectonic in Sumatra is part of an active south-western margin of the Sundaland (Sunda Craton), the south-eastern promontory of the Eurasian Plate (Figure 2.1)

Volcanic eruptions produce a large amount of ash which accumulates in screes on top of volcanoes. These products are barren, pervious, sterile, and unstable and tend to move downhill, particularly during heavy rains (Whitten et al. 2000). The products of Sumatra's volcanoes are generally rich in plagioclase and acid (dacitic to liparitic; Laumonier 1997). Andosol is the soil type which have develop on volcanic material,

characterized by the presence of allophones, very porous and rich in organic matter. The most common type is humic Andosols which occur on andesitic rocks on the slopes of the Barisan Range (Laumonier 1997). Therefore, the plants must have long, deep roots for anchorage and to find moisture to be able colonizing such ground. The first pioneers on Mt. Kerinci include Grasses (e.g. *Agrostis*), sedges (e.g. *Carex*) and the composite *Senecio sumatrana* (Frey-Wyssling 1933).

The impact of volcanic deposition on the vegetation

Volcanic eruptions are a major natural disturbances with varied and complex consequences (Del Moral and Grishin 1999). They can affects climate in term of composition of the atmosphere (Robock et al. 2009), and geochemistry on the surface (Arnald 2013). One of the greatest eruption of the past 100,000 years was the Toba super eruption in Sumatra of about 71,000 years BP (Zielinski et al. 1996) which led to a 'volcanic winter', a decrease in temperature between 3 to 5 °C and up to 15 °C in higher latitudes within worldwide (Rampino and Self 1992; Rampino and Ambrose 2000). It is clear that volcanic processes must play an important role in the vegetation history in Sumatra (Laumonier 1997).

The major component of volcanic eruption is a solid, lithic materials or solidifies into large particle referred as tephra or pyroclast as a broader term (Robock 2000; Manville et al. 2009; Schmid 1981; Francis and Oppenheimer 2004). Volcanic ash refers to tephra materials (or pyroclast) with diameter less than 2 mm (Macdonald 1972; De Paepe and Stoops 2007). While lapilli refers to coarse grained (>2 mm) tephra (Fisher and Schmincke 1984). Lapilli fall close to the source, while ash can travel hundreds of km. Ash and sulfuric acid may be erupted into the atmosphere and thus could affect climate or ecosystem hundreds of kilometres away (Inbar et al. 1995).

The volcanic processes (e.g tephra fall or pyroclastic flow) can be followed by one or more disturbance mechanisms such as erosion, abrasion, burial, heating, and impact force (Swanson and Major 2005; Peters et al. 2011). Tephra deposits usually spread homogenously at a landscape scale. They may cover large regions and their depth varies depending on distance to volcanic source (Del Moral and Grishin 1999). The impact of the eruption can create harsh conditions for plant establishment, either in sites affected by tephra deposition where either primary or secondary succession can occur, or in areas covered by lava flows where primary succession occurs (Titus and Tsuyuzaki 2003). The damage depends also on grain size of ash and season of disturbance (Mack 1981; Hotes et al. 2004). Tephra depth limits plant survival and growth because the tephra layer prevents the roots for reaching the pre-eruption fertile soil (Gomez-Romero et al. 2006). This suggests that thick tephra burial impedes survival and ensues primary succession. However, tephra can increase succession rates on lava if the vegetation still has root (Tagawa et al. 1994).

After the eruption occurred, several effects are possible on the ecosystem (Kuhry 1988; Crowley et al. 1994; Kovar-Eder et al. 2001; Hotes et al. 2001, 2006; Payne and Blackford 2008): (1) Physical impact of tephra which may lead to abrasion of plant surfaces, photosynthesis inhibition, blocking of stomata,

increased reflectivity, limitation in gas exchange between soil and atmosphere and crushing of plant tissues (Eggler 1948; Wilcox 1959; Cook et al. 1980; Bjarnason 1991; Clarkson and Clarkson 1994); (2) Impact on hydrology. The inclusion of tephra could increase the aeration (Hotes et al. 2004) and the deposition of thick tephra layers could set a surface ponding (Crowley et al. 1994); and (3) Chemical impact of tephra and tephra leachates. The elements released from volcanic eruption may be released both on initial contact with water (cf. Wissmar et al. 1981) and through longer-term leaching. Tephra leaching released most commonly elements including Cl, S, Na, Ca, K, and Mg (Smith et al. 1983). It is possible that tephra leachates might constitute either as supply nutrients (such as K) in an oligotrophic ecosystem or release elements that may be toxic to some organisms (such as Zn, Cu, Cd, Pb and Ba) (Gorham et al. 1987).

Theme 2: Human History in Sumatra

History of man and cultural phases in Sumatra

First settlement in Sumatra began with the ‘Hoabinhian’ who lived between 7000 and 12,000 years ago (Glover 1979) when man used stone implements (Forestier 2007) and develop culture stage of hunting-gathering (Whitten et al. 2000). The archaeological evidence from Tianko Panjang Cave in Central Sumatra indicates that human have only been present for 10,000 years (Bronson and Asmar 1975). Afterward, the only clear evidence of post-Hoabinhian pebble tool was found in the southern valley of Lake Kerinci in Air Hitam region (Bonatz 2006). Another finding in Bukit Arat, a production site of an early obsidian tools, which is located in the edge of modern rice fields in the fertile valley of Renah Kemumu, shows that in the past the settlement had been develop remarkably early (Bonatz 2012). From a chronological perspective, Bukit Arat marks the beginnings of a verifiable Neolithic settlement development in Highland Jambi about 4000 years ago with remains of tools such as axes, pottery, mats, and nets (Whitten et al. 2000). The highland-lowland connection already existed during this time, as evidenced by the finding of flake tools from chert and chalcedony which support the flake industry at Bukit Arat. The later phase of Bronze-Iron Age period, began around 3000 years ago (Harrison 1958), characterized by the evidence of elaborate pots and the first metal (Widianto 2009).

The next step in the settlement history of Highland is marked by an increasing degree of territorialisation to which both jar burial and megalithic sites in Renah Kemumu in Serampas and Lolo Gedang (Bonatz 2009) can assess. This ‘megalithic period’ in Highland Jambi lasted at most from the late 1050-650 cal yr BP and had its peak about 850 cal yr BP (Bonatz 2005; Tjoa-Bonatz 2009) evidenced by a single stone in connection to a house which was found in the excavated sites. Following the abandonment of the megalithic sites during the ‘Dark Age’ within 550-450 cal yr BP, the lowland-highland connections revived through trade under the influence of the Islamic rulers in Jambi during the late period of 350-250 cal yr BP. According to the manuscripts found in Kerinci, Serampas and Sungai Tenang (Bonatz

2012; Znoj 2009; Teh Gallop 2010), the population in Highland Jambi was considerably higher before it dropped off after 150 cal yr BP and early on the first millennium AD (Bonatz 2012; Neidel 2009).

History of human activities

The evidence of early human activities in Sumatra is still very limited, however recent palynological study from Sumatran lakes gave a hint based on the vegetation history (i.e Flenley 2013, 1988; Maloney 1980, 1981; Morley 1980, 1982; Whitehead 1985; Morley and Flenley 1987). Based on this kind of analysis, it was found that the first anthropogenic impact on the landscape dated about 7500 cal yr BP (Epipaleolithic) in where the forest clearing was linked to shifting cultivation (Laumonier 1997). However, the firmest evidence of forest clearing was dated after 6000 cal yr BP (Beginning of

Mesolithic) based on the palynological investigation from Danau Diatas (Lake Diatas), a mountain in the south of Padang (Maloney 1985) and in the Sungai Penuh valley in the south of Kerinci region at about 4000 cal yr BP (middle Neolithic).

Nevertheless, the first permanent clearing started about 2000 cal yr BP (Flenley 1988). A strong evidence from the Toba Plateau in the northern highland of Sumatra shown a major clearance which may relate to the introduction of rice cultivation around 2600 cal yr BP (Maloney 1985). The continuous expansion of anthropogenic vegetation may indicate the forest clearance intensification. This is possibly related to a change in agricultural practice or introduction of new technology (Maloney 1985).

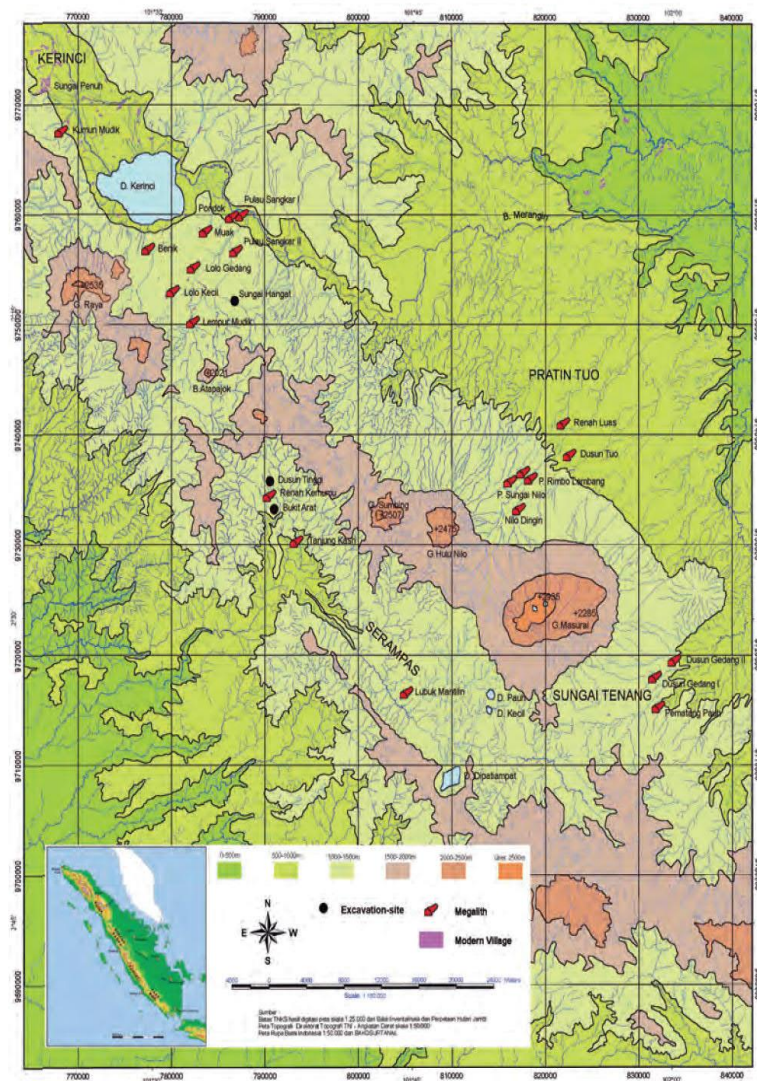


Figure 2.2 Location of archaeological and megalith sites in the Jambi Highland (from Bonatz 2012)

Theme 3: Mangroves and sea-level change

What is mangroves ecosystem and how do they work?

Mangroves are unique and complex ecosystems which consist of trees and shrubs that mainly grow along tropical and some of subtropical coastal regions (Choong 1990; Li et al. 2012). They form forests of salt-tolerant species, with complex food webs and ecosystem dynamics (Macnae 1968; Lugo and Snedaker 1974; Tomlinson 1986) and they are the transition between land and sea, thriving under adverse condition (Choong 1990). As a consequence their existence and diversity is strongly influenced by climate and coastal physiography (Grindrod et al. 2002) and factors such as salinity, soil type, temperature, duration and frequency of inundation, tidal and wave energy, accretion of silt, and periodic events such as cyclones and floods (Lugo and Snedaker 1974; Hutchings and Saenger 1987). The most suitable conditions for mangroves are provided by sheltered tidal settings, muddy sediments and high rainfall (Yulianto et al. 2004). To survive this environmental conditions, mangroves developed special morphological and physiological adaptation such as aerial roots, tidal dispersal of propagules, rapid rates of canopy production, viviparous embryos, absence of growth rings and highly efficient nutrient retention (Wegner 2010; Naskar and Palit 2015).

Sea-level change

Besides human activities (Richard and Friess 2015; Ilman 2016), the other major factor that can threat mangroves existence is climate change, especially sea-level rise (SLR; Krauss et al. 2014). A period of rapid rising in sea-level has started globally in the mid to late 19th century (Church et al. 2008), with an estimated increase of 3.2 mm/yr in the recent decades (Church and White 2011). Projections indicate this increase will continue to reach a SLR between 0.28 and 0.98 m by 2100 (IPCC 2013). The best scenarios suggest an average SLR of 40 cm (26-55 cm), whilst the worst scenarios anticipate an average of 63 cm (45-82 cm) by 2081-2100 (Godoy and Lacerda 2015). While, the current global mean for SLR for the last 20 years is 3.23 ± 0.4 mm/yr (Godoy and Lacerda 2015), it is estimated that SE Asia and the Western Pacific region will experience rise in sea-level in the range of 5-20 mm/yr (Nicholls and Cazenave 2010). These global estimates are however of little importance in this contest, as it is clear that SLR can be very different depending on the location (e.g Slangen et al. 2012; Perrette et al. 2013; Strassburg et al. 2015).

In Indonesia where thousands of island and large low elevation coastal areas are found, the current rate of SLR is much higher than the global mean (ca. 7.5 mm/yr; Nerem et al. 2010) and is predicted to accelerate in the future (Nicholls and Cazenave 2010). The SLR projection by 2100 will be 80 cm. This projection is slightly lower than the 1 m future global SLR predicted by the IPCC (2013). However, estimates vary depending on the period recorded, methodology and location. The eastern coast of North Sumatra shows a mean SLR of 5.0 mm/yr from a study using satellite altimetry for the period 1993-

2016 (Lumban-Gaol et al. 2017). In general, the rise in sea-level will have a significant impact on Indonesia coastal region, specifically on the mangrove ecosystem survival ability (Duke et al. 2007; Alongi 2015).

Mangrove adaptation and resilience to sea-level change

The response of mangroves to SLR projection scenario depends on the ability of species-specific physiological threshold to tolerate the frequency and duration of inundation as well as salinity level (Ball 1988; Friess et al. 2012). However, it is believed that mangroves can abide the risk of drowning, if they can keep up with rising sea level (Gilman et al. 2008). This ability is mostly related to their capacity of increasing surface accretion and positive surface elevation change (SEC; Krauss et al. 2010; Lovelock et al. 2010; McKee et al. 2012; Krauss et al. 2014), and their ability to migrate inland if necessary (Krauss et al. 2014). One of the major factor in determining these process is the availability of allochthonous sediment (Ellison and Stoddart 1991) which is allocated from river transport in deltaic riparian settings. Mangroves extensive root systems facilitate sediment increment processes through organic matter production and accretion, as well as mineral sediment trapping and intake (Krauss et al. 2014). While SLR causes subsidence to increase and sediment supply to decrease (Alongi et al. 2005), mangroves can counteract with their capacity to maintain soil elevation sufficient for plant growth through vertical sediment increment. This is the process that allows mangroves to avoid inundation and keep pace with SLR (Kirwan and Megonigal 2013).

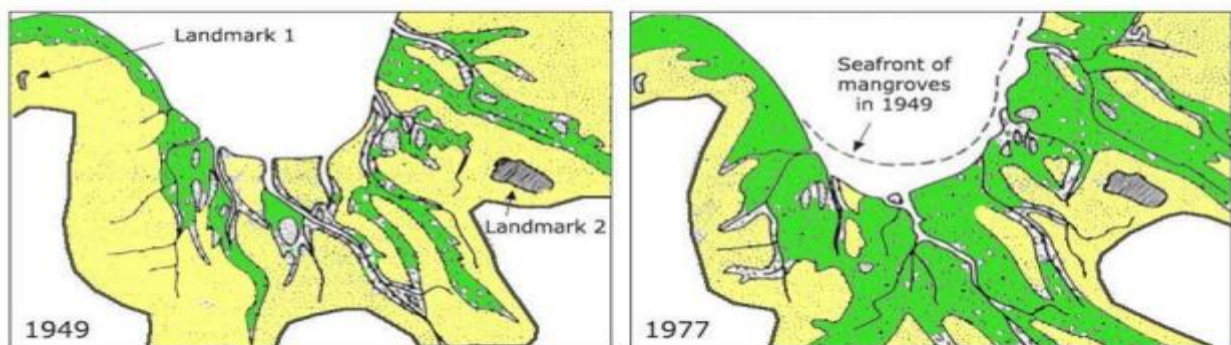


Figure 2.3 Successful mangrove landward adaptation to sea-level rise. Comparisons of mangrove distribution between 1949 and 1977 when mangroves have successfully encroached landwards (from Semeniuk 1994)

The second mechanism that allow mangrove to adapt to SLR is landward migration (Figure 2.3). If landward migration is not impeded by a strong increase of the topographical gradient, under low to medium sea level rise mangroves can shift without significant losses. In summary, mangroves ability to adapt to SLR depends on the availability of sediment and migratory paths inland (Krauss et al. 2014).

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CHAPTER 3: PALAEOECOLOGY

The multi-proxy approach in Palaeoecology

Ecosystems provide a balance interaction between biotic and abiotic components with internal and external driving factors (Birks and Birks 2006). In order to study the dynamics of a tropical ecosystem, past ecosystem reconstruction and biotic responses using the changes in fossil organism records and sediment characteristics ('proxy' data) are needed (Birks and Birks 2006). The used of more than one biological proxies to reduce the misinterpretation of single proxy-data is called multi-proxy (Birks and Birks 2006). This study was conducted using a multi-proxy approach in two different ecosystems in Sumatra, the mountain rainforest in the west and the mangrove forest in the east coast. Coring of sediment archives in Sumatra was obtained from two swamps in the highlands in the Kerinci Seblat National Park (KSNP) and one core was recovered from a secondary mangrove forest in the coastal area of Mendahara Ilir (MI). Palaeoecological proxies used include pollen, spores, non-pollen palynomorphs (NPPs) and charcoal. Further details on the application and methods will be given in the next part.

Palynology –methods and application

The words palynology derives from Greek (*παλύνειν*/palynein - to scatter and -logy) and literally defined as the "study of dust" or "particles that are strewn" (Faegri and Iversen 1989). Palynological study is one of the most widely used research tools in Quaternary studies. This analysis are used as an instrument to record the past and present vegetation composition and includes quantitative study of palynomorphs, which are objects microscopic in size of both plants and animal resistant to decay. The most widely used palynomorphs are pollen and spores. Pollen grain refers to a fine to coarse powder containing the male reproductive cells (Raven et al. 2000) which is formed in the anthers of the flower. Pollen grains are morphologically distinct for each plant so that it is possible to identify plant taxa, occasionally down to species by only investigating the pollen grains (Faegri and Iversen 1989). Spores are the microscopically, unicellular asexual or asexual reproductive units of cryptogams (such as algae, bryophytes, ferns and fungi).

The laboratory methods for pollen and spores are applied using standard techniques by Faegri and Iversen (1989) including HF 48% treatment and acetolysis (Figure 3.1). In pollen preparations, we often found other microfossils of various origins which are preserved in the sediment, such as algae (Korde and Juse 1966; Jankovská and Komárek 2000), eggs produced by aquatic flatworms (Haas 1996), Bacteria (Nilsson and Renberg 1990). The analysis of pollen are often combined with the study of these 'extra' microfossils called non-pollen palynomorphs (NPPs). The aim is to gain more information from

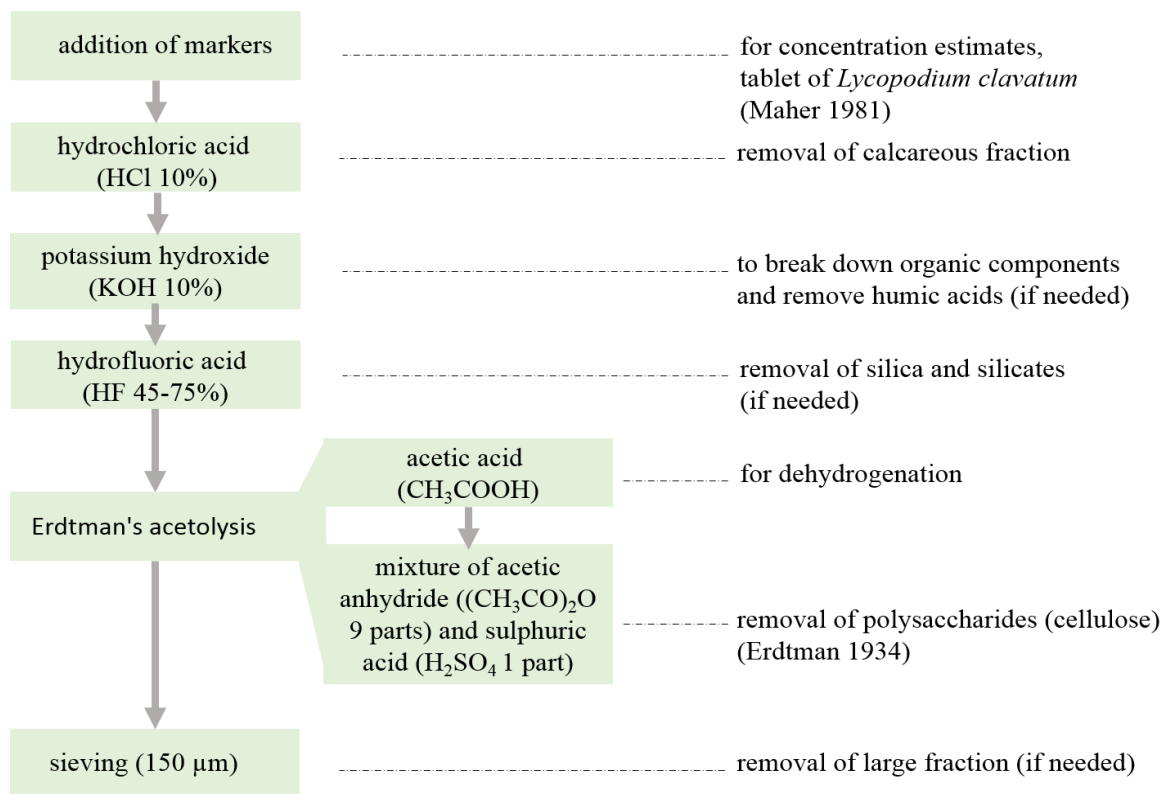


Figure 3.1 Workflow of palynological method applied in the research (modified from Faegri and Iversen 1989)

other palaeoenvironmental indicators (van Geel 2002). For examples specific NPPs can be used to link current environment condition with land-uses, or substrates, to modern NPPs assemblages from mosses, soils, litter, or even dead wood or water (Mulder and Janssen 1999; Mulder et al. 2003; Blackford and Innes 2006; Graf and Chmura 2006; Prager et al. 2006; Yeloff et al. 2007). They can also be used to assess the presence of past fauna, in particular herbivores (wild or livestock; e.g. van Geel et al. 1983, 2003; Davis 1987; Ralska-Jasiewiczowa and van Geel 1992; Hausmann et al. 2002; Bos et al. 2006; Davis and Shafer 2006; Mazier et al. 2009). Among the extra fossils usually studied are spores of fungi, remains of algae, cyanobacteria (formerly known as blue-green algae) and invertebrates (van Geel 2002).

Reconstruction of fire regime history

Fires can occur when there is sufficient combustible biomass (fuel) and an environmental condition that allow fuel and fire sustainability (e.g source of ignition and favourable weather). Environmental condition such as dry climate could increase fire as the biomass fuel become more combustible (Figure 3.2). Also human activities such as agriculture, logging and hunting are linked to burning. These conditions can translate in a different pattern, intensity and frequency of fire, which are characteristic elements for fire regime (Herawati and Santoso 2011).

Fire produces ash when the oxygen is abundant and combustion completely occurs. However, incomplete combustion of organic matter leads to carbonization or pyrolysis which produced an inorganic carbon compound called charcoal (Clark 1984; Patterson et al. 1987; Braadbaart and Poole 2008). Charcoal is produced in a high temperature between 280 and 500°C (Chandler et al. 1983). Lower or higher temperature will not convert the material into charred particles. Charred particles of

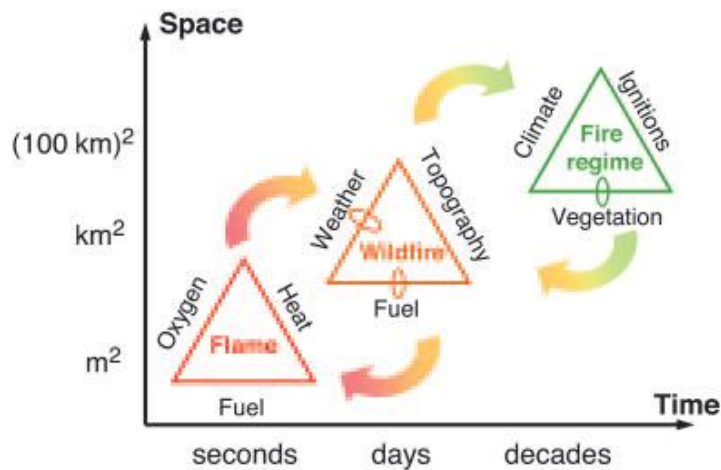


Figure 3.2 Controls on fire including broad scales of space and time, small loops, and feedbacks between processes at different scales a flame, a single wildfire, and a fire regime (shown with arrows) (from Moritz et al. 2005)

charcoal are deposited and preserved in a natural paleo-archives (lake, swamp, peats) during or following fire events due to its resistance to oxidation and microbial activity. There are two types of charcoal: (1) Primary charcoal, the material that is introduced during or shortly after a fire event; and (2) secondary charcoal is introduced during non-fire years, for examples as a result of surface run-off or erosion (Whitlock and Larsen 2001).

Charcoal analysis is used to reconstruct long-term variations in fire occurrence. The applications of charcoal as a paleofire proxy for paleoecologist include: investigating the link of climate-fire-vegetation study (e.g. Clark and Royall 1995; Gavin et al. 2006), analysis of prehistoric use of fire (e.g. Pitkänen and Huttunen 1999; Wick and Möhl 2006) and the investigation of regional and global biomass burning related to carbon cycle and the effects on the global atmospheric CO₂ concentration (e.g. Carcaillet et al. 2002). In general pollen and charcoal data from the same cores are used to study the past linkages between climate, vegetation, fire and anthropogenic activities (Whitlock and Larsen 2001).

Charcoal particles derived from plants and are visually recognizable as black, opaque, brittle and angular, with an elongate prismatic appearance possibly displaying some cellular structure (Swain 1973; Clark 1982; Griffin and Goldberg 1983; Patterson et al. 1987; Enache and Cumming 2009). Other black particles in the sediment such as fragments of plant, mineral and insect cuticles may sometimes be misinterpreted with charcoal (Whitlock and Larsen 2001). Charcoal particles can be differentiated morphologically (e.g bark, trunk, leaves and branches) but their shape depends also on the temperature of formation beside the fuel. Additionally, the initial morphology is often modified through taphonomic processes (Enache and Cumming 2009), as charcoal fragments can be transported for kilometres before to burial (Garstang et al. 1997; Clark et al. 1998; Pisaric 2002). Charcoal size are classified into two classes based on the distance from fire source and the signal they bare as: microscopic (micro) charcoal with size <125 µm (e.g. Swain 1973; Cwynar 1978; Clark 1982) for regional or long distance-transported signal of fire reconstruction and macroscopic (macro) charcoal with size >125 µm to

reconstruct local signal of fire (fires (e.g. Millspaugh and Whitlock 1995; Long et al. 1998; Mohr et al. 2000; Hallett and Walker 2000).

Micro-charcoals have mostly been examined on the same slides used for pollen analysis (e.g. Swain 1973; Cwynar 1978; Clark 1982). The sample preparation procedure was therefore following the

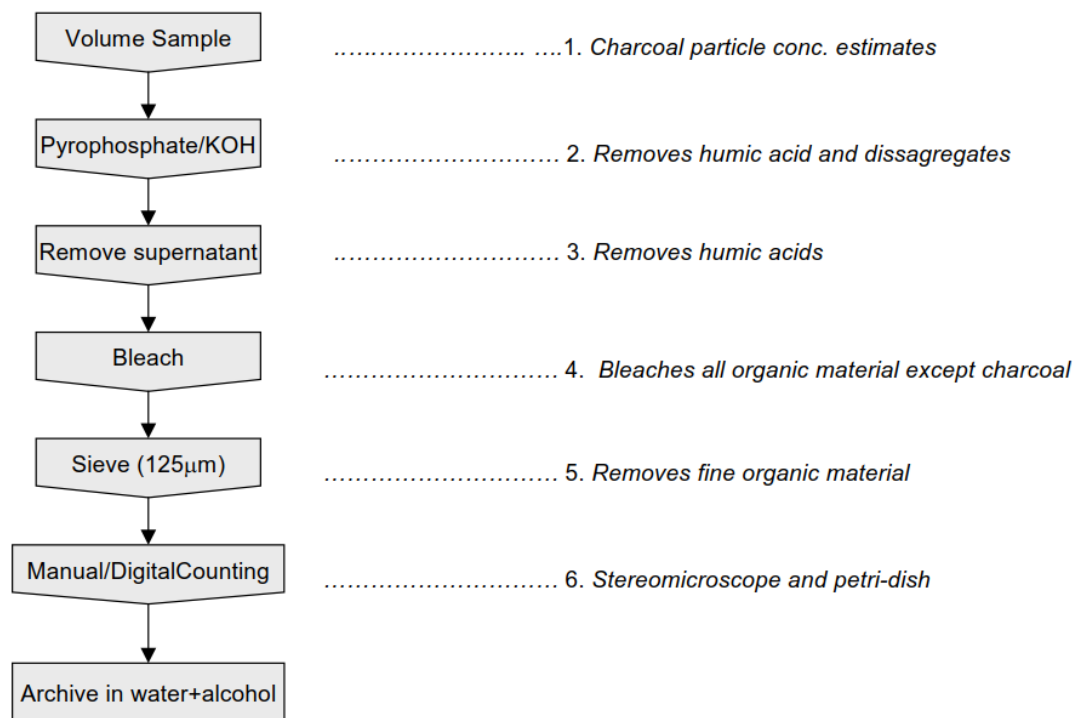


Figure 3.3 Outline schematic flow method the preparation and quantification of macroscopic charcoal (from Stevenson and Haberle 2005)

standard pollen laboratory preparations (Sadori and Giardini 2007). The used of pollen-slide charcoal as a fire proxy was first introduced by Iversen (1941). This method is complex and strongly influenced by long-distance transported micro-charcoal particles. It is therefore best used to infer regional biomass burning in connection to for example climatic reconstructions (Carcaillet et al. 2001). A more suitable method to reconstruct local fire signal is by quantifying macro-charcoal particles using the sieving-method. This method will retain only large charcoal particles ($>125\ \mu\text{m}$) so that the fragmentation is reduced and the macro-charcoal could be applied to reconstruct the local signal of fire (Stevenson and Haberle 2005).

Multi-variate data analysis

In the past two decades, the subject of Paleoecology became more dynamics and more quantitative than qualitative and subjective (Toledo et al. 2009). The use of quantitative analysis in paleoecology is needed because the data are complex, multivariate, and often stratigraphically ordered. Therefore a numerical analysis can help the interpretation of the data by detecting temporal patterns as well as past environmental reconstruction (Birks 2012a).

The first step in numerical analysis is Exploratory data analysis (EDA) which mainly present graphical tools such as histograms, box-plots, scatter-plots, pie-charts, smoothers, co-plots, and scatter-plot matrices (Juggins and Telford 2012). One of program to analysing and visualising palaeoenvironmental data with stratigraphical plots is C2 (Juggins 2007; Chapter 4, 5, 6). While the local zonation can be defined via constrained cluster analysis using the software CONISS (Grimm 1987, 1993; Chapter 4 and 6).

Graphical display of multivariate data can be obtained from such techniques as ordination or scaling or clustering or partitioning. Clustering or data partitioning were done based on the similarities or dissimilarities among objects (Legendre and Birks 2012). This technique is very useful in analysing large, multivariate data-sets (Everitt et al. 2011; Wehrens 2011). Ordination techniques are used in general category of classical or indirect gradient analysis (ter Braak 1987; ter Braak and Prentice 1988; Wehrens 2011). Such techniques including principal component analysis (PCA; Jolliffe 2002; Chapter 4, 5, 6) and correspondence analysis (CA; Greenacre 1984, 2007; Greenacre and Blasius 2006; Chapter 4) can provide a multivariate data in a low-dimensional ordination plot with highest similarities between the objects in the original multi-dimensional space of the data (ter Braak 1987; Husson et al. 2011). CANOCO software is one of ‘user friendly’ program to perform ordination (Ter Braak and Smilauer 2002; Chapter 4, 5, 6). The CANOCO adviser assists in choosing data transformation and methods of analysis.

Besides the ordination, the patterns in taxa composition within the stratigraphic sequence can be summarized with the Principal curves technique (PCs; Chapter 4). PCs is a smooth, one-dimensional curve best fitted through the data in number of dimension (De’ath 1999; Hastie et al. 2011; Simpson and Birks 2012). The axes one and two scores of PCA, CA, and DCA axis are often used to illustrate the major changes in taxa composition (Birks 2012b). Additionally, the distance along the PC is used as an expression of the rate of change (RoC) per 1000 years (kyr) between samples for the pollen and spores dataset. The PC and RoC can be implemented using R software (R Core Team 2015; Chapter 4). In order to analyse sediment-charcoal record, a set of diagnostic and analytical tools called CharAnalysis (<https://sites.google.com/site/charanalysis/>; Higuera 2009; Chapter 4 and 5) has been designed. Basically, the analysis is used to reconstruct ‘local’ fire history by adjusting the charcoal record into low and high frequency component (Long et al. 1998; Carcaillet et al. 2001; Gavin et al. 2006) and using a locally-defined threshold to clean the signal of the fire peaks from noise (e.g. Clark and Royall 1995; Long et al. 1998; Gavin et al. 2006).

Study sites – the Kerinci Seblat National Park and mangrove forest

The first study site is located in the submontane rainforest in the Kerinci Seblat National Park, while the second study site is located in the east coast of Sumatra Island (Figure 3.4). Detail information of the sites and sediment material studied are given in Table 3.1.

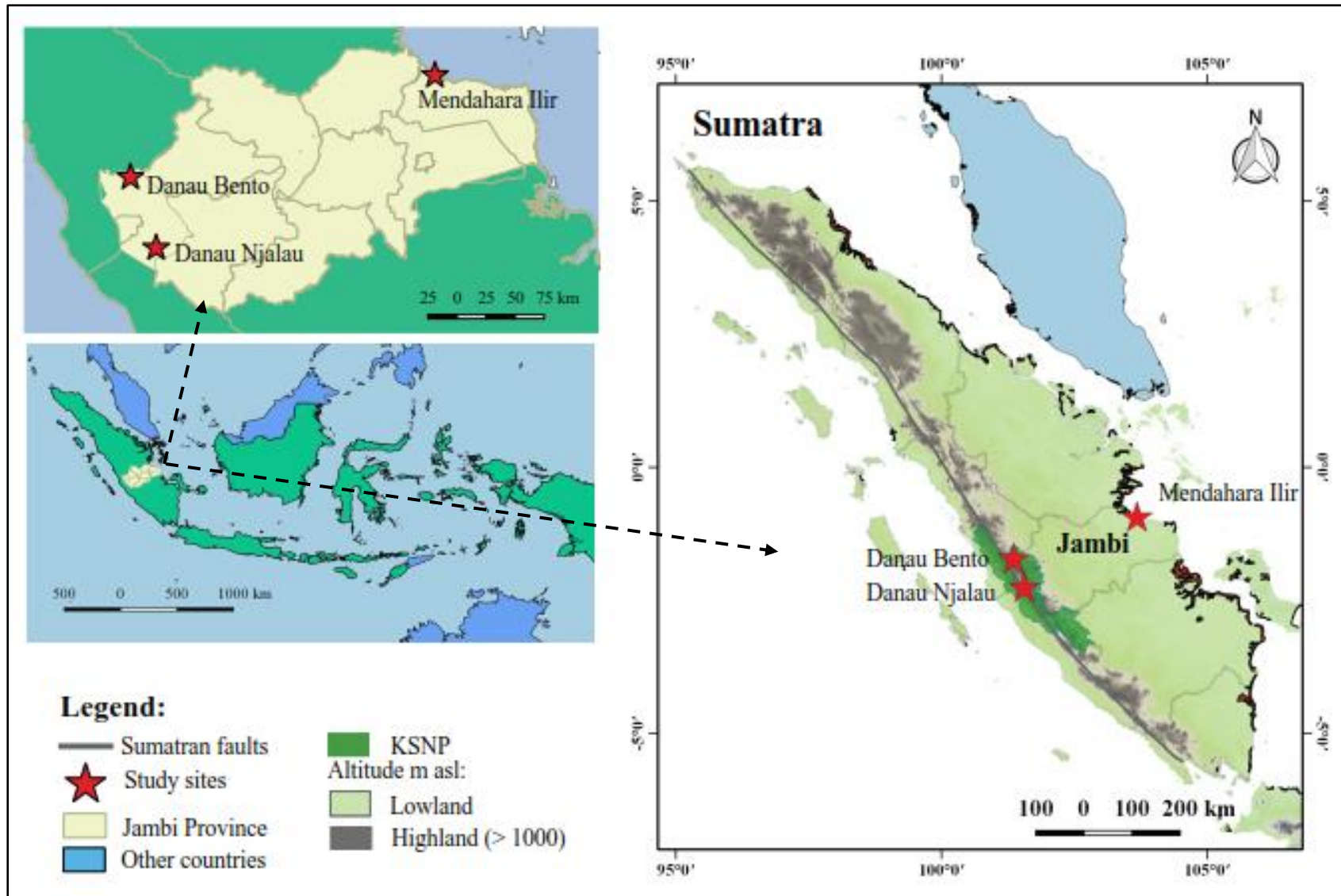





Figure 3.4 Location of the studied sites in the Jambi Province, Sumatra Island (red star). Data source for Digital Elevation Model (DEM) for highland (altitude >1000 m asl): ASTER GDEM Version 2 from METI and NASA. Red line shows the mangrove distribution along the Sumatran coastline (data mangrove distribution from Spalding et al. 2010)

Table 3.1 Detail information of the study sites and sediment material studied.

| | Highlands (mountain) | | Coastlands (mangroves) |
|--------------------------------|---|--|---|
| | Danau Njalau | Danau Bento | Mendahara Ilir |
| |  |  |  |
| Location (latitude, longitude) | 2.27°S, 101.56°E; submontane | 1.734428°S 101.359748°E; swamp forest | 0°57'14.6"S 103°40'45.0"E |
| Altitude (m asl) | 1040 | 1434 | 3 |
| Core material | peat organic sediment | organic mud | Mangrove-swamp sediment |
| Core length (cm) | 491 | 600 | 500 |
| Age (cal yr BP) | 5000 | 4300 | 2300 |
| Proxies | Pollen, spore, charcoal, NPPs (<i>Botryococcus</i> and <i>Glomus</i>) | Pollen, spore, charcoal, NPPs (<i>Coprophilous</i> fungal) | Pollen, spore |
| Chapter | 4 | 5 | 6 |

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CHAPTER 4 – paper 1

The effect of volcanism on submontane rainforest vegetation composition: Paleoecological evidence from Danau Njalau, Sumatra (Indonesia)

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Keywords

Volcanic deposition, Kerinci Seblat National Park, Sumatra, Holocene, palynological analysis, volcanophile

Abstract

Volcanic processes might have played an important role in the vegetation history of Sumatra, one of the largest and most tectonically active region in Southeast Asia. Palynological and macro-charcoal analysis results from Lake Njalau in the Kerinci Seblat National Park (KSNP) in Sumatra (Indonesia) provide an understanding of interactions between the volcanic deposition and vegetation in the past 5000 years. The deposition of volcanic material in the depression of the Lake Njalau (5100–4400 cal yr BP) led to the dominance of pioneer species of *Casuarina* and *Myrica*, which grow in deforested land and volcano slopes (volcanophile taxa). The formation of the modern forest composition took several centuries after the volcanic deposition in the soil ended (ca. 900 years at ca. 2400 cal yr BP). This suggests that the vegetation changes were not driven by a successional pattern, and soil formation was the most important environmental factor explaining this slow change in composition. The palynological records show no evidence for prehistoric human–landscape interactions in the area despite the close proximity to known megalith sites. The local fire regime reconstructed using macro-charcoal analysis indicates that fire was rare for the last 5000 years, and the average fire return interval was ca. 500 years. Phases of increased fire frequency could not be linked to either any of the vegetation phases or regional climatic changes, suggesting that fire occurrences were stochastic events. Our results overall suggest that volcanism has acted as one important driver of changes in the rainforests of the KSNP.

Introduction

Volcanic activities and high biodiversity coexist in Southeast (SE) Asia, where the second largest area of rainforest in the world is found (Whitmore 1998) in the middle of the so-called Pacific Ring of Fire (Kozák and Cermák 2010). The high tectonic activity resulting from the inter crossing of the Eurasian plate and the Indo-Australian plate gave rise to numerous active volcanoes (Francis 1993; Figure 4.1a). One of the largest islands and the most tectonically active place in SE Asia is Sumatra (Salisbury et al. 2012), where 35 volcanoes are listed as active (Smithsonian Institution 2013; Figure 4.1a). In the past 100 years alone, more than 13 volcanic eruptions were reported to have occurred in this island (Salisbury et al. 2012; Smithsonian Institution 2013). Due to this, the island has been known as arc of volcanoes. It is well known that volcanic eruptions are a major natural disturbance (Gómez-Romero et al. 2006), largely affecting species composition, competition, diversity, and succession of the vegetation around volcanoes or on volcanic islands (del Moral and Grishin 1999; Krebs 2008). It follows that volcanic processes must have played an important role in the history of the vegetation in Sumatra (Laumonier 1997). The west coast of Sumatra where the arc of volcanoes is found (Figure 5.1a) is dominated by the Barisan Mountains that run for the whole length of Sumatra (Whitten et al. 2000). A significant part of this mountain is located within the boundaries of the largest national park in Sumatra, the Kerinci Seblat National Park (KSNP; ca. 1.4 million hectares; Bramley et al. 2004).

While most of Sumatran rainforests have been rapidly converted to plantations and agricultural fields in the past 30–40 years (Drescher et al. 2016), the forests of the KSNP have been little affected and have remained relatively pristine. Well embedded in this rich and diverse protected montane rainforests, more than five active volcanoes, including the highest peak in Sumatra, Mount Kerinci (ca. 3805 m), are found (Ohsawa et al. 1985; Figure 4.1a). The area of Kerinci is, therefore, perfectly suitable to study the effect of volcanic eruption in the valleys of the Barisan montane range.

In the KSNP, when looking at the centennial to millennial timescale, volcanism can be considered as one of the most important disturbance factors. Volcanic eruptions produce a large amount of ash which accumulates in screes on top of volcanoes. These products are barren, pervious, sterile, and unstable

and tend to move downhill, particularly during heavy rains (Whitten et al. 2000). The effect and damage that the ash deposition can exert on the vegetation depend on the thickness of the ash layer and size of the ash grain among other things (Hotes et al. 2004; Mack 1981).

The effect might be of increase susceptibility to forest fires and the establishing of harsh condition for certain plants in those areas most affected by tephra deposition such as topographic depressions (Titus and Tsuyuzaki 2003). We hypothesize that this must have had a critical influence on the composition, structure, and dynamics of the rainforest vegetation in the KSNP. To test this hypothesis, we carried out paleoecological multi-proxy analysis from a sediment core taken in a tectonic depression where a small lake is formed (Danau Njalau) in close vicinity to the active volcanoes in the KSNP (Figure

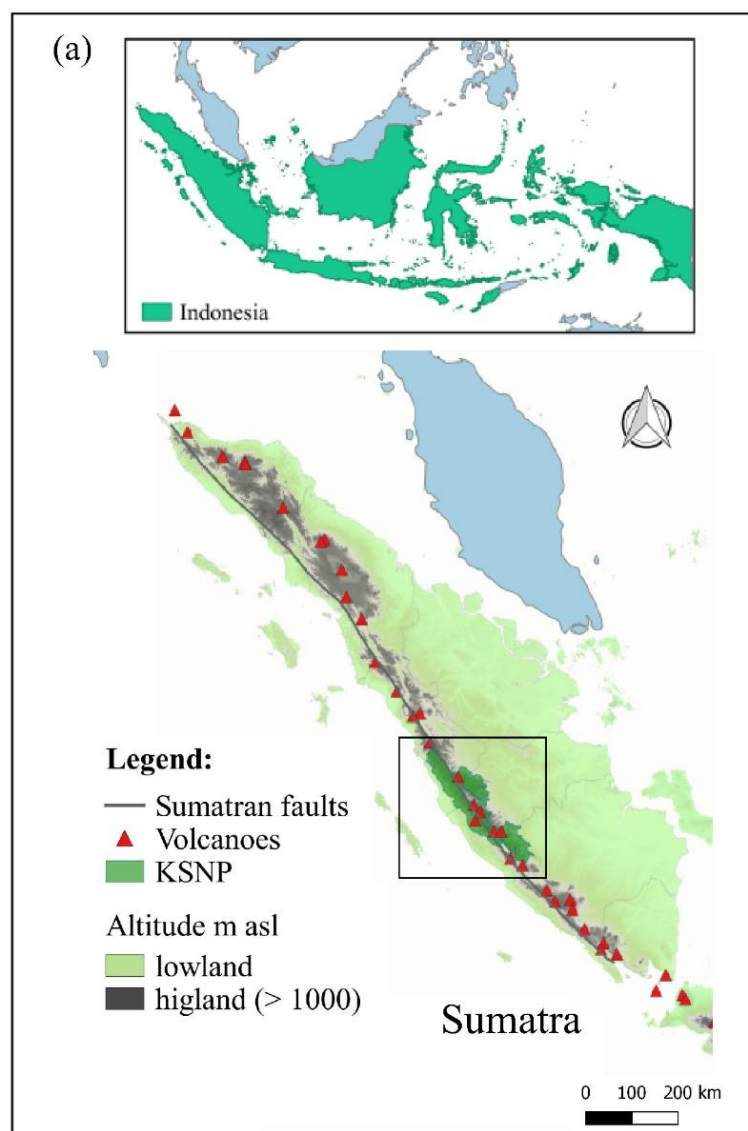


Figure 4.1a Maps of the study area: the location of the studied region, the Kerinci Seblat National Park (KSNP) in Sumatra Island, Indonesia. The red triangle shows active volcanoes along the active tectonic faults in the islands. Data source for Digital Elevation Model (DEM): ASTER GDEM Version 2 from METI and NASA, and volcanoes from Global Volcanism Program 2013 (Volcanoes of the World, v.4.5.3. Venzke, E. Smithsonian Institution. Accessed 19 December 2016. <http://dx.doi.org/10.5479/si.GVP>)

4.1b). Pollen and spore analyses are used to reconstruct the vegetation dynamics around the site. We carried out macro-charcoal analysis to reconstruct the local fire regime and used *Botryococcus* and *Glomus* concentrations as proxies for disturbance. We compared these results with the composition of the sediments in order to assess long-term effect of volcanic deposition and disturbance on the vegetation history of the site.

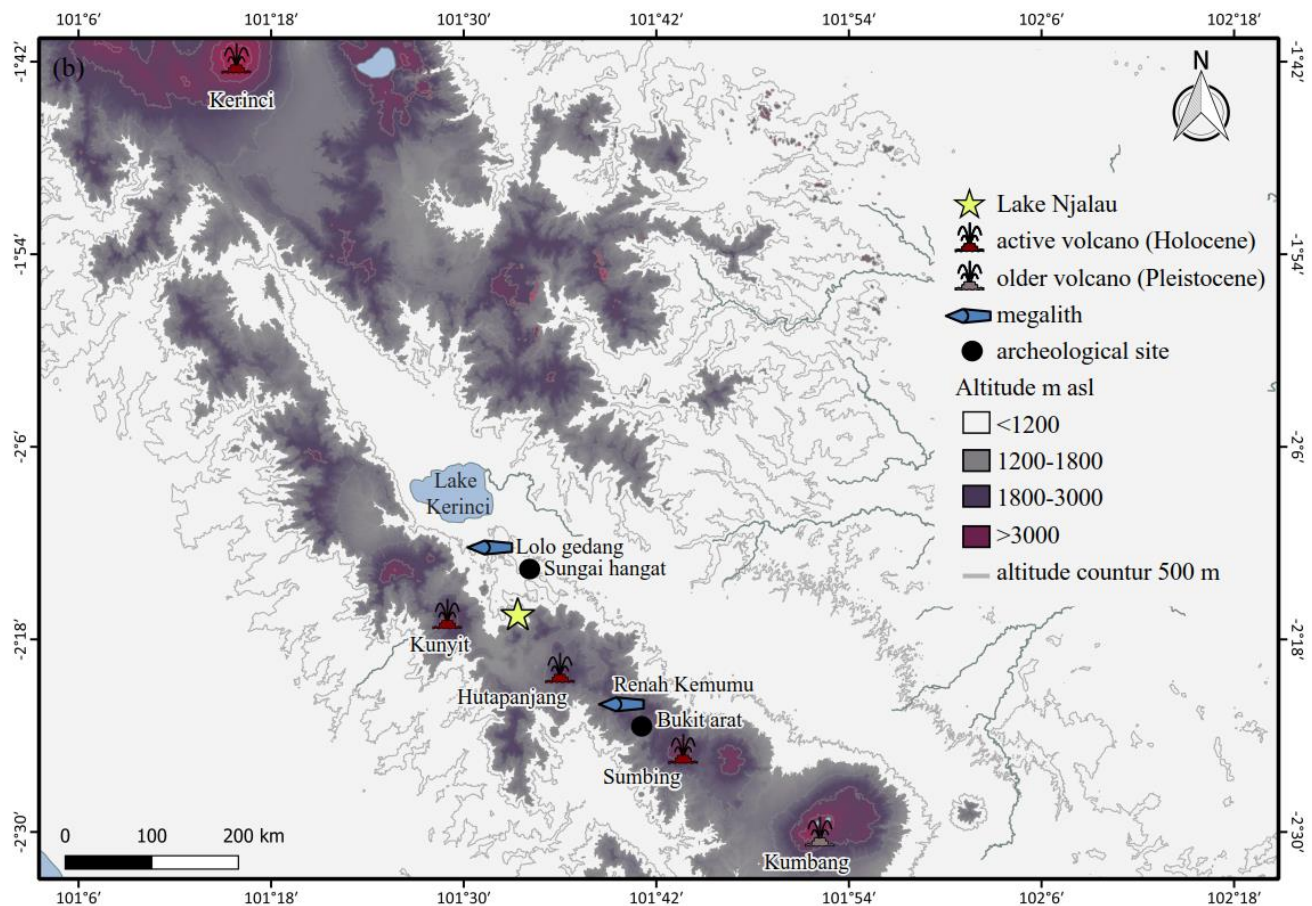


Figure 4.1b Maps of the study area: the study site, Danau Njalau (Lake Njalau) marked with a yellow star. The red volcano symbol represents active volcanoes during the Holocene and the grey volcano symbol is for an ancient Pleistocene volcano. The archeological sites (Bonatz, 2012) mentioned in the text are also shown. Data source for Digital Elevation Model (DEM): ASTER GDEM Version 2 from METI and NASA, and volcanoes from Global Volcanism Program 2013 (Volcanoes of the World, v.4.5.3. Venzke, E. Smithsonian Institution. Accessed 19 December 2016. <http://dx.doi.org/10.5479/si.GVP>)

This study provides a different picture from the previous palynological and paleoecological studies in Sumatra (e.g. Flenley and Butler 2001; Maloney 1980, 1985; Maloney and McCormac 1995; Morley 1982; Newsome and Flenley 1988; Stuijts et al. 1988). For the first time, paleoecological analyses are used to investigate the interactions between volcanic deposition and the rainforests ecosystems of western Sumatra, thus helping improving our understanding of their disturbance regimes in the long term.

Environmental settings of the study site

The study site is located in the southern part of the KSNP within the Barisan mountain range in Sumatra (Figure 4.1a). A small marginal depression where the Lake Njalau is found (Danao Njalau, also known as Danao Nyalo; 2.27°S, 101.56°E; 1040 m a.s.l.) was chosen as the catchment area is small (1–2 ha), and it is located in a remote area at the end of a valley side of Mount Kerinci. The depression probably originated from tectonic activity as it is located in the southwestern edge of the Rift Valley. A volcanic origin as an extinct crater is also possible (Flenley and Butler 2001) as a quiescent volcano Mount Kunyit (2151 m a.s.l.) lies some 20 km in the western side of the depression. This volcano is part of a series of active Holocene and older Pleistocene volcanoes surrounding the Lake Njalau depression (Figure 4.1b).

A ring of grasses and sedges surrounds the lake, but vegetation quickly changes to forest on the relatively steep slopes around it. The mountainous areas surrounding the lake are dominated by submontane vegetation (800–1400 m), where dominant families are Fagaceae, Lauraceae, and Myrtaceae (Laumonier 1997). Most of the forest is still in old grown condition, although some clearing occurred to plant cinnamon (*Cinnamomum burmannii*) in the northern part of the lake and dry rice (*Oryza sativa*; Flenley and Butler 2001). Additionally, embedded in the forest, gardens from local farmers can be seen. These are small monocultural ‘estates’ (Laumonier 1997) for home gardening (in Indonesian language: berkebun), usually for planting annual crops and vegetables such as chili (*Capsicum* spp.), corn (*Zea mays*), eggplant (*Solanum melongena*), and fruit such as banana (*Musa* sp.). Central Sumatra is characterized by wet tropical climate as it lies within the Intertropical Convergence Zone (ITCZ). The mean annual rainfall for the area of the KSNP is about 2990 mm and annual temperatures average 20°C (Karger et al. 2016; <http://chelsa-climate.org/>; see Figure 4.6a). Rainfall seasonality is not usually marked, but a long rainy season of 9–10 months is alternated with a shorter drier season of 2 or 3 months from June to August (see Figure 4.6b). This seasonality is the results of monsoon dynamics over the region where the wet northwest (NW) monsoon peaks from December to February (DJF) and the dry southeast (SE) monsoon from June to August (JJA; see Figure 4.6b; Kalnay et al. 1996). Inter-annual variability in rainfall pattern is controlled by the changes in the phase of El Niño-Southern Oscillation (ENSO) and particularly in western Sumatra, by the Indian Ocean Dipole (IOD; Abram et al. 2007; Saji et al. 1999; Webster et al. 1999).

Materials and methods

A 491-cm-long sediment core (DN) was collected in 2013 on the shore of the Lake Njalau, in a swamp depression using a Russian peat corer (Jowsey 1966). The core was photographed and described lithologically at the University of Jambi, Sumatra, using sediment and attributes including color, texture, and plant part composition. Afterward, the core was transported to the Department of Palynology and Climate Dynamics, University of Göttingen, for further analyses. Eight samples

consisting of plant materials and organic bulk sediment were sent to Erlangen Laboratory in Germany, Poznan Radiocarbon Laboratory in Poland, and the NTUAMS Laboratory in Taiwan for accelerator mass spectrometry (AMS) radiocarbon dating (Table 4.1).

Table 4.1 List of accelerator mass spectrometry radiocarbon dates from DN core. Calibration done with R script in CLAM 2.2, calibration curve is the Southern Hemisphere SHCal13.14C (Hogg et al. 2013)

| depth (cm) | Lab code | Material | pMC | ¹⁴ C BP | cal yr BP |
|------------|-------------|---|------------|--------------------|-----------|
| 98 | Erl-19237 | Plant material (bark, stalk and part of leaf) | 97.48±0.42 | 205±34 | 208±77 |
| 140 | NTUAMS-2703 | Plant material (bark, wood, seed) | 88.87±0.66 | 948±7 | 737±64 |
| 218 | Erl-19236 | Plant material (stalk) | 73.93±0.43 | 2427±47 | 2522±222 |
| 290 | NTUAMS-2704 | Plant material (wood) | 69.44±0.37 | 2930±16 | 3261±119 |
| 373 | Erl-19235 | Organic bulk sediment | 62.55±0.33 | 3769±43 | 4535±300 |
| 422 | NTUAMS-2705 | Organic bulk sediment | 62.12±0.32 | 3825±20 | 4675±98 |
| 467 | Poz-81603 | Organic bulk sediment | NA | 4255±30 | 4694±69 |
| 489 | Erl-19234 | Organic bulk sediment | 59.11±0.32 | 4223±44 | 5314±273 |

Palynological analysis

A total of 32 subsamples for palynological analysis were collected along the core at different intervals to account for changes in sediment accumulation rate. The subsamples were processed for pollen and spores using standard techniques (Faegri and Iversen 1989) including HF 48% treatment and acetolysis. Each subsample consisted of 0.5 cm³ of sediment. One tablet of *Lycopodium clavatum* spores was added to each subsample to estimate palynomorph concentrations (Stockmarr 1971). Residues were mounted in glycerol jelly for pollen visualization, identification, and counting. Pollen and spore analyses were carried out using light microscopy. All identified pollen and spore types were photographed using Leica photomicroscope with a 1000× magnification. Pollen and spores were identified using the tropical pollen reference collections of the Department of Palynology and Climate Dynamics which includes specimen collected from the KSNP area. Additional resources used include pollen key and atlases for SE Asia (Bulalacao 1997; Flenley 1976; Garrett-Jones 1979; Huang 1972; Jones and Pearce 2015; Poliakova and Behling 2016; Powell 1970; Stevenson 1998; Wang et al. 1995) and online database (Australasian Pollen and Spore Atlas (APSA) from Australian National University, Canberra – available at <http://apsa.anu.edu.au> and the Pollen and Spore Image Database of the University of Goettingen – available at <http://gdvh.uni-goettingen.de/>).

The pollen grains were counted to a minimum of 300 grains per subsample, except for the two subsamples at 475 and 485 cm core depth, where a count of 300 could not be achieved due to low pollen concentrations. The identification was conducted at low taxonomic level as far as possible. However,

some pollen grains are morphologically indistinguishable under the light microscopy and were summed together. These include pollen from family Moraceae and Urticaceae (Moraceae/Urticaceae) excluding *Ficus*, family Melastomataceae and Combretaceae (Melastomataceae/Combretaceae), pollen from *Casuarina* (Casuarinaceae), and *Myrica* (Myricaceae; *Casuarina/Myrica*), as well as pollen from *Lithocarpus* and *Castanopsis* (Fagaceae; *Lithocarpus/Castanopsis*).

Pollen counts were standardized to percentages based on the total pollen sum. Fern spores were counted along with the pollen grains and are expressed as percentage of the pollen and spores total sum. Pollen and spore taxa were grouped into sub-montane rainforest taxa including primary rainforest taxa and secondary rainforest taxa, volcanic indicator taxa (volcanophile), open and disturbance (anthropogenic) taxa and fern according to their ecology, habitus, and distribution (Flora Malesiana collection: <http://portal.cybertaxonomy.org/flora-malesiana/>; Prosea collection: <http://proseanet.org>; Laumonier 1997). Concentrations are calculated using the *Lycopodium clavatum* marker and are expressed as number per cubic centimeter of sediment. The algae *Botryococcus* and the fungal spores of *Glomus* were also counted and concentrations calculated (number per cubic centimeter of sediment). The software C2 was used for calculation of percentages and plotting of diagrams (Juggins 2007). Local pollen assemblage zones are defined via constrained cluster analysis using the software CONISS (Grimm 1987, 1993). All pollen and spores taxa are included in the analysis.

Macro-charcoal analysis

Macro-charcoal particles (>150 μm) were counted in contiguous subsamples at 2-cm intervals along the sediment core (250 samples). Subsamples of 2 cm^3 were prepared following the methods for macro-charcoal analysis (Rhodes 1998; Stevenson and Haberle 2005). Low concentration of hydrogen peroxide (6% H_2O_2) was applied to partially digest and bleach organic material in the sediment samples. The macro-charcoal particles were counted under a binocular dissecting microscope. Results are expressed as the number of charred particles per cubic centimeter.

Numerical data analyses

Palynological diversity index (PDI) was estimated via ‘rarefaction analysis’ (Siegel 1986). A small sample (low count, i.e. 10) was used as studies suggest that this pollen type diversity index correlates to the landscape diversity around the deposit (Matthias et al. 2015).

Principal curves (PCs) reduce the complex multivariate data in one-dimensional data space, and they are a powerful technique to summarize taxa compositional changes in the stratigraphic sequence. PC is the smooth, one-dimensional curve best fitted to the data in a number of dimensions (De’ath 1999; Hastie and Stuetzle 1989; Simpson and Birks 2012). Pollen percentage data were transformed using the Hellinger transformation. The sample scores of the first correspondence analysis (CA) axis were used as starting points, and smoothing splines are fitted through these points. The penalty that determines the

degree of smoothness was set to 2 because of the small dataset (31 subsamples; De'ath 1999). Sample age was used as the sole covariate in the model, and the PC scores were extracted for each fit and arranged based on the time order. The curve is then modified through several iterations using a local averaging to reduce the sum of orthogonal distances between the PC and the observed data (De'ath 1999; Simpson and Birks 2012). To avoid overfitting of the curve, general cross-validation was done at each iteration step, and the degree of smoothness is allowed to vary between the different pollen taxa (Herzschuh et al. 2016).

Additionally, the distance along the PC is used as an expression of the rate of change (RoC) per 1000 years (kyr) between samples for the pollen and spores dataset. The PC and RoC were implemented using R version 3.3.2 (R Core Team 2015) using the following packages: *vegan* 2.4-1 (Oksanen et al. 2013) and *analogue* 0.17-0 (Simpson 2007; Simpson and Oksanen 2016).

Fire regime characteristics were reconstructed using the software CharAnalysis (Higuera 2009). The raw charcoal data were converted to charcoal accumulation rates (CHAR; particle/cm²/yr), and the CHAR time series was interpolated according to the median temporal resolution. Background CHAR was defined by smoothing the CHAR record over a 1000-year window with a lowest smoother robust to outliers. A Gaussian mixture model was used to separate the noise from the significant fire-related peaks, which exceeded locally defined thresholds in the noise distributions. The local signal-to-noise index (SNI), as developed by Kelly et al. (2011), was used to verify that the separation between the identified charcoal peaks and the noise distribution of the charcoal series was statistically significant (Kelly et al. 2011).

Multivariate statistical analysis was done to highlight the most important environmental factors driving vegetation dynamics in time. All identified pollen and spore percentage data were included in the analysis. The calculated DCA (with detrending by segments and Hill's scaling) returned a length for the longest axis of 1.5 standard deviation (SD) units, thus linear ordinations were carried out. First, we used an unconstrained ordination (principal component analysis (PCA)) to highlight patterns in compositional change of pollen and spore assemblage. Rare taxa were not down-weight and the Hellinger transformation was applied (Simpson and Birks 2012). Environmental variables are used as supplementary explanatory and are type of sediment (as factors: ash and lapilli and non-volcanic), soil thickness (expressed as vertical distance along the sequence from the volcanic deposit), fire frequency as obtained from the CharAnalysis results as indicator of fire regime changes, and non-pollen palynomorphs as indicators of soil erosion and nutrient supplies (*Glomus* and *Botryococcus*; Kołaczek et al. 2013; Smittenberg et al. 2005; van Geel et al. 2011). Following this, we carried out a constrained ordination (redundancy analysis (RDA)) in order to extract the variation that is directly explained by the environmental variables. PCA and RDA were performed using CANOCO 5 (Ter Braak and Smilauer 2002).

Results

Core descriptions and chronology

The DN core consists mainly of two deposits: the lower volcanic layer (491–375 cm) and the upper peaty organic layer (375–0 cm). The volcanic layer consists of coarser volcanic lapilli embedded in an organic-rich matrix (491–426 cm), followed by finer volcanic ashes embedded in an organic-rich matrix with fine fibers (426–375 cm). The upper peat layer can be divided into two sublayers. The first one consists of hemic peat (375–29 cm), while the second represents the top little decomposed fibric peat layer (29–0 cm). A detailed description of the stratigraphic lithology of the core is shown in Figure 4.7. The chronology of the DN core is obtained from eight AMS radiocarbon dates (Table 4.1). The calibration of the radiocarbon dates is performed using Clam 2.2 (Blaauw 2010) script in R (R Core

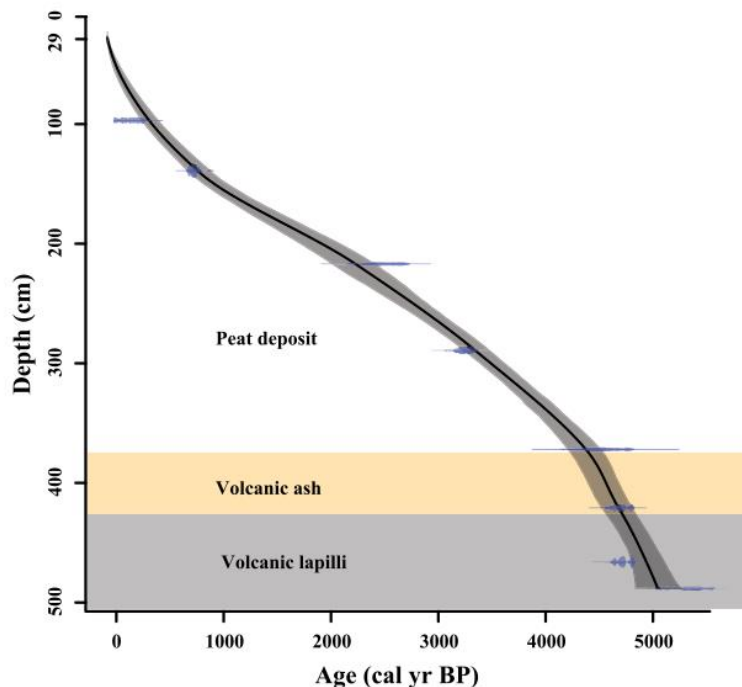


Figure 4.2 Age–depth profile of the DN core. A locally weighted spline (LOESS) is the best fitted model with extrapolated basal point and surface age set at –63 cal yr BP (AD 2013, year of the coring) starting at 29 cm

Team 2015) using the Southern Hemisphere SHCal13.14C calibration curve (Hogg et al. 2013). The top of the core (29–0 cm) is characterized by organic material rich in roots, and it is probably contaminated by modern material (Hogg 1982). This part is, therefore, excluded from the model, and the modern date for the age–depth model is fixed at 29 cm.

The dates are fitted into a locally weighted spline (LOESS) model. The results from the age–depth model indicate that the DN core records the last ca. 5000 years. The depth versus age

relationship (Figure 4.2) suggests an irregular sediment accumulation through time. The volcanic deposit corresponds to ca. 700 years of deposition (491–375 cm; 5100–4400 cal yr BP; average sedimentation rate 1.7 mm/yr). A synchronous or slump deposition is not considered likely due to the stratigraphic characteristics of this deposition (from bottom to top: coarser to finer). Additionally, the organic material is embedded in the volcanic material suggesting a slow accumulation through time. Peat accumulated at the site for the past ca. 4400 years and a total of ca. 4 m of deposit are now found. The peat accumulation rate is initially low (375–110 cm; 4400–400 cal yr BP; average 0.70 mm/yr) and

subsequently progresses to a more rapid rate of accumulation (110–29 cm; 400 cal yr BP–present; average 1.7 mm/yr).

Palynological results

In total, 72 pollen taxa and 15 different spore taxa are identified in the 32 sediment subsamples (3 rare pollen taxa and 4 spore taxa remain unknown). Pollen and spore grains are well preserved, and average concentration is high along the core (average 70,000 grains/cm³). The bottom part (491–475 cm; 5100–5000 cal yr BP) records low pollen concentration (average pollen concentration 50,000 grain/cm³). The pollen concentration values then significantly increased (475–355 cm; 5000–4200 cal yr BP; average pollen concentration 110,000 grains/cm³) and subsequently decreased to about 44,000 grains/cm³ (355–290 cm; 4200–3300 cal yr BP). Afterward, the pollen concentration shows an increasing trend up to the top of the sediment core (290–0 cm; 3300 cal yr BP–present; average pollen concentration 64,000 grain/cm³).

The pollen diagram illustrates percentages of the dominant and most important taxa, which are grouped based on their ecology and habitat occurrences in the KSNP (Figure 4.3a and b; see Table 4.3). ‘Others’ corresponds to pollen grains of taxa that can be described as generalists as they occur in all habitats considered. Based on the cluster analysis, the DN record is divided into two palynological zones (Figure 4.3a and b) which are described below:

Zone DN-1 (491–275 cm; ≥5100–3100 cal yr BP; 12 subsamples). This zone marks the dominance of volcanophile taxa in particular *Casuarina/Myrica* and can be divided into two sub-zones based on the change in volcanophile composition: subzone DN-1a and subzone DN-1b. At the beginning of subzone DN-1a (491–425 cm; 5100–4700 cal yr BP; four subsamples), where volcanic lapilli are deposited, the DN core records high volcanophile pollen taxa *Casuarina/Myrica* (average 38%) and fern spores such as *Phymatosorus* (average 9%), while other montane rainforest pollen and spore taxa are low. Subzone DN-1b (425–275 cm; 4700–3100 cal yr BP; eight subsamples) starts when the deposition shifted to volcanic ash. The volcanophile pollen grains markedly decreased but remained dominant (average 17%). At the same time, other rain-forest pollen taxa, that is, *Ficus*, start to increase (average 11%) and fern spores decrease (average 2%).

Zone DN-2 (275–0 cm; 3100 cal yr BP–present; 20 subsamples). This zone shows a gradual increase in rainforest pollen and spore taxa and a decline of volcanophile taxa. This zone can be divided into two subzones: subzone DN-2a and subzone DN-2b. In subzone DN-2a (275–120 cm; 3100–500 cal yr BP; 14 subsamples), *Ficus* pollen marked an increase in primary rainforest taxa (average 13%) in parallel with the increase in secondary rainforest taxa such as *Saurauia* (average 14%), while *Casuarina/Myrica* started to decline before it finally almost disappears from the record (average 1%). The subzone DN-2b (120–0 cm; 500 cal yr BP–present; six subsamples) is characterized by an increase in primary rainforest taxa *Ficus* (average 16%), mirrored with the decrease in secondary forest taxa *Saurauia* (8%). Additionally, the algae colonies of *Botryococcus* increased markedly in this zone (152–95 cm; 900–300

cal yr BP; average 30,000 grains/cm³). A high peak of the fungal *Glomus* spores was recorded at 2 cm (2000 spores/cm³).

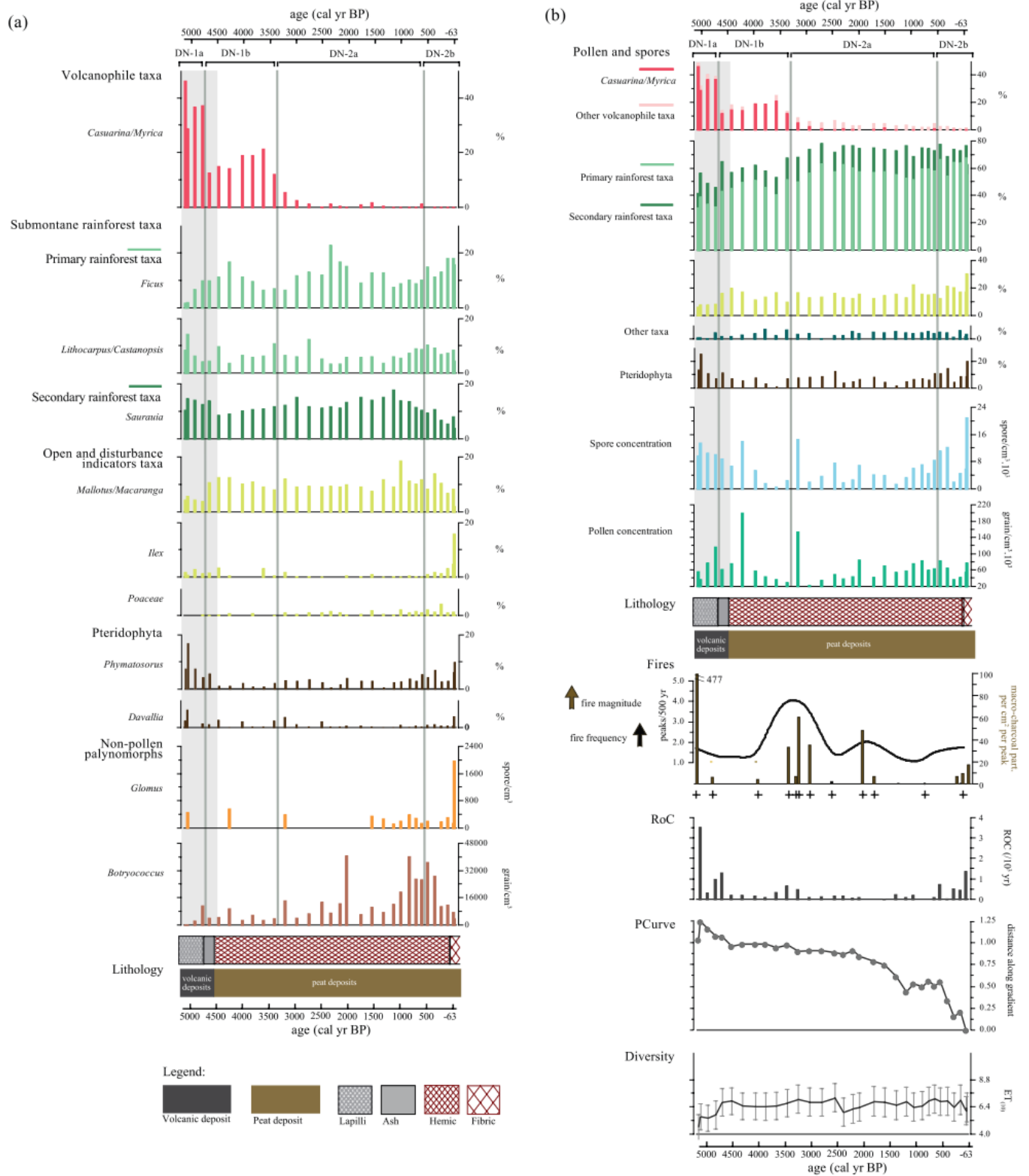


Figure 4.3 Palynological diagram of the DN core: (b) percentage of the dominant and most important pollen and spore taxa for each ecological group. CharAnalysis results (fire peaks, peaks magnitude and fire frequency) and palynological numerical analysis results including the Principal curve (PCurve), Palynological Diversity Index (Diversity/ET₁₀) and rate of compositional change/velocity (RoC)

Macro-charcoal and fire regime

Macro-charcoal analysis resulted in a low number of counting along the DN sediment core. Macro-charcoal concentration marked relatively high values within subzone DN-1a (491–425 cm; 5100–4700 cal yr BP) in the volcanic lapilli deposit (Figure 4.3b). Subzone DN-1b (425–355 cm; 4700–4200 cal yr BP) initially shows a decrease in macro-charcoal concentration and then it started to increase until the end of the zone (355–275 cm; 4200–3100 cal yr BP). In zone DN-2 (275–0 cm; 3100 cal yr BP–present), macro-charcoal concentrations are more stable (minimum concentration: 16 particles/cm³ and maximum concentration: 64 particles/cm³). Using the CharAnalysis software (Higuera 2009), the raw charcoal data are interpolated into 22 years (the median temporal resolution), and the peak signals of fire episodes are modelled while removing the background noise. A total of 12 fire peaks are detected along the core. The local SNI values for the DN macro-charcoal data are fluctuating above 3, indicating significant signals for fire peaks (Kelly et al. 2011). The mean fire return interval (FRI) is 523 with mean frequency of fire of 2 peaks/1000 years (maximum 5 peaks/1000). Fire frequency within zone DN-1 is low (ca. 5 peaks/1000). Zone DN-2 is marked by an increasing trend, and the highest fire frequencies are found within this zone (7 peaks/1000). High magnitude of peak (>100 particles/peak) are found in zone DN-1 (1 peak), while in zone DN-2 are detected lower in magnitude peaks but higher fire frequency (5 peaks; Figure 4.3b).

PDI, PC, and RoC

PDI (PDI/ET₍₁₀₎) values are initially low in subzone DN-1a (37 pollen and spore types). They show an increase at 425 cm depth (4700 cal yr BP), to remain stable afterward (Figure 4.3b). The PC using CA as a starting point converged after five iterations, and the final curve explains 51% of the variance. The distance along the gradient of the subsample composition shows three main phases of compositional change: from 4700 to 4400 cal yr BP, from 3300 to 2400 cal yr BP, and from 500 cal yr BP to present. By scaling these changes per unit of time (RoC per 1000 years; Figure 4.3b), it can be seen that of these three phases, the ones characterized by the most rapid changes, are (in order) the oldest change (from 4700 to 4400 cal yr BP) and the most recent (from 500 cal yr BP to present).

The individual response curves of the six most important pollen taxa are shown in Figure 4a–f. In summary, the DN record shows a high response in terms of compositional changes only for the volcanophile taxa *Casuarina/Myrica*, while the other most represented pollen taxa show no marked change in time but rather slow changes.

PCA and RDA

The result from the PCA indicates that 47% of the total variance is explained by the first (39%) and second (8%) axes (Figure 4.5a and b). Pseudo-canonical correlation for the supplementary environmental variables shows high correlations with the first (0.95) and second (0.96) axes,

respectively. The results from the RDA reveal that 51% of the variation can be explained with the environmental variables and show which environmental variables significantly explain the variance in pollen and spore composition (Table 4.2). The simple effect model (i.e. the independent effects of individual environmental variables) shows that all environmental variables are significantly correlated with the variance in taxa composition ($p < 0.005$ adjusted from false discovery rate) except for ash, erosion (*Glomus* spore), and fire. However, the largest part of the variance (34.5%) is explained by soil thickness (distance from the volcanic deposition; Table 4.2, RDA – simple term effects). The conditional effect model summarizes the conditional effect of each environmental variable after accounting for the effect of the variable placed above each (in order of their decreasing explained variation). The results of this model indicate that only soil thickness (34% variation explained) and lapilli (7% variation explained) are significant ($p < 0.005$ adjusted from false discovery rate; Table 4.2, RDA – conditional term effects).

Discussion

Effects of volcanic deposition on the vegetation

Central Sumatra is possibly reckoned as the source area for the most frequent and large explosive eruptions in Sumatra (Salisbury et al. 2012). The volcano formation in Sumatra is formed either by the uplift of sedimentary deposits, that is, in the Bukit Barisan mountain range or by the volcanic activity, that is, Mount Kerinci, Mount Sinabung, and Mount Singgalang (Whitten et al. 2000). In Sumatra, volcanic activity might have been continuous for millions of years, with evidence of reduced activity only in the Late Miocene (Crow 2005). The volcanoes of the Quaternary period (the last million years) are located in the mountainous areas and are usually associated with faults (Whitten et al. 2000).

The products of explosive volcanic eruptions are commonly rich in plagioclase and acid (damatic to liparitic; Laumonier 1997), and the main long-term effect on the ecosystem is due to the fall-out of this volcanic material. The deposit thickness varies depending on the distance to the volcanic center, and it can interest large areas in the landscape (Del Moral and Grishin 1999). There are several modes of impact of volcanic deposition on ecosystems, including physical impact of tephra on the vegetation (Bjarnason 1991; Clarkson and Clarkson 1994; Cook et al. 1981; Eggler 1948; Wilcox 1959), impact of tephra deposition on the hydrology (Crowley et al. 1994; Hotes et al. 2004), and chemical impact of tephra and tephra leachates (Smith et al. 1983; cf. Wissmar et al. 1982). At the same time, the extent of the impact of volcanic fallout on the ecosystem depends on various factors such as climatic conditions, soil characteristics, as well as grain size and structure of the tephra (Kilian et al. 2006). Vegetation recovery and succession can be affected by the differential survival modes of plants, erosion, concentration of tephra deposits, and many other factors (Del Moral and Grishin 1999; Tsuyuzaki and Haruki 2008; Wang et al. 2010). While in Sumatra, previous research on volcanic impacts on the vegetation has been very limited, there are sufficient evidences to suggest that changes on the vegetation

were significant on the regional vegetation (Fesq-Martin et al. 2004; Kilian et al. 2006; Payne and Blackford 2008).

Paleoecological analysis carried out in lakes and swamps located in valleys surrounded by active volcanoes can be extremely informative on the mode and timing of the effects of volcanic material on the montane ecosystems in Sumatra. The area of the KSNP represents the ideal location to investigate changes in vegetation and test for the most important drivers of change for the past thousands of years. The DN core was taken from a location surrounded by several active volcanoes (Figure 4.1b). The area is characterized by steep slopes where monsoon raining events can cause erosion and deposition of volcanic material from the peaks to the central valley and depressions, such as the one where the site is located (see Figure 4.6b).

The results from the radiocarbon dating of the DN core indicate that there was a rapid initial deposition of volcanic coarse material at the beginning of the record (Figure 4.2). This is likely due to the erosion of volcanic material from the mountain slopes after the eruption event occurred. It is apparent that the DN archive does not include the initial volcanic episode but only the successive re-deposition of volcanic material in the lake catchment area since ca. 5000 cal yr BP. This is confirmed by the nature of the deposits themselves, which are not pure tephra layers but rather a mixture of volcanic and organic mud/peat (Kilian et al. 2006). A gradual decrease in the deposition occurred since 4700 cal yr BP, when volcanic material deposited was finer and erosion from the slopes likely decreased.

The effect of this deposition of volcanic material in the depression of the Lake Njalau is shown from the results of pollen and spore analysis. Parallel to the presence of volcanic material in the soil (5100–4400 cal yr BP; 491–375 cm) was the presence of a vegetation dominated by species of *Casuarina* and *Myrica* and the fern *Phymatosorus* which is often found growing on the volcanic lapilli deposit (Orwa et al. 2009; Pinyopusarerk 1997). Few species can adapt to volcanic soil, while the majority of rainforest species cannot. The fact that the diversity of the vegetation in this phase was low is clarified by the results of the PDI which shows in this phase the lowest values for the entire 5000 years recorded (Figure 4.3b).

Ecological investigations indicate that *Casuarina* and *Myrica* are very successful under stressful condition and highly competitive (Gauthier et al. 1999; Orwa et al. 2009; Potgieter et al. 2014). This can be explained by a combination of traits and factors such as their ability to rapid grew, an early and prolific reproduction, avian seed dispersal, and symbiosis with the actinomycete *Frankia* (Potgieter et al. 2014; Sayed 2011; Vitousek 1990; Vitousek and Walker 1989; Wang and Qiu 2006; Zhong et al. 1994) so that they can colonize nitrogen-deficient deposits. As a consequence, it has been observed that in the KSNP, several species of *Casuarina* and *Myrica* act as pioneer species of both deforested land and volcano slopes (Vitousek and Walker 1989).

These volcanophile taxa slightly decreased when the sediment shifted into volcanic ash deposition and the sediment accumulation slowed down (4700–4400 cal yr BP; 425–375 cm depth). However, after the volcanic deposition in the soil ended (4400 cal yr BP; 375 cm depth), the volcanophile taxa still

persisted in the vegetation with relatively high values (up to 22%) before slowly declining along the record (since ca. 3300 cal yr BP; 290 cm depth). In parallel, other rainforest taxa such as *Ficus* started to increase although the composition of the modern forest took several centuries to complete (ca. 900 years at ca. 2400 cal yr BP).

The results from the PC can help clarifying when most of the variation in taxa composition occurred at the site (Figure 4.3b). Major changes in the composition of pollen and spores occurred only three times in the recorded 5000 years. These episodes are recorded from 4700 to 4400 cal yr BP, from 3300 to 2400 cal yr BP, and in the last ca. 500 years. The first two episodes correspond to the changes from lapilli to ash in the sediments and when the volcanophile taxa decreased markedly around 3300 cal yr BP (Figure 4.3b). When rescaling the PC per unit of time (1000 years), RoC analysis can show how fast those changes were. From this, we can discern that the first episode of change was much more rapid compared with the second decrease in volcanophile taxa, thus suggesting a slow pace of change in this second episode (Figure 4.4a–f). The PC from the most represented taxa in the record highlight an important trend in the vegetation dynamics. The only taxa which shows a major trend (decreasing) is *Casuarina/Myrica*, while the other most important taxa such as *Moraceae/Urticaceae*, *Lithocarpus/Castanopsis*, and *Ficus* show a slow increase through time. This suggests that following the deposition of volcanic material at the beginning of the record, the vegetation changes were not driven by a successional pattern which would be otherwise clear in the PC. The most likely explanation

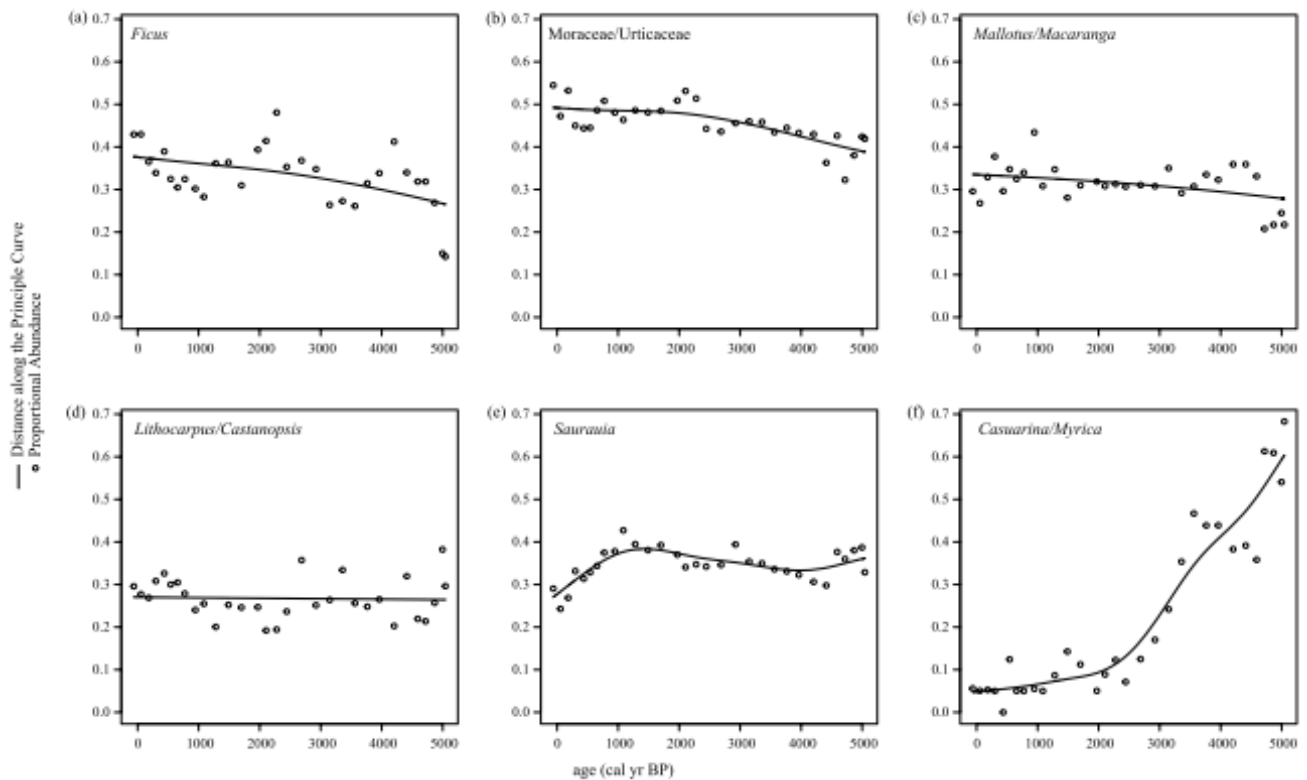


Figure 4.4 Fitted response curves for the six most abundant pollen taxa in the DN records as estimated using a principal curve with CA as the initial starting point. Open circles are the observed proportional abundance and the solid line is the optimized smoother from the final iteration of the PC

for this trend is that competition played the major role in shaping plant composition in the area. Species of *Casuarina* and *Myrica* were successful in dominating patches of the forest until other rainforest taxa e.g. *Ficus* and Moraceae/Urticaceae), conquered back the space in the landscape, reducing the representation of *Casuarina* and *Myrica* markedly.

There are several environmental factors which might have played a role in driving this competition. The PCA and RDA show that the two most important and significant factors were the presence of lapilli in the soil at the beginning of the record and the subsequent formation of soil. The presence of lapilli in the first 400 years of the record explains 7% of the variation in the record. The deposition of this barren material likely marked the first expansion of the volcanophile *Casuarina/Myrica*. Although this cannot be tested with our data, it is likely that soil acidification might have played an important role favouring their expansion and, at the same time, causing dying off and/or impeding the development of the other rainforest taxa (Potgieter et al. 2014).

However, our results suggest that the most important factor explaining the majority of the variance in our record is soil thickness (34%). It is likely that the presence of volcanic material in the soil limited plant survival and growth by preventing root from reaching the below organic soil (Gómez-Romero et al. 2006). This suggests that the dominant presence of *Casuarina* and *Myrica* in the Lake Njalau depression was largely affected by the presence of volcanic material in the soil layer where trees have their roots. Once the peaty organic soil accumulated above such a layer, species of *Casuarina* and *Myrica* could no longer outcompete against other rainforests species and rapidly decreased.

Other possible drivers of change: Fire and human activities

Fire regime shifts can occur in tropical rainforests as a consequence of climate variability (e.g. ENSO, IOD; Gaveau et al. 2014; Kita et al. 2000; Page et al. 2002; Siegert et al. 2001; Van Der Werf et al. 2004; Wang et al. 2004) or due to human activities (Bowen et al. 2001; Cole et al. 2015). Our results for the high-resolution macro-charcoal analysis and CharAnalysis reveal that fire episodes were extremely rare at this site. In average, the FRI was of a fire episode per 523 years with only 12 major fire episodes detected over the past ca. 5000 years. The general low return interval as well as the lack of any trend in the fire frequency through time suggests that the occurrence of fires at the site were stochastic events, most likely as a consequence of occasional storms and lightening (Stolle et al. 2003). Additionally, the RDA indicates that there was no significant correlation between vegetation composition and fire frequency (Table 4.2), thus suggesting no link between vegetation changes and fire regime in the long term.

The first evidence of arrival of *Homo sapiens* in Sumatra trace back to 12,000 years ago at the beginning of the Holocene (Forestier et al. 2006) with the Hoabinhian hunter-gatherer civilization (12,000–7000 yr BP; Glover 1979). In the KSNP area, palynological evidences seem to point toward an increase in deforestation and fires because of human activities already starting from ca. 7000 cal yr BP (Flenley

1988; Flenley and Butler 2001; Morley 1982). However, the first cultural evidence of human presence dates back to the Neolithic periods around 3400–2900 cal yr BP when stone artifacts and obsidian tools are found in the Sungai Hangat and Renah Kemumu regions (Bonatz 2012; Figure 4.1b).

Table 4.2 Results from the redundancy analysis (RDA) with the (a) simple term effect and (b) conditional term effect (significant results with $p < 0.005$ in bold)

| Name | Explains % | pseudo-F | P(adj) |
|------------------------------------|-------------|-------------|----------------|
| (a) RDA – simple term effects | | | |
| Soil thickness | 34.5 | 15.3 | 0.00233 |
| Peat | 25.4 | 9.9 | 0.00233 |
| Lapilli | 20.7 | 7.6 | 0.0035 |
| Nutrient (<i>Botryococcus</i>) | 15.5 | 5.3 | 0.00233 |
| Ash | 7.9 | 2.5 | 0.0378 |
| Erosion (<i>Glomus</i>) | 3.5 | 1.1 | 0.33833 |
| Fire (macro-charcoal) | 3 | 0.9 | 0.425 |
| (b) RDA – conditional term effects | | | |
| Soil thickness | 34.5 | 15.3 | 0.0035 |
| Lapilli | 6.7 | 3.2 | 0.0035 |
| Ash | 3 | 1.4 | 0.126 |
| Peat | 3 | 1.4 | unknown |
| Fire (macro-charcoal) | 3.1 | 1.5 | 0.07933 |
| Nutrient (<i>Botryococcus</i>) | 2.2 | 1.1 | 0.4858 |
| Erosion (<i>Glomus</i>) | 1.9 | 0.9 | 0.67317 |

Afterward, the settlement history in the Kerinci area is marked by the ‘Megalithic period’ which lasted from the late 10th century until the 14th century AD (900–1300 yr BP) and had its peak during the 12th century AD (1100 yr BP; Bonatz et al. 2006; Tjoa-Bonatz et al. 2009). What is left of this culture is outstanding stone megaliths and burial jars as well as remnant of single stones which are usually placed in connection to a house in a small-scale settlement. These megalithic remnants are found around the

KSNP area in cultural clusters close to the villages of Renah Kemumu in Serampas region, Lolo Gedang in the Kerinci area, Sungai Hangat, and Bukit Arat region (Bonatz 2012; Figure 4.1b).

Despite the close proximity of the DN site to these clusters of cultural human phases, no evidence of prehistorical human–landscape interactions was found in the palynological record from the Lake Njalau catchment area. As shown by the PC, RoC, PCA, and RDA, the major changes in vegetation composition can be explained with effect of volcanic deposition in the area.

However, a dynamical phase is recorded for the top part of the record from ca. 500 cal yr BP (AD 1450) to present. This phase is characterized by rapid changes (PC and RoC, Figure 4.3b) and a composition of pollen and spores which was not found in any of the samples before as shown in the PCA (Figure 4a and b). Three high in magnitude fire peaks were recorded at ca. –63 (present time), 47, and 157 cal yr BP which might indicate anthropogenic burning activities. These fire episodes coincide with an increase in *Glomus* spores which can be used as an indicator of soil erosion (Kołaczek et al. 2013). Thus, the synchronous occurrence of fires and the increase in *Glomus* might be related to deforestation and burning of the surrounding forest. However, no evidence could be found of other activities such as Cinnamon and ‘berkebun’ cultivation. This suggests that either there was little human disturbance on the vegetation during the past 5000 years or the DN core was too remote and isolated to record even close by activities in the Kerinci area.

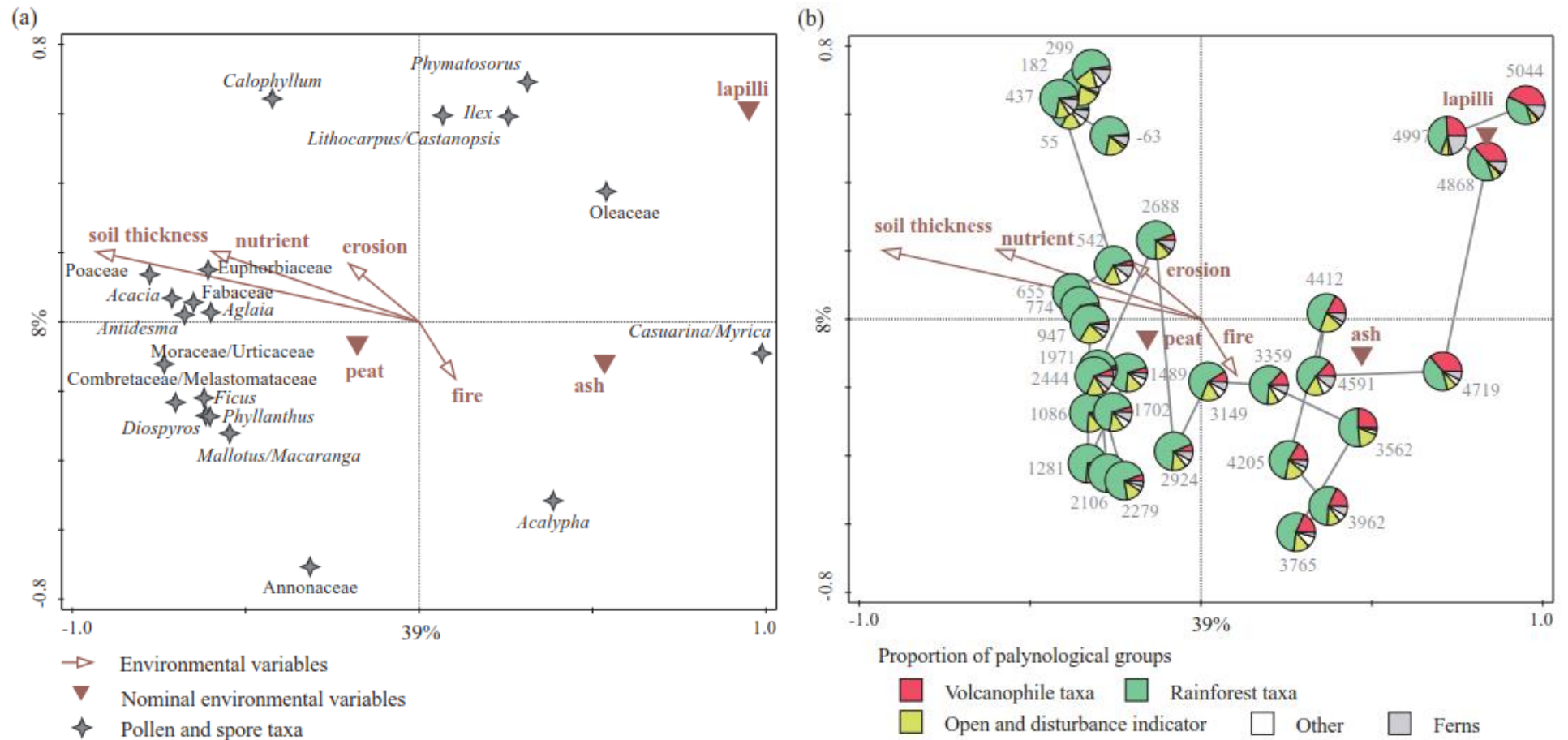


Figure 4.5 Principal Component Analysis (PCA) of all percentage data of identified pollen and spore taxa after Hellinger transformation. Environmental supplementary variables are type of sediment (peat, ash and lapilli as nominal variables), fire frequency from the results of the CharAnalysis, non-pollen palynomorph concentrations for erosion and nutrient status (*Botryococcus* and *Glomus*) and the soil thickness (vertical distance in cm from the volcanic deposit). First two axes are shown (39% and 8% of the variation in composition). (a) Pollen and spore taxa scatterplots; (b) Samples scatterplots represented as pie charts of the relative abundance of pollen and spore taxa groups. Numbers in grey are estimated age of each sample (cal yr BP)

Conclusion

This study was conducted with the aim of investigating the effects of volcanic depositions on the highly diverse tropical montane ecosystems of the KSNP in Sumatra, Indonesia. The use of paleo-ecological analysis increased our understanding of this interaction, by adding a long-term temporal view to the modern understanding of these ecosystems (Simpson and Birks 2012).

The DN core taken from this depression dates back to ca. 5000 years ago, and it revealed a secondary deposition of volcanic material at the beginning of the record. The results from the radiocarbon dating indicate that this re-deposition occurred at a slow pace (ca. 700 years), while the results from pollen and spore analysis indicate that the presence of this barren material in the soil had a strong impact on the plant composition in the area. Species of *Casuarina* and/or *Myrica* were advantaged by this condition and dominated the depression in this phase, leading to low diversity. When the deposition of volcanic material decreased and finally ended ca. 4400 years ago, the presence of these volcanophile pioneer taxa remained frequent in the area. The establishment of the modern submontane rainforests took ca. 900 years.

Such a long-time dynamic is unlikely to have been driven by succession, as this kind of recover pattern after volcanic eruption has been shown to have taken less than 100 years, for instance, in the island of Krakatoa in Indonesia (Whittaker et al. 1989). This is confirmed by the PCA of the pollen and spore data which highlight that this decreasing trend was not characterized by temporal succession of different taxa but by a continuous decrease in *Casuarina/Myrica* and a slow but continuous increase in several other rainforest taxa (i.e. *Ficus*, Moraceae/Urticaceae, and *Mallotus/Macaranga*). Several environmental factors might have contributed to this slow increase in submontane species including soil thickness, erosion, and disturbance and human activities. We tested for these different factors using multivariate statistical analyses on the pollen and spore assemblage. The environmental explanatory variables used were type of sediment (as factors: ash and lapilli and non-volcanic), soil thickness (expressed as vertical distance along the sequence from the volcanic deposit), fire frequency as obtained from the CharAnalysis results as indicator of fire regime changes, non-pollen palynomorphs as indicators of soil erosion, and nutrient supplies. The constrained ordination (RDA) results indicate that among those factors which were significantly correlated with the decrease in volcanophile taxa, soil thickness was the one that explains most of the variance. We conclude that the presence of volcanic material in the soil layer where trees have their roots limited the survival and growth of most of submontane rainforests taxa rather than *Casuarina/Myrica*. Once the peaty organic soil accumulated above such a layer, species of *Casuarina* and *Myrica* could no longer outcompete against other rainforests species and rapidly decreased.

Other than the effect of volcanic material in the soil, disturbance caused by human activities, climatic variability, and fire regime changes can be considered strong drivers of ecosystem dynamics in the tropical montane rainforests in Indonesia (e.g. Biagioni et al. 2015, 2016; Haberle 2007; Haberle et al.

2001; Hope 1998; Kirleis et al. 2011; Maloney 1980; Maloney and McCormac 1995; Morley 1982). Despite the close vicinity of the site to known archaeological sites, we did not find compelling evidence for prehistoric disturbance of the vegetation due to human activities such as deforestation and agriculture. Additionally, the high-resolution macro-charcoal analysis of local fire history at the Danau Njalau depression indicated that fire never had a strong influence on the vegetation for the past 5000 years. Fire episodes were extremely rare and, therefore, cannot be linked to any causality (i.e. human cultural phases and climate variability).

While it should be noted that this is a single case study and more records are needed to confirm these results, our record from the KSNP suggests that the effect of volcanism on the western side of the Sumatra island might be spatially and temporally more important than so far assumed in shaping the composition and structure of the diverse rainforests we see today.

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Supplementary materials

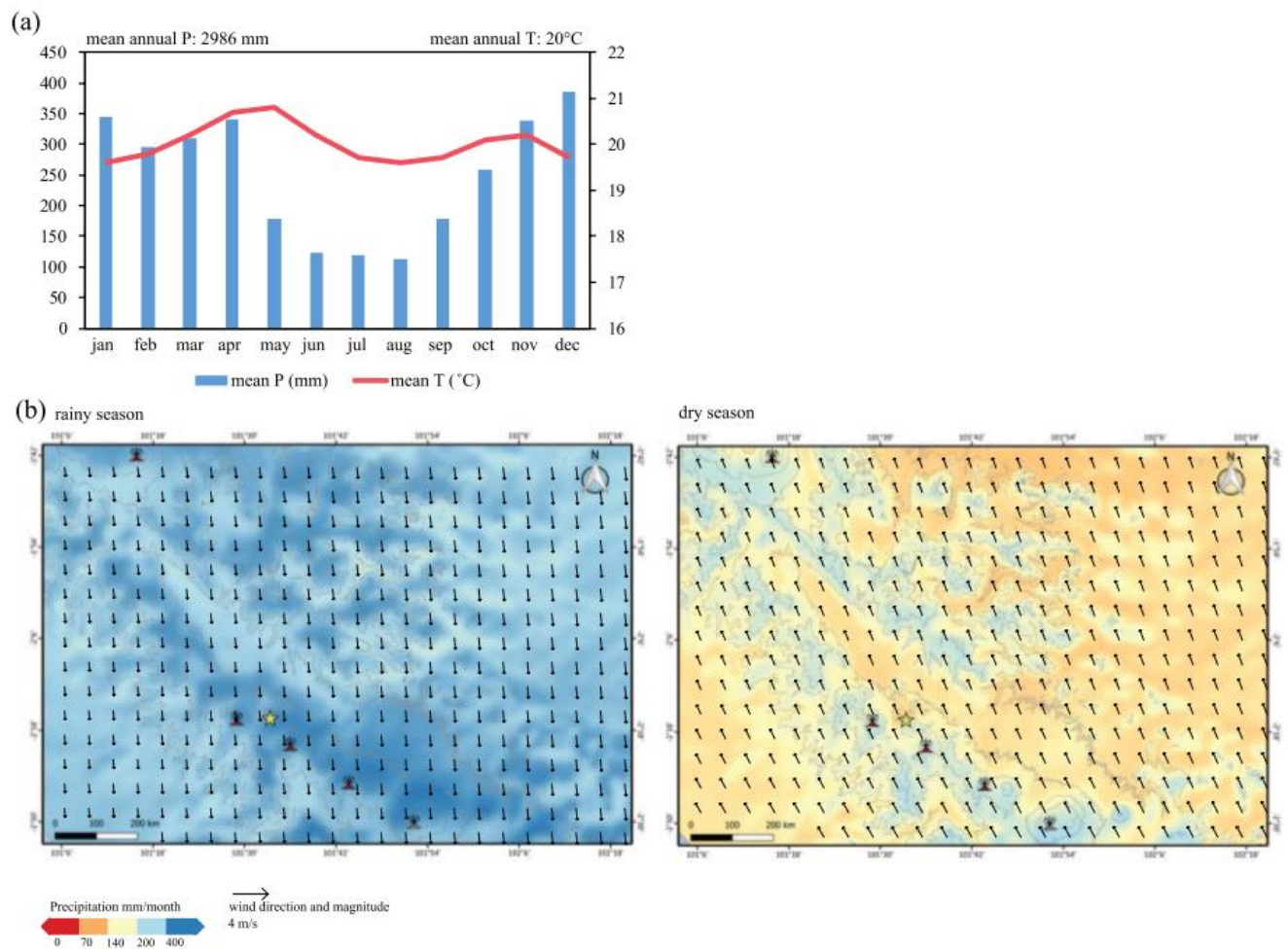


Figure 4.6 (a) Mean monthly and annual precipitation and temperature of the studied area. Data source for precipitation from CHELSA 30 arcsec time period 1979–2013. Available at: <http://chelsa-climate.org/> (Karger et al. 2016). (b) Wind pattern and mean precipitation (mm/month) for the rainy (December, January, and February) and dry (June, July, and August) seasons in the study area. Data source for wind direction and magnitude from NCEP reanalysis of vector surface wind (1000 mb) done within time period 1950–2015 (Kalnay

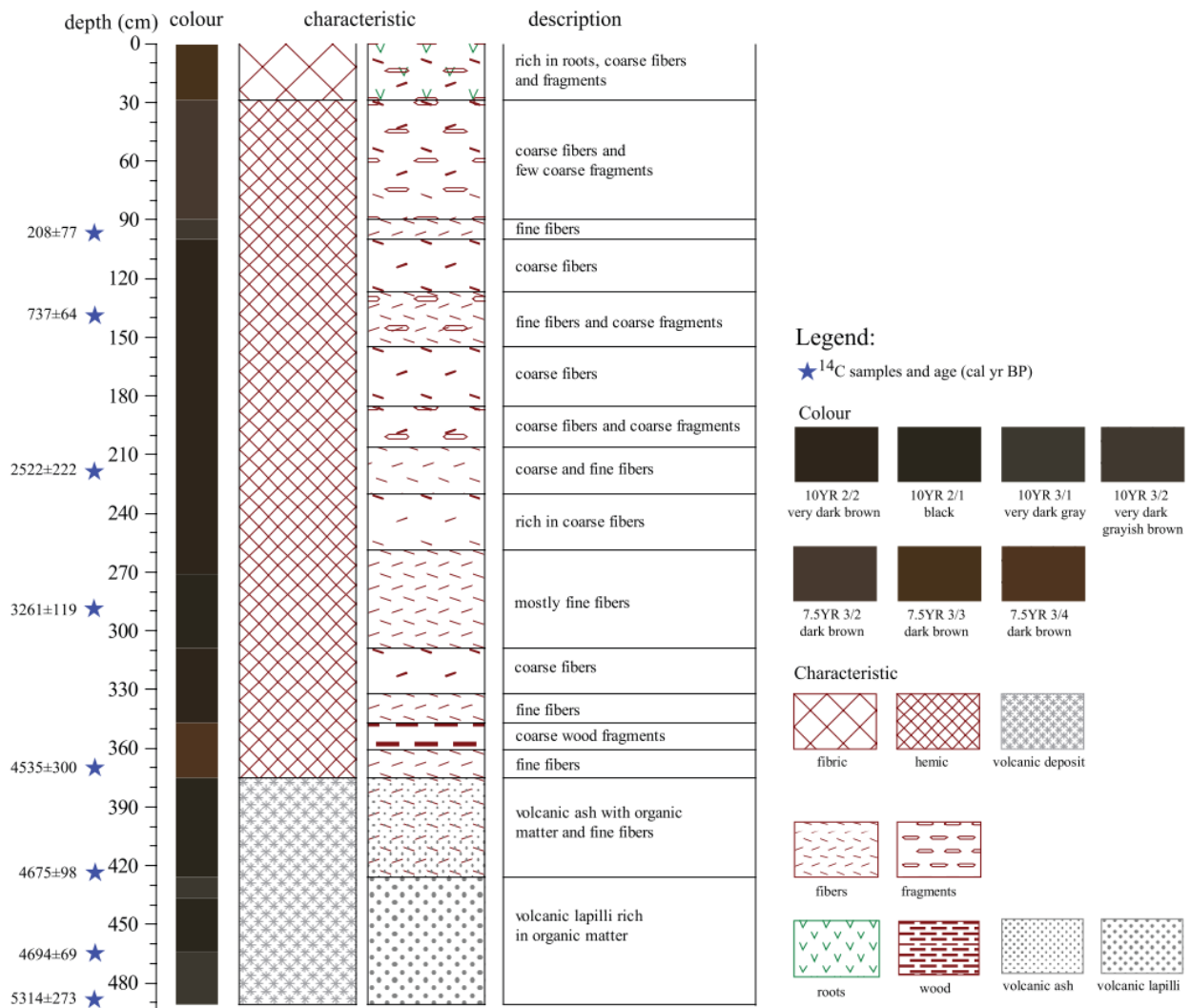


Figure 4.7 Detailed lithological profile of the sediment from the DN core and calibrated AMS radiocarbon dates shown as star symbols

Table 4.3 List of pollen and spore taxa identified in the DN core and grouping based on their ecological distribution: submontane rainforest taxa, volcanophile taxa, open and disturbance indicator taxa, and Pteridophyta. Other taxa correspond to pollen grains of taxa that could not be included in any of the defined group

| Sub-montane rainforest taxa | | Volcanophile taxa | "Others" |
|----------------------------------|---------------------------|--|-------------------------------|
| <i>Acacia</i> | Myristicaceae | <i>Aglaia</i> | Annonaceae |
| <i>Acalypha</i> | Myrsinaceae cf. Aegiceras | <i>Casuarina/Myrica</i> | Celastraceae |
| <i>Ambrossia</i> | Myrtaceae | <i>Celtis</i> | Loranthaceae |
| <i>Antidesma</i> | <i>Nauclea</i> | <i>Podocarpus</i> | Ericaceae |
| Arecaceae | <i>Pandanus</i> | <i>Pometia</i> | Euphorbiaceae undiff |
| <i>Bischofia</i> | <i>Phyllanthus</i> | <i>Dacrycarpus</i> | Fabaceae undiff |
| <i>Blumeodendron</i> | <i>Pinus</i> | | Malpighiaceae |
| <i>Canarium</i> | Rutaceae | | Malvaceae |
| Combretaceae/ Melastomataceae | Sapindaceae | Open and disturbance indicator taxa | Oleaceae |
| <i>Diospyros</i> | <i>Saurauia</i> | <i>Arenga</i> | <i>Oncosperma</i> |
| <i>Dipterocarpus</i> | Verbenaceae | Asteraceae | <i>Randia</i> |
| <i>Dysoxylum</i> | <i>Zanthoxylum</i> | <i>Baccaureae</i> | Rosaceae |
| Elaeocarpaceae | | <i>Calophyllum</i> | Rubiaceae undiff. |
| <i>Engelhardtia</i> | | <i>Macaranga/Mallotus</i> | Sapotaceae |
| <i>Ficus</i> | | <i>Prunus</i> | Tilioideae |
| Flacourtiaceae | | <i>Trema</i> | Pteridophyta |
| <i>Gardenia</i> | | <i>Vernonia</i> | Cyatheaceae |
| <i>Glochidion</i> | | <i>Ilex</i> | <i>Davalia</i> |
| <i>Gnetum</i> | | Poaceae | <i>Phymatosorus</i> |
| Hamamelidaceae | | Liliaceae - Iridaceae | Marattiaceae |
| <i>Homalanthus</i> | | Cyperaceae | <i>Ophioglossum</i> |
| Lauraceae | | Mimosoideae | Polypodiaceae |
| <i>Leea</i> | | | <i>Pteris</i> type |
| <i>Lithocarpus/Castanopsis</i> | | | <i>Schizaea</i> |
| <i>Livistona</i> | | | <i>Selaginella</i> |
| Menispermaceae | | | <i>Stenochlaena palustris</i> |
| Moraceae/Urticaceae | | | <i>Thelypteris palustris</i> |

CHAPTER 5 – paper 2

First palaeoecological evidence of Buffaloes husbandry and rice cultivation in the Kerinci Seblat National Park in Sumatra, Indonesia

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Keywords

Holocene, palynological analysis, rice introduction, buffalo husbandry, coprophilous fungi, Kerinci valley

Abstract

Rice is one of the most important subsistence crops, however evidence of the origin and domestication of rice cultivation is still scarce in Indonesia. This study aims to trace the beginning of rice cultivation and buffalo husbandry in Sumatra, Indonesia. We carried out palaeoecological multi-proxy analyses of pollen and spores, non-pollen palynomorphs (NPPs) and macro-charcoal analysis on a sediment core from the swamp forest of Danau Bento (DB) in the Kerinci Seblat National Park (KSNP). Our results provide first evidence of buffalo husbandry in the Kerinci at least 4300 years ago, in line with the migration of the Austronesians to Sumatra. NPPs and pollen results indicate the existence of grassland until about 3200 cal yr BP around the site, which was used for buffalo grazing and not for rice cultivation. The rise of Poaceae about 2500 cal yr BP suggests the beginning of rice cultivation in the swamp contemporary with a decline in grazing as shown by the NPPs. However, this phase lasted only few centuries until ca. 2100 cal yr BP. Following the decline of rice cultivation, the swamp remained in use as a grassland for grazing.

Introduction

In Asia, rice is the most important cereal crop and it has shaped the cultures, diets and economies of the people (Gnanamanickam 2009). Cultivated rice (*Oryza sativa* L.) belongs to the grass family (Family: Poaceae; USDA-NRCS PLANTS Database, Hitchcock 1950) and was domesticated from wild rice (*O. rufipogon* Griff.). Physical remains (phytolith and rice husks) from archaeological sites and genetic evidence indicate that rice was domesticated ca. 8500 cal yr BP in China (Higham and Lu 1998; Zhao et al. 1995; Khush 1997; Liu et al. 2007; Zong et al. 2007; Fuller et al. 2009). Subsequently, rice cultivation expanded to Cambodia, Vietnam and southern India. Afterward, the derived species of *O. japonica* and *O. indica* were distributed to other Asian countries, such as Korea, Japan, Myanmar, Pakistan, Sri Lanka, the Philippines and Indonesia (Gnanamanickam 2009).

Indonesia is today one of the largest consumers and the third-largest rice producing country in the world after China and India (Setyanto et al. 2018; Statistic Indonesia 2017). However, the origin and domestication history of cultivated rice in Indonesia are still unknown (Maloney et al. 1989). It is thought that the agricultural system in Indonesia started in the mountainous area with shifting cultivation of root crops, and only afterward migrants introduced cultivated rice (Maloney 1996). However, evidence of this is still scarce (Figure 5.1).

The oldest evidence of rice in Indonesia comes from the island of Sulawesi dated to about 4000 cal yr BP as a charred rice remain in pottery (Bronson and Glover 1984; Maloney 1991; Bellwood 2008; Bulbeck 2008; Barton 2015). Close to Indonesia, in the Malaysian part of the island of Borneo, rice-tempered pottery from two coastal lowland sites of the Gua Sireh cave (Datan and Bellwood 1991) and

Table 5.1. Review of early evidence of rice cultivation in Asia

| Region | Site | Type of evidence | Age (BC) | Age (cal yr BP) | References |
|----------|---|--|------------------|------------------|--|
| China | Lake Dongting, Middle Yangtze valley | Husk and chaff as temper in pottery, rice macrofossil | 6000-5000 | 8000-7000 | Pearson and Underhill 1987; Maloney 1991 |
| China | Hemudu, Lower Yangtze valley | Rice macrofossil, well known site of early rice cultivation | 5000-4600 | 7000-6600 | Liu 1985; Pearson and Underhill 1987; Chang 1990 |
| India | Ganges valley, Koldihwa | Rice husk and chaff as temper I pottery | 4000-2000 | 6000-4000 | Sharma 1985 |
| Thailand | Bang Pakong valley | Pollen and phytolith | 4000 | 6000 | Kealhofer and Piperno 1994 |
| Vietnam | Xom Trai Cave | - | 4000-2000 | 6000-4000 | Maloney 1991 |
| Borneo | Niah Cave | Rice embedded in pottery | 3400-3900 | 5900-5400 | Doherty et al. 2000 |
| Thailand | Ban Chiang, Korat Plateau | Rice husk as temper in pottery | 3500 | 5500 | Maloney 1991 |
| Borneo | Cave of Gua Sireh | Rice embedded in pottery | 2300 | 4300 | Datan and Bellwood 1991; Bellwood et al. 1992; Beavitt et al. 1996 |
| Thailand | Khok Phanom Di | Rice straw as temper in pottery | 2000-1500 | 4000-3500 | Maloney et al. 1989; Maloney 1991 |
| Sulawesi | Ulu Leang, South Sulawesi | Rice macrofossil | 2000 | 4000 | Bronson and Glover 1984; Bellwood 2008; Bulbeck 2008 |
| Sumatra | Toba Plateau, Highland of North Sumatra | Pollen of rice (large Poaceae) with phytolith and microfossil charcoal | 600 | 2600 | Maloney 1996 |

Ages are reported as BC and calibrated BP. The bold numbers show the original ages mentioned in the references

the Niah cave (Doherty et al. 2000; Hunt and Rushworth 2005) returned an older age for rice introduction (4300 cal yr BP and 5900–5400 cal yr BP, respectively; Table 5.1). The island of Sumatra is located in the western part of Indonesia and it has a strategic location as a hub to mainland Asia. The east coast of Sumatra through the Straits of Malacca might have provided a gateway path for introduction of rice from Asia to other islands such as Borneo and Java. The population that now inhabits the islands descends from Southern Mongoloid and speaks Austronesian languages (Bellwood 1985). Evidence of dentate stamped pottery suggest that they migrated southward from Taiwan across other islands of SE Asia (Bellwood and Dizon 2005; Hung 2005; Bellwood 2007) and reached Sumatra about 3500 cal yr BP (Bellwood 2007). By this time, rice had long been cultivated in China and the Austronesian speakers supposedly brought their crop with them (Maloney 1996). Currently the only evidence for rice cultivation introduction in Sumatra is from the highland of North Sumatra at the Toba Plateau, indicated by the rise of rice pollen (Poaceae) and rice phytoliths (Maloney 1996). This evidence suggests that rice cultivation might have begun as late as 2600 cal yr BP when the Batak, predominant people in the highland of Toba, had already inhabited the area for more than 3000 years (Maloney 1996). This is a very late date, considering the Bellwood model (Bellwood 1985, 2007) and the indication from pollen analysis that forest clearing had already started in Sumatra at 7500 cal yr BP (Maloney 1985; Flenley 1988).

One of the most important variations in rice cultivation is whether rice was cultivated under dry-field or wet-field conditions. Initially, early rice domestication in China was developed in wet-fields as suggested by the composition of phytoliths in association with grasses on sites with rice cultivation (Fuller et al. 2016). Wetland rice is often referred to as paddy, being cultivated in controlled flooded fields with developed irrigation systems (Falvey 2010). In Sumatra, it was suggested that initially rice could have been introduced as both a dry-land and a wet-land crop simultaneously (Maloney 1996) as evidenced in the Toba Plateau (Maloney 1982).

Paddy is cultivated in bounded fields (= sawah in Bahasa Indonesia, Maloney 1996; Bellwood 2007) and associated with tillage using the hoe or the plough (Maloney 1996). Before the introduction of machinery in SE Asia, water buffalos (*Bubalus* sp.) were used in wet-rice cultivation to plough wet-rice fields. The wild Asian buffalo (*Bubalus arnee* Kerr, 1792) extends across South and SE Asia from Mesopotamia to Indo-China (Barker 2014) and is considered as the most probable ancestor for water buffalo *B. bubalis* (Cockrill 1984; Colli et al. 2018). The Asian domestic water buffalo (*B. bubalis* Linnaeus, 1758) is today widely distributed around the world through historical migration events and recent importations, especially during the last century (Cockrill 1974). *B. bubalis* is classified based on morphological and behavioural criteria into two types: river buffalo *B. bubalis bubalis* and swamp buffalo *B. bubalis carabensis* (MacGregor 1941). The swamp buffalo was most likely domesticated in a region close to the border between China and Indochina (Zhang et al. 2011, 2016; Wang et al. 2017) about 5000–4000 years ago (Cockrill 1981). Following domestication in this region, genetic evidence indicates that it spread via the southern route through peninsular Malaysia to the Indonesian islands

(Sumatra, Java and Sulawesi, Figure 5.1) and via the northern/northeast route into central China, and then through an eastern island route via Taiwan to the Philippines and Borneo (Barker 2014; Colli et al. 2018). Finding evidence of the presence of swamp buffaloes can provide important information regarding rice cultivation and its introduction in Sumatra.

Palaeoecology can be used to trace back the history of rice cultivation and buffalo husbandry. For instance, pollen and spore analyses can be used as evidence of rice cultivation and vegetation changes (e.g. Maloney et al. 1989; Huang and Zhang 2000; Hunt and Rushworth 2005; Zong et al. 2007; Yang et al. 2012; Qiu et al. 2014; Jones et al. 2016; Liu et al. 2016). Non-pollen palynomorphs (NPPs), in particular the fossils of ascospores of coprophilous fungi can be used to assess the existence of past fauna, especially wild or livestock herbivores, as several studies have shown (e.g. Davis 1987; Hausmann et al. 2002; van Geel et al. 2003; Bos et al. 2006; Davis and Shafer 2006; López-Sáez and López-Merino 2007; Mazier et al. 2009; Cugny et al. 2010; Raczka et al. 2016).

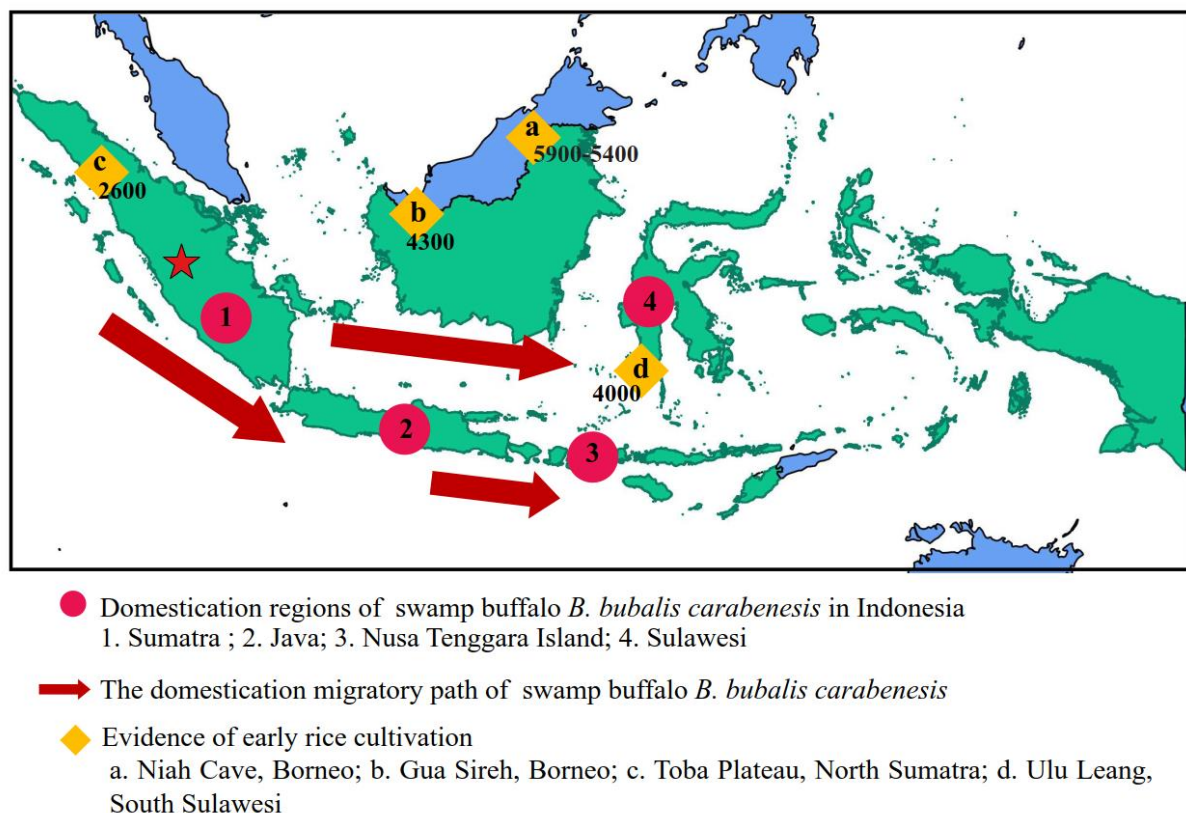


Figure 5.1. The domestication region and migratory path of swamp buffalo *B. bubalis carabensis* (MacGregor 1941) in Indonesia (Colli et al. 2018). Red arrow show the domestication migratory path and the regions are shown in red circles. The first evidence of rice cultivation in Indonesia and its surrounding shown in yellow diamonds (Datan and Bellwood 1991; Doherty et al. 2000; Hunt and Rushworth 2005; Chacornac-Rault 2005; Maloney 1991). The red star is the location of our study area (Danau Bento). Numbers show oldest dates of rice evidence in the region (in cal yr BP)

The Kerinci valley is one of the most fertile areas in the highlands of Sumatra (Miksic 2015). The rich volcanic soil in the large alluvial valley makes it a highly suitable place for rice cultivation (Bonatz 2006). Archaeological evidence shows a long history of human occupation in Kerinci (Bonatz 2012). There is however no clear evidence as to when rice was first introduced in the area. In the Kerinci valley

today, water buffalos are used extensively in farming in swampy grassland areas. It has been hypothesized that a complementarity existed between raising livestock, introduction of wet-rice cultivation in Indonesia and farming grassland (Brookfield et al. 1995). To test the reciprocal introduction of wet-rice cultivation and swamp farming in the Kerinci valley, we conduct palaeoecological multi-proxy analysis on a sediment core taken from a grassland swamp (Danau Bento) in the Kerinci valley. Pollen and spores are used to reconstruct past vegetation changes around the site. NPPs of coprophilous fungi are used as markers for grazing activities and macro-charcoal analysis is used to reconstruct the local fire regime. This study aims to trace back the beginning of rice cultivation and buffalo husbandry in the Kerinci valley. Thanks to this new evidence, we can improve our understanding of historical and prehistorical agriculture and human activities in SE Asia.

Study area

Environmental setting of the study area

Sumatra Island is forming part of the so-called Sundaland (Laumonier 1997), a biogeographic area between mainland Asia to the west and the Wallace and Sahul shelf to the east. The west coast of Sumatra Island is dominated by the Barisan Mountains that run the whole length of Sumatra (Whitten et al. 2000). A significant part of this mountain range falls within the boundaries of Kerinci Seblat National Park (KSNP), the largest national park and one of biodiversity hotspots in Sumatra (ca.1.4 million ha, Bramley et al. 2004). The national park area consists of steeply sloping land and numerous active volcanoes, including the highest peak in Sumatra, Mount Kerinci (3805 m, Ohsawa et al. 1985). The Kerinci valley is a large fertile rift (Bonatz 2012) where today rice is cultivated. The slopes of the valley are covered with primary montane rainforest, tea plantations and cinnamon agroforest.

Danau Bento is a unique wetland ecosystem in the KSNP (Figure 5.2a; Natividad and Neidel 2003). It is one of the highest freshwater swamps in Sumatra lying at about 1300–1400 m a.s.l. and covering approx. 1000 ha. Despite its name, Danau Bento (i.e. Danau means lake in the Indonesian language) is not a lake but a large swath of freshwater marshland (Natividad and Neidel 2003). The area is located about 12 km south from Mt. Kerinci and about 20 km south-west of Danau Gunung Tujuh, two of the most prominent volcanic features of Kerinci. The water system originates from Danau Gunung Tujuh, with Sungai Sangir (Sangir River) crossing the swampy ecosystem to a small lake in the centre (Natividad and Neidel 2003). The vegetation of this small lake consists of swampy peat grassland and swamp forest. Along the Sungai Sangir, open wetlands with Enceng Gondok (*Eichhornia crassipes*) and Kayu Apu (*Pistia stratiotes*) can be found.

The fringing areas of the Danau have been converted into wet-rice fields. The surrounding open swamps are covered with *Leersia hexandra*, and other grasses from the families of Poaceae and Cyperaceae. The swampy forest is dominated by *Eugenia spicata*, *Palaquium* sp. and *Syzygium* sp. The mountainous

areas surrounding the swamp are characterized by submontane vegetation (800–1400 m), with tree species from the families of Fagaceae, Lauraceae and Myrtaceae (Laumonier 1997).

A sediment core (DB) was collected from the Danau Bento in the fresh water swamp forest. The site is located in the margin between the rice plantations, farmed grassland for buffaloes and the steeper submontane forest (Figure 5.2b). The site was chosen due to its proximity to archaeological sites, location in the fertile Kerinci valley and the marginal position between natural (swamp forest) and open (grassland and rice plantations) systems.

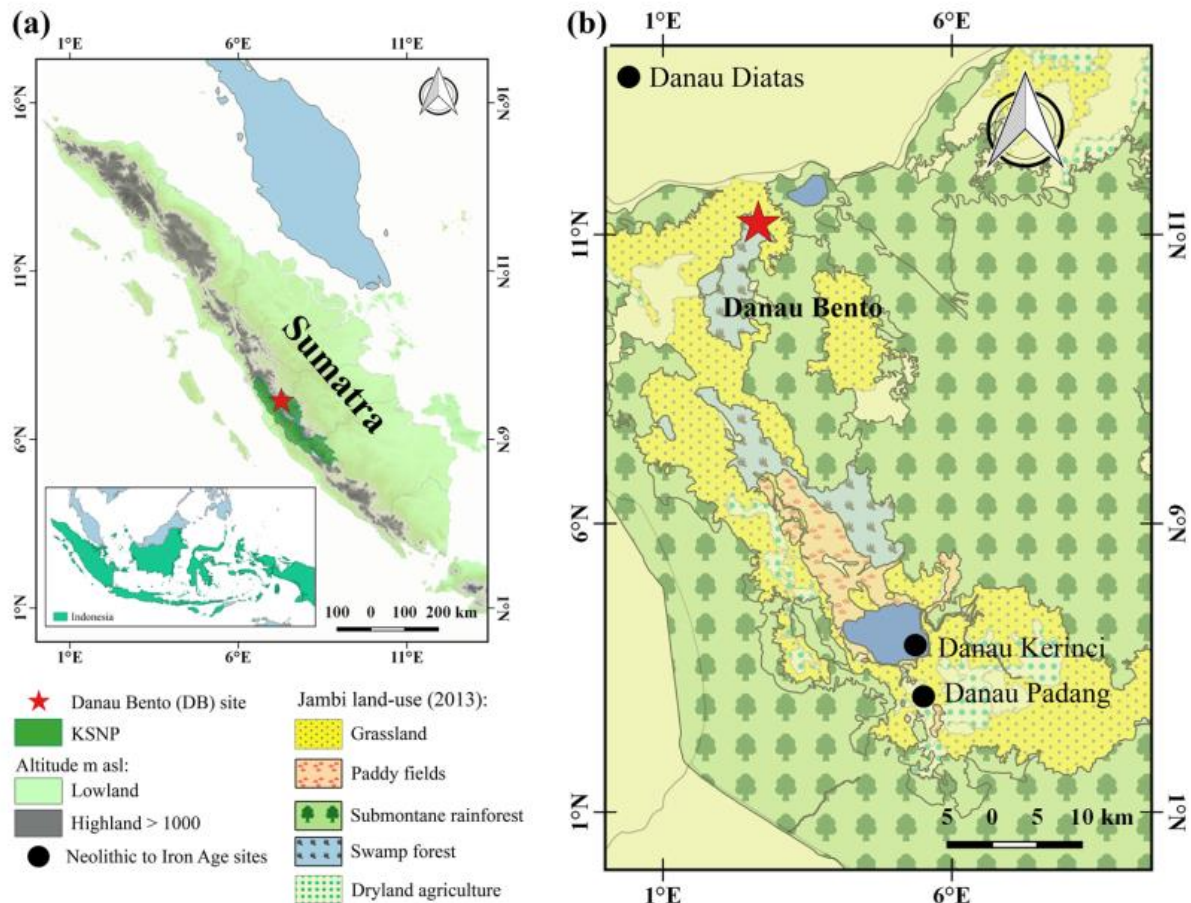


Figure 5.2 Maps of the study area: a) the location of the studied region, the Kerinci Seblat National Park (KSNP) in Sumatra Island, Indonesia. The red star shows the location of the study site (Danau Bento) in the KSNP; b) the study site, Danau Bento (DB) marked with a red star. The land-use data are from Melati et al. (2015). The possible Neolithic to Iron Age sites at Danau Diatas and Danau Padang (Lolo Gedang region) are from Bellwood (2017) and Flenley (1985); and the Danau Kerinci site from van Heekeren (2013)

Prehistory and history of Sumatra's highlands

Palynological studies from the highlands in Sumatra (Morley 1982; Flenley 1988; Maloney 1996; Flenley and Butler 2001) suggest forest clearance since 7500 years ago (Morley 1980, 1982). These findings might provide the first evidence for settlement in this region by cultivators. However, there were no direct associations with the archaeological records (Bellwood 2007). A pollen record from Pea Sim–Sim Swamp near Lake Toba in northern Sumatra (Maloney 1996) indicates forest clearance could

have started as early as 6500 cal yr BP, however the evidence of increase in large grass pollen began only from 2600 cal yr BP onward (Maloney 1996). A similar sequence is from Lake Diatas near Padang (Newsome and Flenley 1988) in central Sumatra where the initial forest clearance was linked to shifting cultivation, which allowed complete forest regeneration (Flenley 1988). This was shown not by Poaceae pollen grains, but other secondary pollen indicators like *Trema* and *Macaranga*. The rise in Poaceae grains started only about 2000 years ago (Flenley 1988).

Based on archaeological evidence, rice introduction in Sumatra might have started with the Austronesian (Malayo-Polynesian) migration out of Taiwan about 4000 years ago (Bellwood 2007). With this migration the local Neolithic period started in the area of Kerinci as indicated by archaeological remains (Whitten et al. 2000). During this cultural phase, man was cultivating rice and other crop plants such as sago and had domestic animals such as pigs *Sus scrofa* (Medway 1973) and dogs *Canis familiaris* (Clutton-Brock 1959; Medway 1977). The animal domestication evidence also records the use of swamp buffalo as livestock cattle. It is estimated that the introduction of water buffaloes in Sumatra and Java started about 4000–3000 years ago along with the spread of the agricultural system (Lei et al. 2007) from China to mainland SE Asia (Zhang et al. 2011). The later prehistoric phases in Sumatra such as the Bronze-Iron Age are not clear, despite the dating from about 3000 years ago evidenced by bronze kettle drums near Lake Kerinci, Bengkulu and Lake Ranau, other bronze vessels from the Kerinci area, and statues from Bangkinang in West Riau (van Heekeren 2013).

Material and methods

A 600 cm-long sediment core (DB, 1.734428S 101.359748E; 1430 m a.s.l.) was collected in 2013 in the forest margin of Bento swamp using a Russian peat corer (Jowsey 1966). The core was described lithologically and photographed at the University of Jambi, Sumatra. Six samples consisting of plant materials and organic bulk sediment were sent for Accelerator Mass Spectrometry (AMS) radiocarbon dating to the Erlangen Laboratory in Germany and Poznań Radiocarbon Laboratory in Poland (Table 5.2).

Palynological analysis

A total of 39 subsamples for palynological analysis were collected along the core at different intervals to account for changes in sediment accumulation rate. Each subsample consisted of 0.5 cm³ of sediment and was processed for pollen and spores using standard techniques (Fægri and Iversen 1989) including HF 48% treatment and acetolysis. One tablet of *Lycopodium clavatum* spores was added to each subsample to estimate palynomorph concentrations (Stockmarr 1971). Pollen and spores analyses were carried out using light microscopy. All identified pollen and spore types were photographed using a Leica photomicroscope with a 400 × magnification. Pollen and spores were identified using the tropical pollen reference collections of the Department of Palynology and Climate Dynamics which includes

specimens collected from the KSNP area. Additional resources used include pollen keys and atlases for SE Asia (Powell 1970; Huang 1972; Flenley 1976; Garrett-Jones 1979; Wang et al. 1995; Bulalacao 1997; Stevenson 1998; Jones and Pearce 2015; Poliakova and Behling 2016) and the online database of the Australasian Pollen and Spore Atlas (APSA) from the Australian National University, Canberra (available at <http://apsa.anu.edu.au>) and the Pollen and Spore Image Database of the University of Göttingen (available at <http://gdvh.uni-goettingen.de/>).

The pollen grains were counted to a minimum of 300 grains per subsample. The identification was conducted at the lowest taxonomic level possible. However, some pollen grains are morphologically indistinguishable under light microscopy and were summed together. These include pollen from Moraceae and Urticaceae (Moraceae/Urticaceae) excluding *Ficus*, Melastomataceae and Combretaceae (Melastomataceae/Combretaceae), as well as pollen from *Lithocarpus* and *Castanopsis* (Fagaceae; *Lithocarpus/Castanopsis*), *Mallotus* and *Macaranga* (Euphorbiaceae; *Mallotus/Macaranga*), *Casuarina* (Casuarinaceae) and *Myrica* (Myricaceae; *Casuarina/Myrica*). The monoporate pollen grains from the family Poaceae were separated into small Poaceae (< 40 µm in size, Page 1978; Köhler and Lange 1979; Dickson 1988) for wild grasses and large Poaceae (> 40 µm in size, Chaturvedi et al. 1998) for cultivated rice (*Oryza sativa*-complex); however, Yang et al. (2012, 2018) found the majority of grains were < 40 µm in their studies. As other wild Poaceae species can also be larger than 40 µm, single occurrences of large Poaceae were not considered compelling evidence for rice cultivation.

Pollen counts were standardized to percentages based on the total pollen sum. Fern spores were counted along with the pollen grains and are expressed as percentage of the pollen and spores total sum. Pollen and spore taxa were grouped into swamp forest taxa, forest disturbance and open vegetation taxa, submontane forest taxa, and ferns according to their ecology, habitus and distribution (Flora Malesiana collection: <http://portal.cybertaxonomy.org/flora-malesiana/>; Prosea collection: <http://proseanet.org>). Concentrations are calculated using a *Lycopodium clavatum* marker and are expressed as number per cm³ of sediment. The software C2 was used for calculation of percentages and plotting of diagrams (Juggins 2007).

Macro-charcoal analysis

A series of contiguous subsamples at 2 cm intervals were taken along the sediment core (275 samples) for macro-charcoal analysis (> 150 µm). Subsamples of 2 cm³ were prepared following the methods for macro-charcoal analysis (Rhodes 1998; Stevenson and Haberle 2005). A low concentration of Hydrogen Peroxide (6% H₂O₂) was applied to digest and bleach organic material in the sediment samples. The macro-charcoal particles were counted under a binocular dissecting microscope. Results are expressed as the number of charred particles per cm³.

Non-pollen palynomorphs analysis

Non-pollen palynomorphs (NPPs) were prepared and counted together with the pollen grains until a minimum of 300 pollen grains was counted). Coprophilous fungal spores and other palynomorphs were identified and interpreted according to the NPPs references (van Geel et al. 1983, 2011; van Geel and Andersen 1988; Gelorini et al. 2011; Shumilovskikh et al. 2017). Most NPPs types are identified and grouped together into coprophilous fungal spores (CF), aquatic freshwater spores (AWF), decaying wood fungal spores (DWF) and others. ‘Others’ (OF) represents NPP types that could not be identified to a specific grouped taxon.

Numerical data analyses

Multivariate statistical analysis (principal component analysis—PCA) was done to display the vegetation changes deriving from pollen and spore analysis in time. Based on these results, local pollen assemblage zones were defined. All pollen and spores taxa are included, rare taxa were not down-weighted and the square-root transformation was applied (Simpson and Birks 2012) using the software CANOCO to perform the analysis (ter Braak and Šmilauer 2002). Non-pollen palynomorph percentage values are used as additional environmental explanatory variables.

The software CharAnalysis was used to reconstruct the fire regime characteristics (Higuera 2009). The CHAR time series was interpolated based on the median temporal resolution and the raw charcoal data were converted to charcoal accumulation rates (CHAR, particle/cm²/yr). Background CHAR was smoothed per 1000-year window with a lowest smoother robust to outliers. A Gaussian mixture model was used to separate the noise from the significant fire-related peaks. The local signal-to-noise index (SNI) was used to verify that the separation between the identified charcoal peaks and the noise distribution of the charcoal series was statistically significant (Kelly et al. 2011).

Results

Core descriptions and chronology

The DB core consists mainly of organic mud intercalated with several minerogenic clay layers (132–150 cm, 203–237 cm, 301–320 cm, 380–397 cm, 405–426 cm). However, the clay is still organic with abundant plant and wood material. A detailed description of the stratigraphic lithology of the core is shown in Figure 5.3. The chronology of the DB core is obtained from six AMS radiocarbon dates (Table 5.2). The calibration of the radiocarbon dates is performed using Clam 2.2 (Blaauw 2010) script in R (R Core Team 2015) using the Southern Hemisphere SHCal13.14C calibration curve (Hogg et al. 2013). The dates are fitted into a smooth spline model. The age-depth model results indicate that the DB core records the last 4300 years.

Table 5.2. List of accelerator mass spectrometry radiocarbon dates on organic bulk sediment from DB core

| depth (cm) | Lab code | Material | pMC | BP | Cal yr BP |
|------------|------------|-----------------------|------------|---------|-----------|
| 146 | Poz-101222 | Organic bulk sediment | - | 1595±30 | 1478.5±95 |
| 198 | Erl-19240 | Organic bulk sediment | 80,58±0,43 | 1735±43 | 1616±92 |
| 246 | Poz-101223 | Organic bulk sediment | - | 2640±30 | 2764±93.2 |
| 376 | Erl-19239 | Organic bulk sediment | 68,19±0,39 | 3075±46 | 3233±128 |
| 473 | Erl-19241 | Organic bulk sediment | 65,69±0,35 | 3376±43 | 3550±96 |
| 598 | Erl-19238 | Organic bulk sediment | 62,82±0,35 | 3734±44 | 4022±132 |

Calibration done with R script in CLAM 2.2, calibration curve using the Southern Hemisphere SHCal13.14C (Hogg et al. 2013)

The depth versus age relationship (Figure 5.3) suggests an irregular sediment accumulation in the bottom of the core (567–268 cm) and more stable sediment accumulation rates afterwards (268–0 cm). The sediment accumulation rate is initially high (567–359 cm; 4300–3400 cal yr BP; average 2.4 mm/year), and subsequently decreases to a slower accumulation rate (359–268 cm; 3400–2800 cal yr BP; average 1.8 mm/year). Afterward, the sediment accumulation rate is low and stable until the top of the core (268–0 cm; 2800 cal yr BP to present; average 0.8 mm/year).

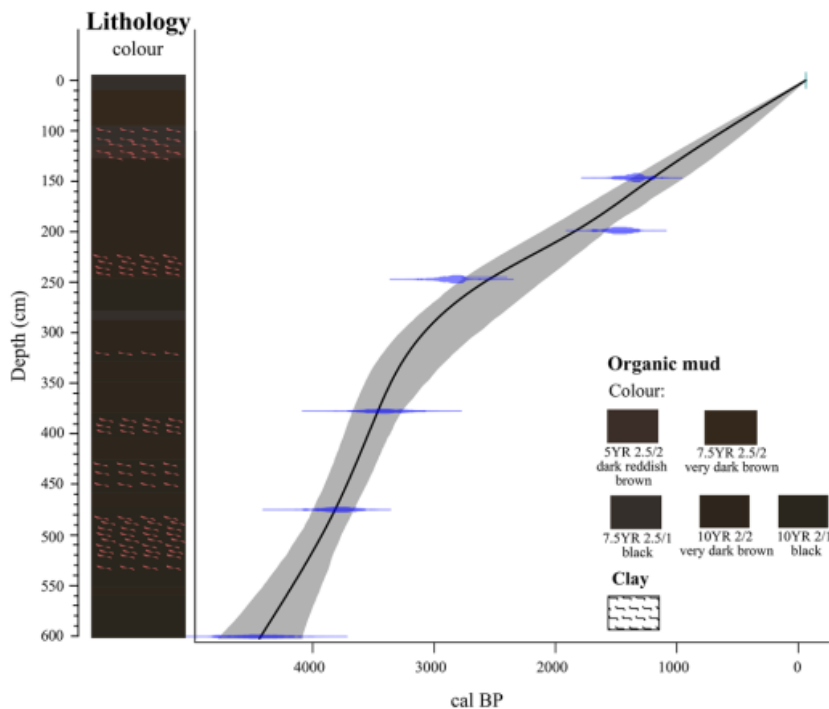


Figure 5.3 Lithological and age-depth profiles of the DB core. The age-depth model is performed using Clam 2.2 (Blaauw 2010) script in R (R Core Team 2015) using the Southern Hemisphere SHCal13.14C calibration curve (Hogg et al. 2013). A smooth spline is the best fitted model

Palynological results

In total, 64 pollen taxa and 20 different spore taxa are identified in the 39 sediment subsamples (eight rare pollen taxa and two spore taxa remain unknown). Pollen and spore grains are well preserved (average 240,000 grain/cm³; the following numbers are in average). The bottom part (567–320 cm; 4300–3200 cal yr BP) records high pollen concentration (320,000 grain/cm³). The pollen concentration

values then strongly decreased (320–242 cm; 3200–2500 cal yr BP; 100,000 grains/cm³). Subsequently, the pollen concentration shows a slightly increasing trend until the top of the sediment core (242–0 cm; 2500 cal yr BP-present; 160,000 grain/cm³). The spore concentrations show a similar trend to the pollen concentration except in the upper part of the core. The initial spore concentration was high (567–320 cm; 4300–3200 cal yr BP; 62,000 spore/cm³), then markedly decreased to 37,000 spore/cm³ (320–242 cm; 3200–2500 cal yr BP). The spore concentration then strongly increased again (242–138 cm; 62,000 spore/cm³), before it finally decreased upto the top of the sediment (138–0 cm; 1100 cal yr BP-present; 18,000 grain/cm³).

The pollen diagram illustrates percentages of the dominant and most important pollen and fern spore taxa, which are grouped based on their ecology and habitat occurrences in the KSNP (Figure 5.4a and Supplementary materials): swamp forest vegetation (SWF), open vegetation and anthropogenic disturbance vegetation (AOF), submontane rainforest vegetation (SMF) and ferns. The DB record is divided into three zones according to the main changes in palynological composition based on the PCA (Figure 5.4a, b, all percentages are averages):

Zone DB-1 (567–320 cm; 4300–3200 cal yr BP). In this zone, the SMF pollen dominates (66%), primarily through Moraceae/Urticaceae (19%) followed by Melastomataceae (11%), *Ficus* (6%); *Glochidion* (7%) and *Lithocarpus/Castanopsis* (5%). The SWF is high (25%), particularly with Myrtaceae which dominates the group (22%). AOF are already present at the beginning of the record in this zone, despite having low values (8%) and are dominated by small Poaceae (6%), but large Poaceae are also found (< 1%).

Zone DB-2 (320–203 cm; 3200–1900 cal yr BP). This zone is further divided into two subzones according to the changes in vegetation composition: DB-2a (320–268 cm; 3200–2800 cal yr BP) and DB-2b (268–203 cm; 2800–1900 cal yr BP). In subzone DB-2a, the total SMF pollen markedly increased (78%). The SWF pollen of Myrtaceae abruptly decreased (8%), mirrored by the increase of AOF pollen (11%) especially small Poaceae (5%), Asteraceae and *Vernonia* (from < 1% in DB-1 to 2% for both taxa). In sub-zone DB-2b, the total SMF pollen decreased (70%) with a sharp rise of Rutaceae cf. *Melicope* (from 3% in DB-2a to 17%). SWF pollen continues to decrease (5%), especially Myrtaceae (3%). On the other hand, the AOF pollen significantly increased (25%), especially small Poaceae (18%), Asteraceae slightly increased (1.4%) and large Poaceae increase notably here (from < 1% in DB-1 to 5%).

Zone DB-3 (203–0 cm; 1900 cal yr BP to present). In this zone, total pollen SMF increased (87%) with Moraceae/Urticaceae (26%), Melastomataceae (26%) and *Lithocarpus/Castanopsis* (8%). The SWF pollen remains low (5%), whilst the AOF decreased (7%) notably with small Poaceae (4%), Asteraceae (1%) and large Poaceae (< 1%).

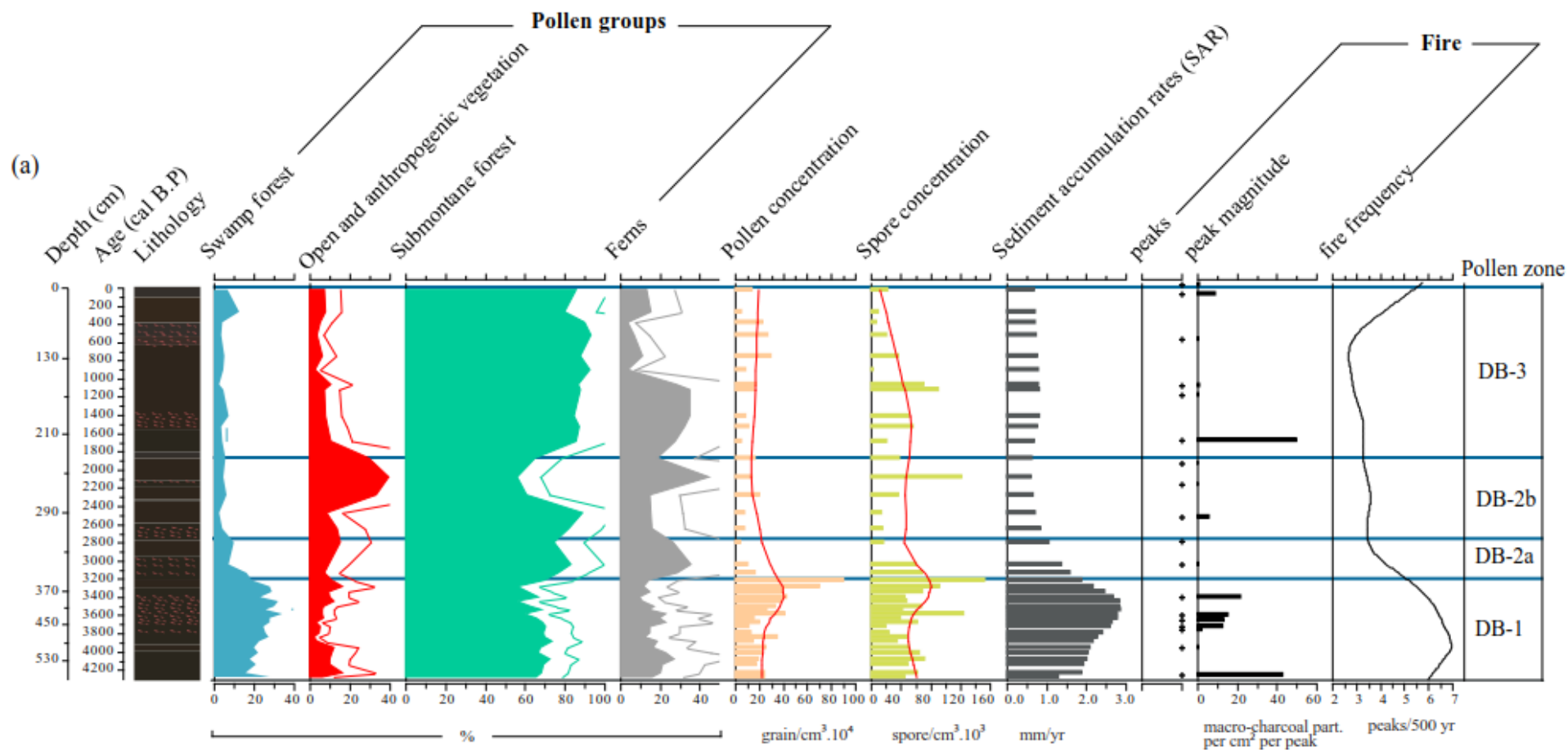
Non-pollen palynomorphs (NPP) results

In total, 16 NPP taxa were identified in the 39 sediment subsamples (six types remain unknown). The NPPs are grouped based on their ecological and habitat occurrences as coprophilous fungal spore (CF), aquatic and fresh water fungal spores (AWF), decaying wood fungal spores (DWF) and others (OF). “Others” corresponds to NPP taxa that cannot be included in the specified group above. The NPP diagram illustrates percentages of the dominant and most important taxa. The NPPs zonation follows the pollen zonation (Figure 5.5, all percentages are averages):

Zone NPP-1 (567–320 cm; 4300–3200 cal yr BP). CF spores are present with relatively high values (16%) primarily with *Cercophora* (8%), and *Sordaria* (7%). The DWF spores are dominant with high values (67%), with Xylariaceae (42%), *Byssothecium* (19.5%) and *Ustulina deusta* (5%). The AWF spores are present in low values (2%), while OF spores are markedly present at 16%, especially Type Hdv-1010 (13%).

Zone NPP-2 (320–203 cm; 3200–1900 cal yr BP). This zone is divided into two subzones: NPP-2a (320–268 cm; 3200–2800 cal yr BP) and NPP-2b (268–203 cm; 2800–1900 cal yr BP). In subzone NPP-2a, the CF spores decreased slightly (14%), especially *Sordaria*, which disappeared in this zone, but with a notable marked increase of *Cercophora* (9%) and *Trichodelitchia* (from < 1% in NPP-1 to 4%). The DWF spores increased slightly (70%) with *Byssothecium* (10%) and *Ustulina deusta* (26%), while Xylariaceae markedly decreased (34%). The AWF spores slightly increased (2.5%). The OF spores decreased (14%), especially Type Hdv-1010 (10%). In subzone NPP-2b, the CF spores slightly increased (15%) with *Sordaria* present again (4%). The DWF spores decreased slightly (35%) especially *Ustulina deusta* (8%) with an increase of *Byssothecium* (25%). The AWF and OF spores also decreased slightly again (2% and 9%).

Zone NPP-3 (203–0 cm; 1900 cal BP to present). In this zone, CF spores increased (18%). The DWF spores abruptly decreased (49%), primarily Xylariaceae (20%) and *Byssothecium* (18%), with a notable slight increase of *Ustulina deusta* (12%). The AWF spores increased slightly (1.6%), while the OF spores increased markedly (31%).



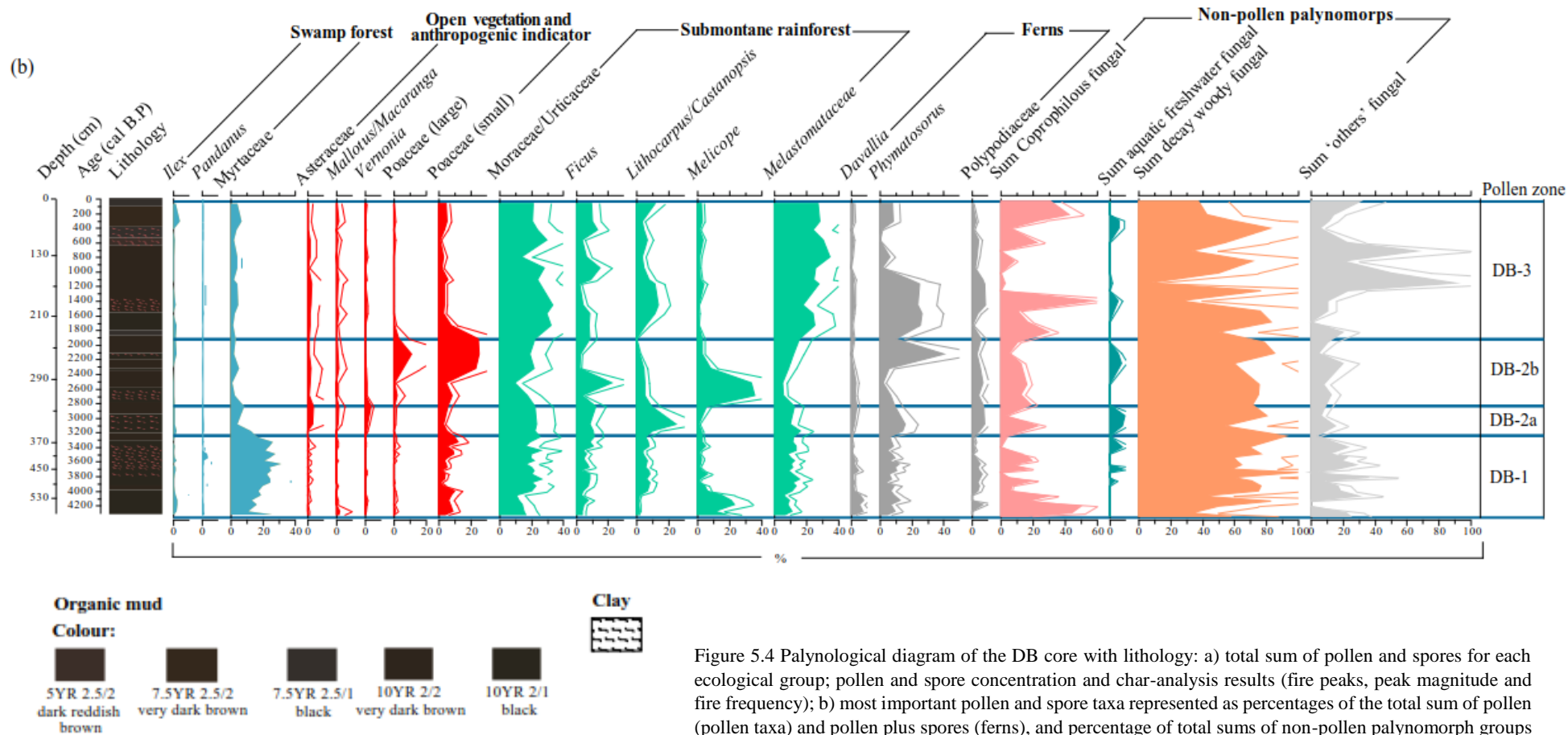


Figure 5.4 Palynological diagram of the DB core with lithology: a) total sum of pollen and spores for each ecological group; pollen and spore concentration and char-analysis results (fire peaks, peak magnitude and fire frequency); b) most important pollen and spore taxa represented as percentages of the total sum of pollen (pollen taxa) and pollen plus spores (ferns), and percentage of total sums of non-pollen palynomorph groups

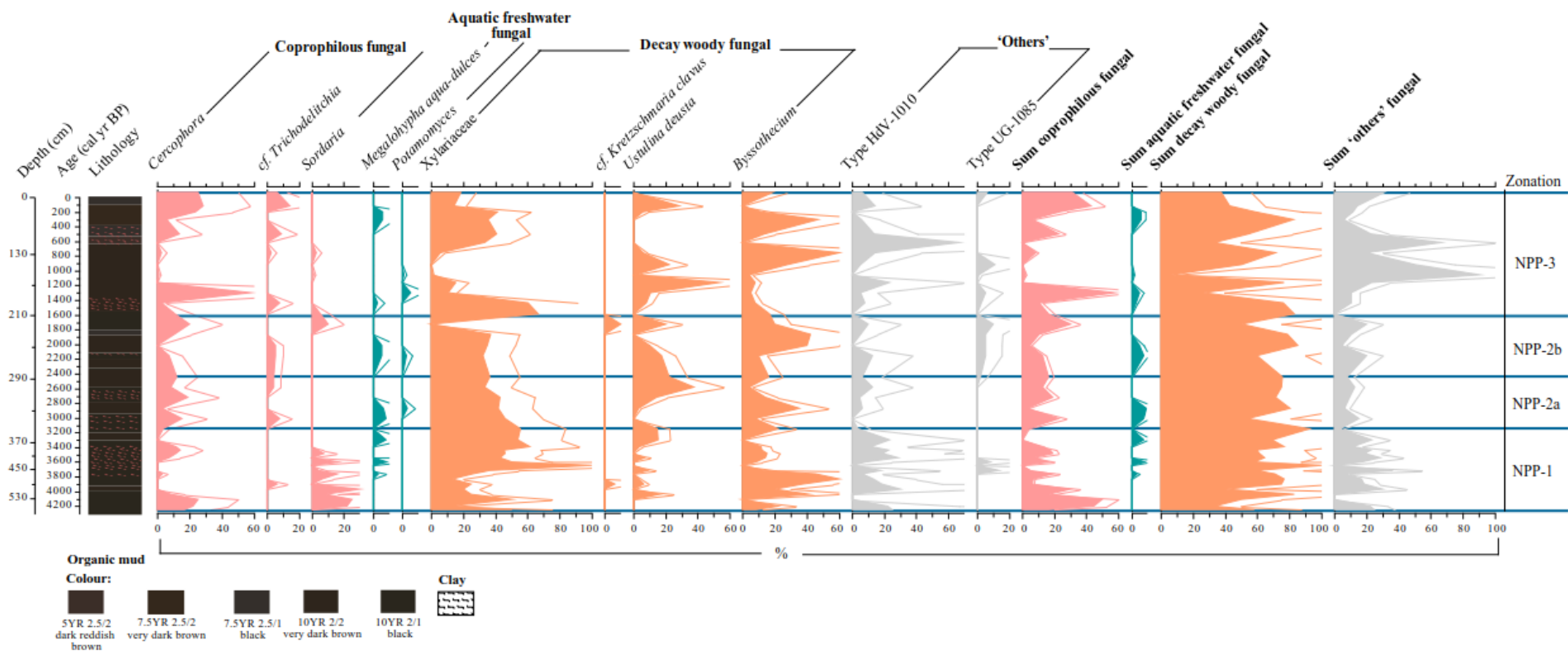


Figure 5.5 Non-pollen palynomorphs (NPPs) diagram of the DB-core with lithology represent the most important NPPs taxa and total sum of NPPs for each ecological group

Macro-charcoal and fire regime

Macro-charcoal analysis resulted in a very low charcoal count along the DB sediment core (minimum count = 0 and maximum count = 28). The macro-charcoal concentration registered low values along the whole sediment core (minimum concentration 1 particle/cm³ and maximum concentration 10 particles/cm³). Using the CharAnalysis software (Higuera 2009), the raw charcoal data are interpolated into a 21-year median temporal resolution, and the peak signals of fire episodes are modelled while removing the background noise. A total of 20 fire peaks are detected along the core.

The local signal-to-noise index (SNI) values for the DN macro-charcoal data fluctuate above 3, indicating a good signal of fire episodes from individual peaks (Kelly et al. 2011). The mean fire return interval (FRI) is 233 with mean frequency of fire of 2 peaks/1000 years (max 5 peaks/1000). Zone DB-1 has the highest number of fire peaks along the record (ca. 7 peaks/1000) with highest magnitude of 44 particles/peak at 4300 cal yr BP. Zone DB-2 records six fire episodes with only two visible detected magnitudes. However, the highest peak magnitude along the record is found within this zone (50 particles/peak, ca. 1700 cal yr BP), while zone DB-3 detected the lowest fire frequency (ca. 5 peaks/1000; Figure 5.4a).

Principal Component Analysis (PCA)

The result from the PCA indicates that 41% of the total pollen and spore variance is explained by the first (24%) and second (17%) axes (Figure 5.6a, b). Pseudo-canonical correlation for the supplementary environmental variables (NPPs) shows high correlations with the first (0.75) and second (0.26) axes, respectively. The PCA explains better the separation between the taxa grouping. This separation was used to define the pollen zonation (Figure 5.6a). The first axis where most of the variance is explained separates the closed swamp forest initial phase (score positive, zone DB-1) from the submontane forest phase (score negative, zone DB-3). A transitional phase is located in-between these two phases (Zone DB-2a). The second axis better explained the separation between these three phases and the open anthropogenic phase which scored positive (zone DB-2b).

While NPP taxa percentage values are used as external explanatory variables they show no clear significant correlation with the palynological phases (Figure 5.6b). The NPP taxa are present in all zonations with no significant grouping. Only the coprophilous fungal spore *Sordaria* is correlated with the swamp forest vegetation of zone DB-1.

Discussion

The Kerinci valley is a tectonic valley surrounded by the Barisan Range and dominated by Mt. Kerinci (3805 m) in the north. The valley is fertile from the volcanic soils and its low lying areas are dominated by grassland, wet-rice cultivation and cinnamon gardens (Aumeeruddy and Sansonnens 1994). The slopes of the valley fall in the protected area of the KSNP and are covered by primary montane rainforest

and agroforestry of Cinnamon cultivation and tea plantation (Laumonier 1997). Embedded in the valley is the unique swamp of Danau Bento (DB). DB is characteristically covered by forest and open grassland. A small patch of swampy area is located in front of the grassland and our results show it is a good location for detecting changes in vegetation linked to anthropogenic activities.

The palynological results from the DB records show 3 distinct vegetation phases which are highlighted in the PCA results (Figure 5.6a) and discussed in detail below:

Phase 1: the swamp forest (4300-3200 cal yr BP)

At the beginning of our record from ca. 4300 years ago, pollen analysis reveals a much more forested swamp than at present. Pollen results indicate that the swamp forest was dominated by Myrtaceae, *Pandanus* and *Ilex*. Surrounding the swamp on the nearby mountain slopes, submontane forest was abundant as it is today with taxa like Fagaceae (*Lithocarpus/Castanopsis*) and Moraceae/Urticaceae (Figure 5.4b). The presence of a larger swamp forest indicates a more natural ecosystem present at the site ca. 4300 years ago compared to today. Additionally, the pollen results confirm that one of the most prominent features of the swamp forest in Sumatra is the dominance of Myrtaceae like *Eugenia* (e.g. Maloney 1980, 1996; Maloney and McCormack 1996). The presence of small Poaceae pollen (6%) shows that grassland has existed around the site since the beginning of the record ca. 4300 years ago.

The stratigraphy of Danau Bento shows that the entire swamp is originally formed on a thick deposit of diatomite or diatom gyttja, which can be found in open water (Hummel 1931). Above this water layer, either swamp forest or swamp grasslands can be formed (Flenley 2013). It is therefore unclear if the grassland is a natural or anthropogenic occurrence at the site. However, while the grassland might be natural in the swamp, the presence of coprophilous fungi hints at grassland cultivation for grazing of livestock like buffaloes. In particular, among the recorded fungal spores were representatives of the Sordariaceae (*Sordaria*) and *Cercophora*. Most of the Sordariaceae are coprophilous and often so specialized that they only grow on the dung of a single or a few species of animals (van Geel 1992). Several studies show that their presence is common at archaeological sites that supported domestic cattle (Graf and Chmura 2006; van Geel and Aptroot 2006). The PCA result (Figure 5.6b) confirms that *Sordaria* is the only coprophilous fungal spore that is positively correlated (first and second axes) with the swamp forest (zone DB-1). *Sordaria* was the major component of change in the swamp in the beginning of this zone (4300–4200 cal yr BP). Additional evidence of herbivory is the presence of *Cercophora*, which is also an indicator for dung (van Geel 2001; van Geel et al. 2003).

In the KSNP, large herbivores such as Sumatran elephant *Elephas maximus sumatranus* and Sumatran rhinoceros *Dicerorhinus sumatrensis* can be found (UNESCO 2014). Besides the mountainous area, the Sumatran elephant is also commonly found in the lowland rainforest and in open lands (Sitompul et al. 2013). However, these species are mainly mixed feeders, not grazers. Therefore, rain forests are their primary habitat not grasslands (Cristoffer and Peres 2003). On the other hand buffaloes are grazers with grassland as their main habitat.

As the presence of coprophilous fungal spores is persistent through the DB record, we can infer that the signal most likely comes from constant grassland feeders in large numbers. The most likely candidate for this are therefore buffaloes. The swamp buffalo type *B. bubalis carabensis* was already domesticated about 5000–4000 years ago (Cockrill 1981) in the region between China and Indochina (Zhang et al. 2011, 2016; Wang et al. 2017), probably associated with the development of rice cultivation 8000 years ago (Bellwood 2008). Cockrill (1981) reported a later period of swamp buffalo domestication about 5000–4000 years ago. It is suggested that with the spread of agriculture, the swamp buffalo then spread to mainland SE Asia through peninsular Malaysia to Sumatra and Java (Zhang et al. 2011) since ca. 4000–3000 years ago (Lei et al. 2007). Our evidence derived from the NPP results seems to confirm that the swamp buffalo was already in the Kerinci valley by at least 4300 years ago, even though the specifically coprophilous fungus *Sporormiella*, common fungal spores on the dung of living domestic herbivores (Davis 1987; Burney et al. 2003; Robinson et al. 2005; Davis and Shafer 2006), was not found in our record. We found however no evidence of rice cultivation in this phase. The lack of large Poaceae and the presence of a much more forested swamp in this early phase might suggest that rice cultivation was carried out far from the swamp. On the other hand, the swamp area might have been used for the grazing of buffaloes, which were used for ploughing wetland agriculture elsewhere in the valley, similarly to what is done today in the area.

Several fires of large magnitude detected in this phase might be associated with grassland cultivation which involved slash and burn activity by humans and ploughing the sod using cattle (Brookfield et al. 1995). For instance, in the Toba area the Batak used the grassland to stall feed the cattle and buffalo, the latter being used to plough nearby wet-rice fields (Sherman 1980). This finding seems to match with our interpretation that the existence of grassland since 4300 years ago might be related to humans and that the area was used as a grazing field for the buffaloes.

This phase and our findings correspond to the inferred migration of Austronesians from Taiwan, which is estimated to have occurred about 4000 years ago (Bellwood 2007, 2008). It is believed that this group of farmers cultivated rice and other crops, and brought material innovations such as pottery and new lithic industries with them (Bellwood 2007). These early farming communities marked the emergence of the Neolithic period, which is a pivotal event in the history of human occupation in Indonesia (Simanjutak 2017). Palynological studies near Kerinci–Sikijang swamp (Flenley and Butler 2001) and Danau Padang (Morley 1982) show forest disturbance from about 7000 years ago, with firmer evidence of forest clearance by man starting later from about 4000 years ago based on the extent of pioneer trees like *Trema* and *Macaranga* (Morley 1982). This suggests that humans already inhabited Kerinci and were clearing the forest about 4000 years ago. However, evidence of permanent clearing, which can better attest to the start of a permanent agroecosystem, started only about 2000 cal yr BP with the increase of Poaceae in association with other cultivation crops such as *Arenga* (Morley 1982). In Sumatra, a Neolithic cord-marked pottery shred was recovered in a site adjacent to Danau Bento, and was dated by thermoluminescence to between 4460 and 3700 yr BP (Flenley 1985). However, the centre

of Neolithic settlement was located further away in the southern part of the valley in Bukit Arat, the first prehistoric open air site in the highland of Jambi and the centre of early obsidian tool production (Bonatz 2012).

Phase 2: the intensification of human activities and rice cultivation (3200-1900 cal yr BP)

A decrease of the swamp forest started from ca. 3200 cal yr BP. This decrease corresponds to an increase of anthropogenic indicators including Asteraceae and *Macaranga/Mallotus* (Figure 5.4b). Small Poaceae began to increase notably around 3000 cal yr BP and reached the highest value of the record at ca. 2100 cal yr BP. Our NPP results show a significant increase of *Byssothecium*, a common fungal spore in (submerged) wood (Crane et al. 1992) between 2500 and 2100 cal yr BP when we have the peak of small Poaceae. While decayed wood is a common component in swamp forest, the signal of opening of the forest coupled with the increase of the NPP woody decay indicator is compelling evidence for the deforestation of the swamp forest and grassland expansion which marks the first intensification of human activity in the swamp. Coprophilous fungal spores decreased in this phase, especially *Sordaria*, which was abundant in the previous zone but abruptly decreased and almost disappeared within this phase.

In the same phase from ca. 2500 cal yr BP, large Poaceae also notably increased and reached their peak (11%). This change can be interpreted as first evidence of occurrence at the DB site of rice cultivation. Interestingly, our results match with the other record in the Toba area in the north Highland of Sumatra based on the increase of grass pollen (Poaceae) in the size range of rice, microfossil charcoal, and phytoliths. That study showed that rice was introduced as both a dry-land crop (= ladang) on the crater slopes and a wet-land crop (= sawah) around 2700 cal yr BP (Maloney 1996).

This period corresponds in Sumatra to the Bronze-Iron Age, marked by archaeological evidence of elaborate pots and the first metal, iron, glass beads and imported ceramics (Harrison 1958). Archaeological evidence of bronze kettle drums near Lake Kerinci and other bronze vessels found in the Kerinci area dated to about 3000 years ago (van Heekeren 2013). Currently nothing is known about the culture of the people in the Bronze-Iron Age in Sumatra nor their interaction with the environment, except that they were cultivators (Whitten et al. 2000). Our results show that during this period rice cultivation intensified becoming common even in swamps like Danau Bento from about 2500 years ago. However, the pollen results show that the peak period lasted only few centuries between 2500 and 2100 cal yr BP. After that the large Poaceae abruptly declined and remained low. This might suggest that rice cultivation in DB was not permanent but part of a shifting practice as found in other Sumatran sites such as in Danau Padang (Morley 1982) and the Toba Plateau sites (Maloney 1996). Bellwood (2007) also hypothesized that most cultivation systems in the area of Austronesian migration, including Sumatra, by 3000 years ago were characterized by shifting and localized swamp cultivation, which subsequently transitioned to wet-rice cultivation in bounded fields (sawah). It is also possible that the swamp area of Bento turned out not to be productive or convenient for rice cultivation compared to other areas in the Kerinci valley and that the cultivation was simply moved somewhere else. Support

for this hypothesis is the continuous abundant presence of small Poaceae after 2100 until 1900 cal yr BP which might indicate that the grassland was found more suitable for grazing activity instead of crop cultivation.

Phase 3: Decline of human activities (1900 cal yr BP to present)

After 1900 cal yr BP the small Poaceae started to decrease but remained stable afterward and coprophilous fungi were also continuously found in the record. As spores of coprophilous fungi and Sordariaceae in particular provide a valuable source of information about past herbivore densities (Eklom and Gillson 2010), our result can be evidence that buffaloes were continuously grazing the grassland (as they do today). This can be confirmed by other recorded coprophilous fungal spores like *Cercophora* and a significant increase of *Trichodelitschia* fungal spores, an indicator for dung (van Geel 2001; van Geel et al. 2003). This suggests that the swamp was not used for rice cultivation, but was used for buffalo grazing since 1900 cal yr BP.

Interestingly, the swamp forest never recovered to the values before disturbance, suggesting that humans kept controlling the site, maintaining the grassland as indicated by the Poaceae values. The CharAnalysis results show that only a few fire peaks were detected within this period with very low magnitude, suggesting that fire probably was a random event and was not used to maintain the grassland. As we have no evidence of fire use for maintaining the grassland, we could infer that it was maintained by grazing of swamp buffalo.

Pollen results also suggest that submontane forest expanded from the slope of the valley toward the site, although this might simply be an effect of the relative low percentage values of swamp forest taxa and not a real increase in submontane forest.

Conclusions

The palynological record from Danau Bento provides the first evidence of buffalo husbandry in the Kerinci area from 4300 years ago based on the NPP results. Our record shows that grassland has existed around the site since the record started along with a larger area of swamp forest. This condition persisted until about 3200 cal yr BP. As palynological results show no clear evidence for rice cultivation, we can infer that the grassland was used for grazing and rice cultivation was carried out somewhere else in the valley. Our record of buffalo husbandry in Sumatra from 4300 years ago is in agreement with the archaeological and linguistic record of the Austronesian migrants to the island and in line with the dates for rice introduction found in Sulawesi and Borneo (4000 and 5900–5400 cal yr BP, respectively).

A rapid decrease of the swamp forest started from about 3200 years ago and the open vegetation and anthropogenic indicators increased. This period highlights the beginning of the intensification of human activities in the swamp forest which was more extensively opened. The increase in large and small Poaceae at 2500 cal yr BP shows clearer evidence of rice cultivation in the Danau Bento swamp. At the

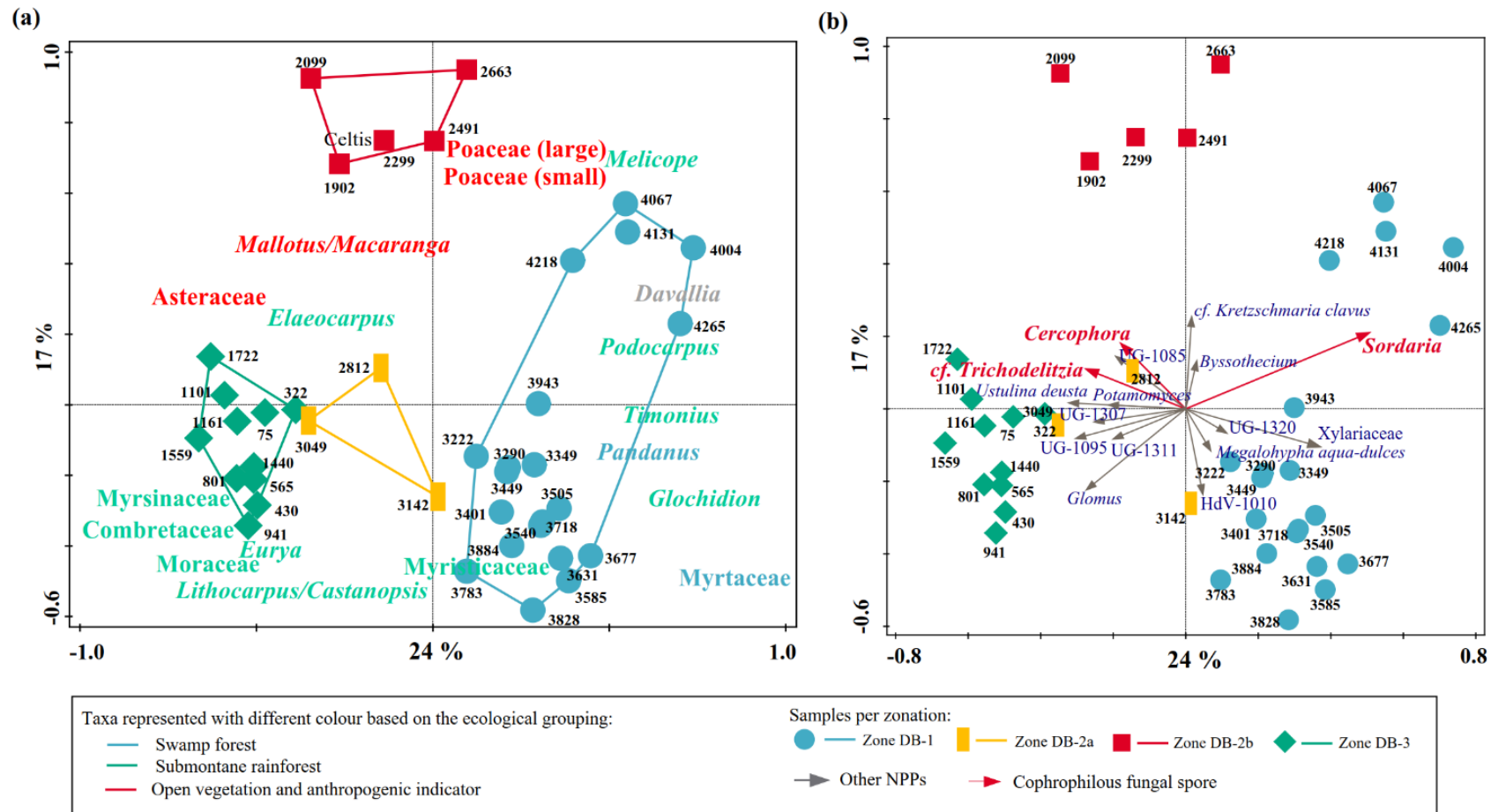


Figure 5.6 Principal Component Analysis (PCA) of all percentage data of identified pollen and spore taxa after square-roots transformation. Environmental supplementary variables used are the percentage of non-pollen palynomorphs taxa. First two axes shown are 24% and 17% of the variation in composition. Numbers are estimated age of each sample (cal yr BP): (a) Samples scatterplots represented pollen zonation and taxa selection on the ordination. Pollen and spore taxa are shown in different colour according to their ecological group as Figure 5.4; (b) Samples score with explanatory variables represented by the NPPs value. Cophrophilous fungal spores are shown in red arrow

same time NPPs show a reduction of grazing activities suggesting a change in the use of the swamp. Our results on intensification of rice cultivation in the swamp at ca. 2500 cal yr BP match the cultivation date found on the Toba Plateau (ca. 2600 cal yr BP). Both of these findings might suggest an increase in population and/or change in technology corresponding to the Bronze Age period in Sumatra. However, our records show that this phase lasted only a few centuries until ca. 2100 cal yr BP. It is not clear if this is due to shifting agricultural practices, or to the swamp turning out to not be very productive for rice.

Following the decline of rice cultivation in Danau Bento, the swamp remained in use as a grassland for buffaloes as shown by the low values of swamp forest pollen and high values of NPP dung indicators. The lack of evidence for systematic use of fire suggests that the grassland was maintained through grazing and without the use of fire. The record shows that since 1900 cal yr BP the human population in Kerinci maintained the swamp open with only a little patch of the swamp forest that dominated the site in the distant past.

Our results are the first evidence of rice cultivation in the Kerinci valley, however more research is still needed using paleo-multiproxy approaches to better elucidate the migration and development of rice cultivation technology in Indonesia.

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Supplementary materials

Table 5.3. List of pollen and spores with different ecological groups for submontane forest vegetation in Sumatra, Indonesia.

| Plant Family | Plant taxon |
|--|--|
| <i>Swamp forest vegetation</i> | |
| Acanthaceae | |
| Anacardiaceae | |
| Aquifoliaceae | <i>Ilex</i> |
| Ericaceae | <i>Vaccinium</i> |
| Myrtaceae | |
| Pandanaceae | <i>Pandanus</i> |
| Potamogetonaceae | <i>Potamogeton</i> |
| Primulaceae | <i>Myrsine</i> |
| Typhaceae | <i>Typha</i> |
| <i>Open and anthropogenic indicator vegetation</i> | |
| Asteraceae | <i>Vernonia</i> |
| Cannabaceae | <i>Trema</i> |
| Cyperaceae | |
| Euphorbiaceae | <i>Mallotus, Macaranga</i> |
| Malvaceae | Sub.fam. Tilioideae |
| Poaceae | |
| <i>Sub-montane rainforest vegetation</i> | |
| Amaranthaceae | |
| Anacardiaceae | |
| Annonaceae | |
| Cannabaceae | <i>Celtis</i> |
| Caprifoliaceae | |
| Casuarinaceae | <i>Casuarina</i> |
| Celastraceae | |
| Combretaceae | |
| Dipterocarpaceae | <i>Shorea</i> |
| Ebenaceae | <i>Diospyros</i> |
| Elaeocarpaceae | <i>Elaeocarpus</i> |
| Euphorbiaceae | <i>Alchornea, Homalanthus</i> |
| Fabaceae | |
| Fagaceae | <i>Castanopsis, Lithocarpus, Quercus</i> |
| Juglandaceae | <i>Engelhardia</i> |
| Loranthaceae | |
| Melastomataceae | |
| Meliaceae | <i>Dysoxylum</i> |
| Moraceae | |
| Myricaceae | <i>Myrica</i> |
| Myristicaceae | |
| Myrsinaceae | |
| Oleaceae | <i>Ligustrum</i> |
| Phyllanthaceae | <i>Antidesma, Glochidion</i> |
| Plantaginaceae | <i>Plantago</i> |
| Podocarpaceae | <i>Dacrydium, Podocarpus</i> |
| Rosaceae | <i>Prunus</i> |
| Rubiaceae | <i>Timonius, Zanthoxylum</i> |
| Rutaceae | <i>Melicope</i> |
| Sapindaceae | <i>Filicium</i> |
| Theaceae | |
| Urticaceae | |

| Plant Family | Plant taxon |
|---------------------|--------------------------------------|
| Winteraceae | <i>Eurya, Drimys</i> |
| <i>Fern</i> | |
| Adiantaceae | <i>cf. Adiantum</i> |
| Blechnaceae | <i>cf. Blechnum</i> |
| Cyatheaceae | <i>Cyathea</i> |
| Davalliaceae | <i>Davallia</i> |
| Dicksoniaceae | <i>Dicksonia</i> |
| Dryopteridaceae | <i>Arachniodes</i> |
| Hypodematiaceae | <i>Leucostegia</i> |
| Lindsaeaceae | <i>Lindsaea</i> |
| Lycopodiaceae | <i>Huperzia, Lycopodiella cernua</i> |
| Marattiaceae | <i>Angiopteris</i> |
| Polypodiaceae | <i>Phymatosorus, Polypodium</i> |
| Pteridaceae | <i>Pteris</i> |
| Schizaeaceae | <i>Lygodium</i> |
| Selaginellaceae | <i>Selaginella</i> |

CHAPTER 6 – paper 3

Response of mangroves to late Holocene sea-level change: palaeoecological evidence from Sumatra, Indonesia

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Keywords

palynology; mangrove; transgression; regression; sea-level rise

Abstract

This study was conducted with aim to reconstruct the late Holocene mangrove history and to investigate if mangroves can be resilient to current and projected sea-level rise (SLR). The palynological record from a sediment core in the Mendahara Ilir region (MI) in Sumatra was compared with available sea level reconstructions from sites close to MI (Malacca Strait and Singapore). The palynological results show that the mangrove swamp forest was already present in MI ca. 2300 years ago. At time, the sea-level was estimated to be ca. 2 m higher than the present level, thus indicating persistence of mangroves in MI for the current global increase scenario of more than 1 m SLR by 2100. However, the estimated rate of change from the MI core are ca. 2.2 mm/yr. These values are much lower than current (5.0 mm/yr) and future (7 mm/yr) estimates. Thus posing a threat on the resilience and the capacity to adapt of the mangrove swamp forest. Additionally, the palynological results indicate that the mangrove swamp forests were quickly moving seaward and landward following regression and transgression phases in MI. Without a clear inland free path, such migration will be impeded under current and future projections of SLR.

Introduction

Mangrove ecosystems are widespread along the coastlines of the vast archipelago of Indonesia, which for two-third is composed of water (Choong et al. 1990). Owing to the availability of enormous coastal habitats with humid tropical climate, Indonesia has the largest mangrove area in the world (nearly 23% of the world's mangrove with ca. 3.2 million hectares; Wilkie and Fortuna 2003; Agency of Survey Coordination and National Mapping Republic of Indonesia 2009). Additionally, mangrove vegetation in Indonesia is one of the most diverse in terms of plant species composition (Spalding et al. 2010; Giri et al. 2011). A total of 202 mangrove plant species are recorded, of those 43 are true mangrove species and the others are associated to mangroves (Kusmana 1993).

Mangroves have an important function for the coastal environments. They provide coastlines protection (Choong et al. 1990; Gedan et al. 2011; Hashim and Catherine 2013), ecological services (e.g Choong et al. 1990; FAO 2007; Alongi 2008; Hutchison et al. 2014; Godoy and Lacerda 2015) and provide socio-economic benefits (FAO 2007; Choong et al. 1990; Ellison and Stoddart 1991). However, despite their ecological and socio-economic functions the present development of mangroves in Indonesia is under threat (Table 6.1). Two main kinds of disturbance are found to be the most important cause of mangrove degradation at present and in the future: sea-level rise and human activities.

One of major concern for mangrove ecosystems is the effect of future sea-level rise (SLR; Krauss et al. 2014) as it is likely that SLR will have tangible effects on the coastal region already in the near future (Duke et al. 2007; Alongi 2015). The mangrove ecosystems existence will be affected due to sediment erosion, increased inundation and salinity stress. Such an effect is aggravated for mangrove stands

whose landward migration is restricted by topography or urban structures (Alongi 2015; Godoy and Lacerda 2015). On the other hand, human activities are responsible for the loss of 40% of mangrove forests in Indonesia in the past three decades alone (FAO 2007; Campbell and Brown 2015). The conversion was caused mainly by the expansion of aquaculture, mangrove wood exploitation and land-use change (Long et al. 2013; Giesen et al. 2007). Aside from the great loss in biodiversity, large-scale mangroves conversion is troublesome because it can lead to coastal erosion, leaving the coastal population centers more susceptible to the effects of storms and flooding (Whitten et al. 2000).

Reconstructions of the mangrove vegetation in the Holocene have shown that mangroves are sensitive to the post-glacial SLR and coast formation in Indonesia and else-where (i.e. Soeriaatmadja 1979; Sukardjo 1979; Sukardjo and Kartawinata 1979; Blasco et al. 1996; Grindrod 1985, 1988; Ellison 1989; Behling and da Costa Behling and da Costa 2001; Behling et al. 2001; Yulianto et al. 2004, 2005; Ellison 2005; Horton et al. 2005; Engelhart et al. 2007; Hait and Behling 2009; Monacci et al. 2009; Li et al. 2012; Punwong et al. 2017). While showing that mangrove pollen and spore assemblage can be used to reconstruct sea-level changes, these studies cannot be used as modern or future analogue for sea-level changes in Indonesia, due to the low temporal resolution and the very different environmental baseline conditions in the early and mid-Holocene (i.e. Sunda shelf exposition and different coastline settings; Hanebuth et al. 2000; Bush and Fairbanks 2003; Sathiamurthy and Voris 2006).

Thus, more long-term studies are needed to improve our understanding of mangrove ecosystem dynamics and its relation with sea-level changes and coastal physical development, particularly in Indonesia. With this study we aim to fill this gap, by providing the first high-resolution palaeoecological record of the last ca. 2300 years from a mangrove ecosystem in Sumatra, Indonesia. Pollen and spores are used as proxies for mangrove dynamics. The results are compared to local past sea-level change data available for the region in order to understand if the mangroves in Sumatra, Indonesia, can be resilient to current and future scenarios of change.

Study area

Mangrove ecosystems in Indonesia are similar to those found throughout South East (SE) Asia and Oceania (Choong et al. 1990). A total of 268 plant species have been listed in SE Asian mangrove with 52 of them are true mangrove species. They are dominated by the family of Leguminosae (Fabaceae), Cyperaceae and Rhizophoraceae (Giesen et al. 2007). In Indonesia, mangroves represent the geographical center for several mangrove genera e.g. *Rhizophora*, *Bruguiera*, *Sonneratia*, *Avicennia*, *Ceriops*, *Lumnitzera* (Chapman 1976).

This study is located in the east coast of Sumatra island, where 600,000 ha of mangroves can be found (Ilman et al. 2016; Figure 6.1a). Mangroves in Sumatra have a low floristic diversity, consist only 17

Table 6.1. Various threats and their predicted impact on mangrove ecosystem in Sumatra from anthropogenic and climate change factors

| Mangrove threats | Possible impacts | Reference |
|--|--|---|
| Human activities | | |
| Timber extraction, agriculture (conversion to plantation, aquaculture, re-settlement/urban development and diversion of freshwater for irrigation) | Higher or lower sedimentation, dissolved oxygen reduced, imbalance in nutrient ratio and water turbidity due to increased eutrophication in the water body. Loss of biodiversity | Diaz and Rosenberg 2008; Alongi 2002; Victor et al. 2006; Thampanya et al. 2006; Wolanski 2007 |
| Climatic factors | | |
| Sea-level rise | Lead to inundation, excess flooding, erosion of the sediments, and inhibition of different nutrient cycling and gaseous exchange | Ellison 2015; McLeod and Salm 2006 |
| Temperature rise | Limiting photosynthesis resulting in species diversity and composition change. Changes in biochemical processes in plants and soils | Ellison 2015; Lovelock and Ellison 2007 |
| Increase atmospheric CO ₂ | Affecting plant growth and development and influences respiration. Increase productivity and more efficient water use in relation with carbon fixation in photosynthesis. Mitigate the negative effects of reduced rainfall and humidity, alter species dominance | Ellison 2015; Drake et al. 1999; Donato et al. 2011 |
| Precipitation changes | Affecting species diversity, height and biomass, and mangrove margins. Reduced rainfall causes decrease in mangrove diversity, photosynthesis activity and growth rates along with substrate subsidence. Increased rainfall will lead to increased sedimentation rates which can result in increase of mangrove productivity and diversity | Duke et al. 1998; Kumara et al. 2010; Smith and Duke 1987; Rogers et al. 2005; Whelan et al. 2005 |
| Storms and high energy wave | Storm could cause defoliation, uprooting and reduced forest cover. Storm impacts can deposit marine sediments into mangrove seaward margins to either cause mortality or build shore parallel sand ridges or chenier ridges. Wave action has increasing impact with higher water levels such as surges, resulting in sedimentation, erosion and forest coverage changes | Lovelock and Ellison 2007; Cahoon 2006 |

Table is modified and integrated from Parida et al. 2014

tree species which belongs to four families (Rhizophoraceae, Sonneratiaceae, Avicenniaceae, Meliaceae; Whitten et al. 2000). The sediment core was retrieved from a mangrove swamp forest in Mendahara Ilir (MI) region in the Jambi Province in Sumatra (0°57'14.6"S 103°40'45.0"E; 3 m a.s.l; Figure 6.1). The MI site comprises the catchment of Sungai Mendahara (Mendahara River) and an extensive tidal flat area which is located in front of the mangroves belt. The Mendahara River channel is ca. 800 m wide and 6 m deep at its mouth (Sanderson and Taylor 2003). The vegetation in the MI area can be described as riverine/fringe mangrove. The coast consists of a narrow band of *Avicennia marina* and the mangroves are dominated by *Rhizophora apiculata* sometimes combined with *Sonneratia alba*. Further inland, the communities are still dominated by *Rhizophora* mixed with *Bruguiera* species (Taylor and Ali 2001).

In the Jambi Province about 4000 ha of land are covered with mangrove vegetation (Laporan Status Lingkungan Hidup Daerah Provinsi Jambi 2014). Similarly, to other parts of the Province, the mangrove forest of MI and the catchment of the Mendahara River are in critical conditions, as they were heavily damaged due to continuous abrasion and encroachment by human activities (Taylor and Ali 2001). Of the total potential mangrove area in Mendahara, only 30% is currently covered with mangrove forests (Dinas Kelautan dan Perikanan Kabupaten Tanjung Jabung Timur 2010). Most of the forest has been converted into mixed dryland agriculture and aquaculture (fish pond). A relatively old settlement is located in the lower part of the river where the inhabitants practice agriculture (i.e. rice and coconut) in a smallholding scale. Recently a new road and new settlement were established close to the old settlement.

The climate in Central Sumatra is tropical humid as it is located within the Intertropical Convergence Zone (ITCZ). The mean annual rainfall for the MI region is about 2400 mm and annual temperatures average 27°C (Karger et al. 2017; <http://chelsa-climate.org>). Rainfall seasonality is associated with wet northwest Asian monsoon, marking a long rainy season of 7 to 9 consecutive months with peaks from December to February (DJF). This is alternated with a shorter drier periods of dry southeast Australian monsoon lasting three or less months from June to August (JJA; Whitten et al. 2000). The inter-annual rainfall variability is controlled by the phase changes of El Niño-Southern Oscillation (ENSO) and the Indian Ocean Dipole (IOD; Saji et al. 1999; Webster et al. 1999; Abram et al. 2007).

Tidal range is one of the most important physical factors for the growth and the formation of zonation in the mangrove ecosystem (Whitten et al. 2000; Lovelock et al. 2015). Tidal amplitude in the shallow seas around Sumatra it is commonly up to 3 m high (Whitten et al. 2000). In particular, the tide in the MI area are microtidal to mesotidal, with a neap tide range of 1.4 m and a spring tide range of 3.4 m (Sanderson and Taylor 2003). Tides are mixed mainly semi-diurnal where two high waters and two low waters with different amplitudes occur daily (Whitten et al. 2000).

Regional past sea-level change and future projection

The sea-level has changed at varying rates, rising and falling hundreds of meters throughout the geological time period (Chappell and Shackleton 1986; Fairbanks 1989). At the last glacial maximum (LGM) ca. 20,000 years ago, global mean sea-level was ca. 130 m below present level (Lambeck et al. 2002) caused by ice caps expansion in the northern hemisphere (e.g. Lambeck et al. 2002; Rohling et al. 2009). In SE Asia Sea, sea-level was ca. 116 m lower at the terminal phase of LGM (Geyh et al. 1979; Hanebuth et al. 2000). Afterward, in the early Holocene sea-level began to rise and experienced an upward trend from a minimum of -22 m (Horton et al. 2005). The mid-Holocene period in SE Asia was characterized by a high stand which is estimated at interval between 3 and 5 m between 6000 and 4000 years ago (Geyh et al. 1979; Scoffin and Le Tissier 1998; Kamaludin 2001; Horton et al. 2005; Tjia 2013). Afterward, in the late Holocene sea-level decreased close to its present level (Nunn 1998) or below present level (Horton et al. 2005).

Over the twentieth century, global sea-level has been increasing due to ocean warming and land ice melting (Church and White 2011). The latest prediction suggest that 95% of the coastal areas worldwide will be affected by SLR, with rates projected between 26 mm and 98 mm by 2100 (IPCC 2013). The best scenarios suggest an average SLR of 40 cm (26–55 cm), whilst the worst scenarios anticipate an average of 63 cm (45–82 cm) by 2081–2100 (Godoy and Lacerda 2015). While, the current global mean SLR for the last 20 years is 3.23 ± 0.4 mm/yr (Godoy and Lacerda 2015), it is estimated that SE Asia and the Western Pacific region will experience SLR of 5–20 mm/yr (Nicholls and Cazenave 2010). In Indonesia, the mean sea-level increased by 1–8 mm/yr as reported by the State Ministry of Environment (SME; 2007) for the entire twentieth century (Asian Development Bank 2009) and it is projected that some parts of Indonesia will experience SLR rate as high as 7.7 mm/yr by 2100 (Nerem et al. 2010). According to BAPPENAS (Indonesian National Development Planning Agency; 2009) the estimated average rate of SLR in Indonesia is around 7 mm/yr and the SLR projection by 2100 will be 80 cm. This projection is slightly lower than the 1 m future global SLR predicted by the IPCC (2013).

Materials and methods

A 500 cm-long sediment core (MI) was recovered from a secondary mangrove forest in the Mendahara Ilir region, Jambi Province in 2014 using a Russian peat corer (Jowsey 1966). The core lithology was described using sediment and attributes including colour, texture and plant part composition. Eleven samples consisting of charcoal, plant materials and organic bulk sediment were sent to the NTUAMS Laboratory in Taiwan and Poznan radiocarbon laboratory in Poland for Accelerator Mass Spectrometry (AMS) radiocarbon dating (Table 6.2). All organic bulk sediments were sieved with a 100 μ m mesh to eliminate fine roots which are a strong source of contamination in mangrove sediments dating.

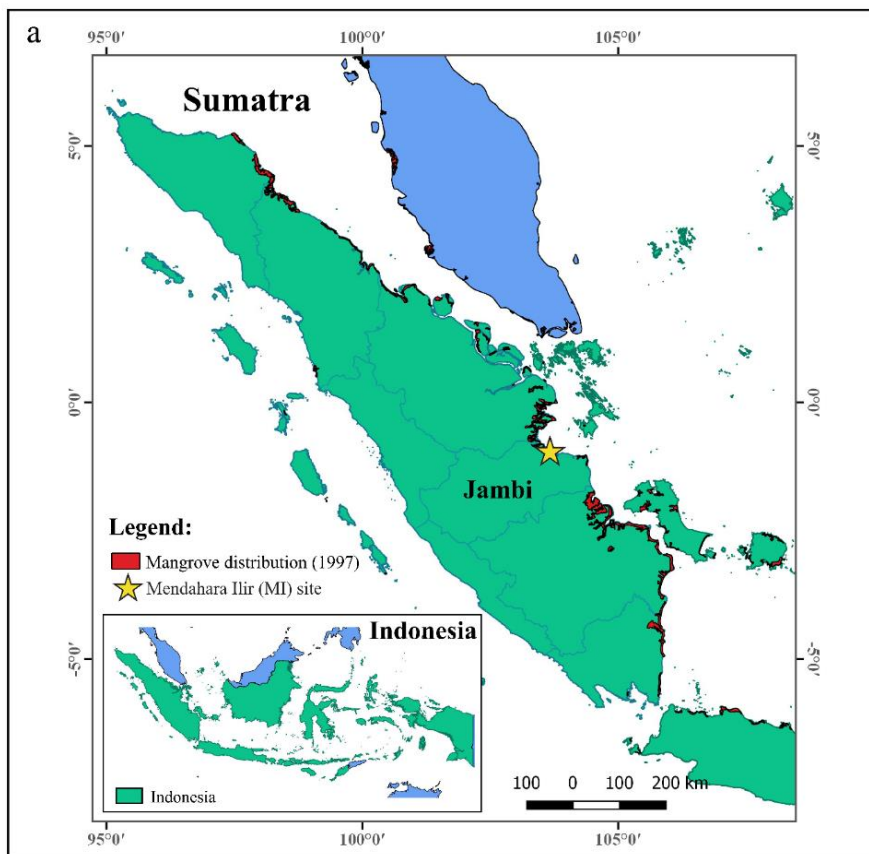


Figure 6.1 Maps of the study area: (a) the location of the studied region, the Mendahara Ilir region in Jambi Province, Sumatra (Indonesia). Red line shows the mangrove distribution along the Sumatran coastline (Spalding et al. 2010); and (b) the study site in Mendahara Ilir (MI), marked with a yellow star. The land-use data are from 2013 (Melati et al. 2015)

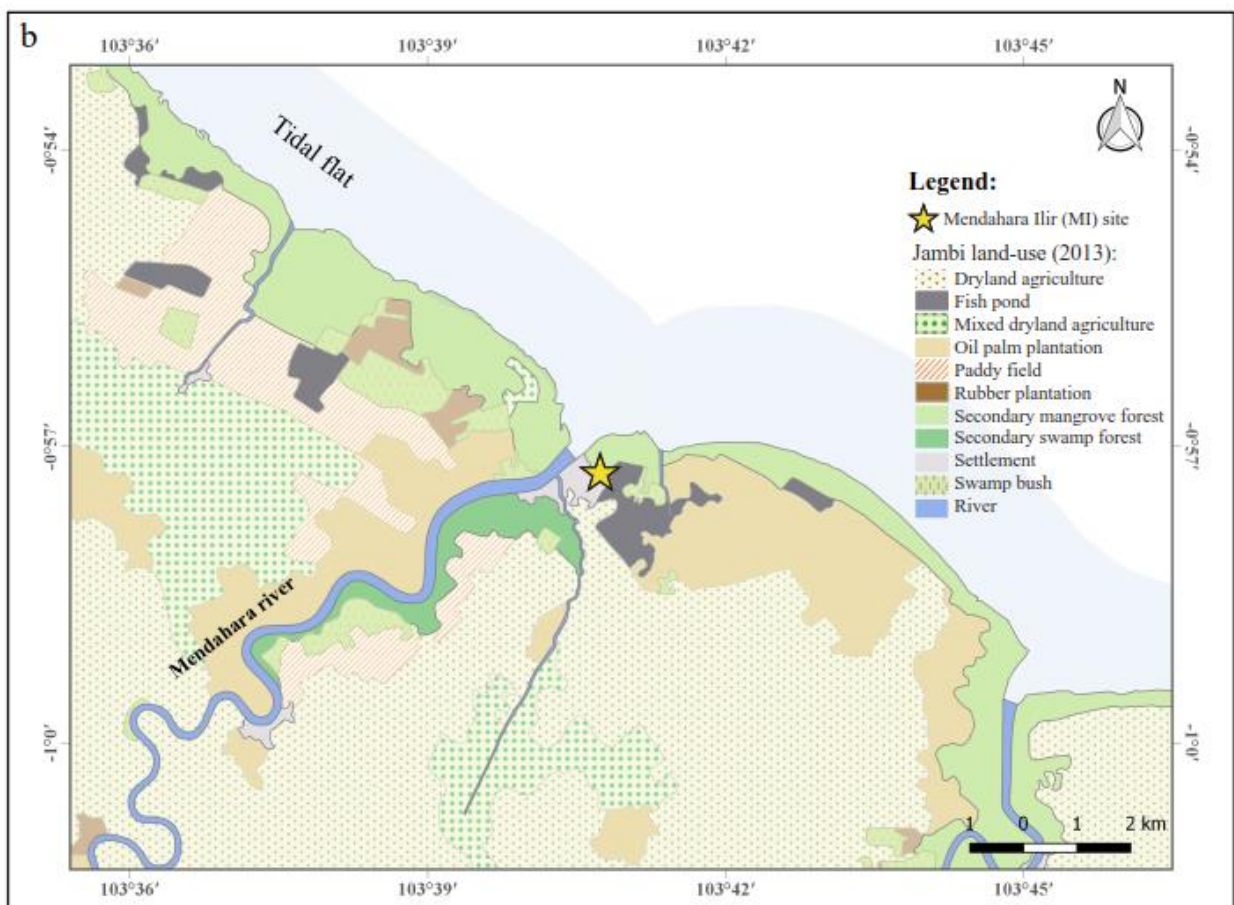


Table 6.2 List of accelerator mass spectrometry radiocarbon dates from MI core

| depth (cm) | Lab code | Material | pMC | cal yr based on pMC | ¹⁴ C BP | cal yr BP ^a |
|------------|---------------|-----------------------|---------------------|---------------------|--------------------|------------------------|
| 26 | NTUAMS-2023-1 | Organic bulk sediment | 106.423 ± 0.456 | -500 ± 34 | NA | modern ± |
| 71 | NTUAMS-1790 | Charcoal | 112.414 | -940 ± 29 | NA* | modern ± * |
| 85 | NTUAMS-2723-1 | Organic bulk sediment | 101.8468 ± 0.416022 | -147 ± 33 | NA* | modern ± * |
| 107 | NTUAMS-2024-1 | Organic bulk sediment | 152.224 ± 0.406 | 3375 ± 21 | NA* | modern ± * |
| 147 | Poz-81604 | Organic bulk sediment | NA | NA | 885 ± 30 | 782 ± 50 |
| 210 | NTUAMS-2025 | Organic bulk sediment | 86.897 ± 0.266 | NA | 1128 ± 3 | 1008 ± 26 |
| 264 | NTUAMS-2026-1 | Organic bulk sediment | 88.156 ± 0.337 | NA | 1013 ± 4* | 932 ± 9* |
| 307 | NTUAMS-2027-1 | Organic bulk sediment | 81.500 ± 0.284 | NA | 1643 ± 6 | 1545 ± 14 |
| 357 | NTUAMS-2028 | Organic bulk sediment | 79.854 ± 0.232 | NA | 1807 ± 5 | 1724 ± 17 |
| 454 | NTUAMS-2029-1 | Organic bulk sediment | 77.749 ± 0.274 | NA | 2022 ± 7 | 1972 ± 26 |
| 498 | NTUAMS-1792 | Plant material (wood) | 74.943 | NA | 2317 ± 13 | 2342 ± 10 |

Date with * symbol is excluded from the age-depth model

^aCalibration done with R script in CLAM 2.2, calibration curve used Southern Hemisphere SHCal13.14C (Hogg et al. 2013)

Palynological analysis

A series of samples for palynological analysis were taken along the core (total 50 samples) at different depth intervals to account for changes in sediment accretion. Subsamples of 0.5 cm³ of sediment were processed using standard techniques (Faegri and Iversen 1989) including HF 40% treatment and acetolysis. One tablet of *Lycopodium clavatum* spores was added to each subsample to estimate pollen and spore concentrations (Stockmarr 1971). Taxonomic identification was carried out using the tropical pollen reference collections of the Department of Palynology and Climate Dynamics. Additional resources used including pollen key and atlases for SE Asia (Huang 1972; Wang 1995; Mao et al. 2012; Li et al. 2012; Jones and Pearce 2015; Poliakova and Behling 2016), the online database of Australasian Pollen and Spore Atlas from Australian National University, Canberra (available at <http://apsa.anu.edu.au>) and the Pollen and Spore Image Database of the University of Goettingen (available at <http://gdvh.uni-goettingen.de/>).

The pollen were counted to a minimum of 300 grains per subsample. Fern spores were counted along with the pollen grains. Pollen and spore counts are express as percentage based on the pollen and spore total sum. Pollen and spore percentage were grouped into: mangrove-seaward vegetation (MS); mangrove swamp vegetation (or mangrove-mesozone vegetation; MM); mangrove-landward vegetation (ML); mangrove-associate vegetation (MA); forest vegetation (FV; including riparian taxa

and lowland/dryland rainforest taxa); herbaceous and fern, according to their ecology, habitus and distribution in the mangrove ecosystem (Flora Malesiana collection: <http://portal.cybertaxonomy.org/flora-malesiana>; Prosea collection: <http://proseanet.org>; Yulianto et al. 2004; Yulianto et al. 2005; Mao et al. 2012; Li et al. 2012; Kusmana 2014). The identified submontane/montane taxa (i.e. *Dacrydium*, Ericaceae, *Lithocarpus* and Podocarpaceae) were excluded from the total sum as long-distance transported grains. Pollen concentrations are calculated using the *Lycopodium clavatum* marker and are expressed as number per cm³ of sediment. The software C2 was used for calculation of percentages and plotting of diagrams (Juggins 2007).

Local pollen assemblages zones are defined via constrained cluster analysis using the software CONISS (Grimm 1987, 1993). All pollen and spores taxa are included in the analysis. The square-roots transformation was applied for pollen and spore percentage data.

Numerical analysis

Principal component analysis (PCA) was performed using CANOCO 5 (Ter Braak and Smilauer 2002) to display the relationship between palynological composition (Figure 6.4) in the subsamples and sea-level change (Table 6.3) for the whole record. The subsamples are classified based on the changes in sea-level phase such as: transgression and regression. All identified pollen and spore percentage data were included in the analysis. Rare taxa were not down-weighted and square-roots transformation was applied.

Review of local sea-level change

To compare palynological results with sea-level changes and to investigate the adaptation of mangroves, we conducted a review of the local sea-level data for the past 2500 years. A detailed description of the records and reference can be found in Table 6.3 and the location of each site is shown in Figure 6.6. In particular, we focus on the past sea-level change recorded from the Malacca Strait (Geyh et al. 1979) and Singapore (Tushingham and Peltier 1992), as these are the closest locations to MI study site and it is clear that sea-level changed differently on different locations (i.e sea-level change in the west and east coast of the Malaysia are comparatively different; Ercan et al. 2013). The resulted data are plotted together with the palynological results in Figure 6.3

Table 6.3 Review of sea-level from several sites in SE Asia for the last 2500 years (in bold the measures which are closer MI site)

| Site | Sea-level (m) | Latitude | Longitude | ¹⁴ C age | ¹⁴ C (error) | calibrated ¹⁴ C | Age (CE) ^a | Reference |
|--------------------------|---------------|-----------------|-------------------|---------------------|-------------------------|----------------------------|-------------------------|------------------------------------|
| Modern sea level | 0 | | | | | | 1900^b | modern |
| Phen Rang Vietnam | 1.2 | 11.3 | 108.8 | 900 | 200 | 863 | 1087 | Tushingham and Peltier 1992 |
| Strait of Malacca | -0.7 | 2.516667 | 101.766667 | 1055 | 85 | 970 | 980 | Geyh et al. 1979 |
| Strait of Malacca | -0.61 | 2.416667 | 101.966667 | 1145 | 80 | 1095 | 855 | Geyh et al. 1979 |
| Tioman Island | 1.1 | 2.75 | 104.25 | 1900 | 90 | 1150 | 800 | Tjia et al. 1983 |
| Tioman Island | 1.6 | 2.75 | 104.25 | 2370 | 120 | 1675 | 275 | Tjia et al. 1983 |
| Singapore | 2 | 1.6 | 103.4 | 2100 | 200 | 2102 | -152 | Tushingham and Peltier 1992 |
| Phuket | 1.34 | 7.75 | 98.416667 | 2210 | 57 | 2205 | -255 | Scoffin and Le Tissier 1998 |
| Chao Phraya Delta | 1.35 | 13.5 | 100.5 | 2250 | 110 | 2325 | -375 | Somboon and Thiramongkol 1992 |
| Chao Phraya Delta | 1.6 | 13.5 | 100.5 | 2250 | 110 | 2325 | -375 | Sinsakul 1992 |
| Phuket | 1.45 | 7.75 | 98.416667 | 2425 | 57 | 2530 | -580 | Scoffin and Le Tissier 1998 |
| Thale Noi TN3 | 2.37 | 7.75 | 100.166667 | 2435 | 50 | 2535 | -585 | Horton et al. 2005 |
| Phen Rang Vietnam | 2 | 11.3 | 108.8 | 2500 | 200 | 2587 | -637 | Tushingham and Peltier 1992 |

^aCalibrated ¹⁴C dates is converted into age CE (common age era)

^bThe Modern sea-level is assign a value of 0 to the year 1900 CE, preceding current observed global rise in sea-level

Results

Core descriptions, chronology and sediment accretion

The MI core consists mainly of two sediment horizons: a clay-loam sediments (500–26 cm) and a loam organic sediments (26–0 cm). The clay-loam deposit is embedded in rich organic material with several layers containing shell remains (493–452 cm, 357–300 cm, and 246–233 cm). The loam consists of rich organic materials with plant woody fibers and roots. A description of the stratigraphic lithology of the core is shown in Figure 6.2.

The first part of the core (0–107 cm) is characterized by organic material rich in roots and dating was difficult due to the high contamination by more recent root material. Therefore, the modern dates which resulted from this part are excluded from the age-depth model and the actual age control for the top of the core is unknown. There could have been erosion or a hiatus. The results from the age-depth model indicate that the MI core records the last 2300 years with an average sediment accumulation rate of 2.2 mm/yr.

The depth versus age relationship (Figure 6.2) suggests a relatively regular sediment accretion through time. The depth of 500–447 cm (ca. 290–45 BCE) record an average accretion rate of ca. 2 mm/yr and

subsequently at 447–315 cm (ca.45 BCE–460 CE) progressed to a more rapid sediment accretion rate ca. 2.6 mm/yr. The sediment accretion attained lower rate ca. 2.1 mm/yr at 315–109 cm (ca. 460–1430 CE). Subsequently, the sediment accretion was the lowest rate along the core ca. 1.86 mm/yr at 109–0 cm (ca. 1430 CE – modern). Additional loss on ignition (LOI) results at the first 100 cm show that organic matter and carbonate matter content range from 17% to 32% and 2% to 5%, respectively.

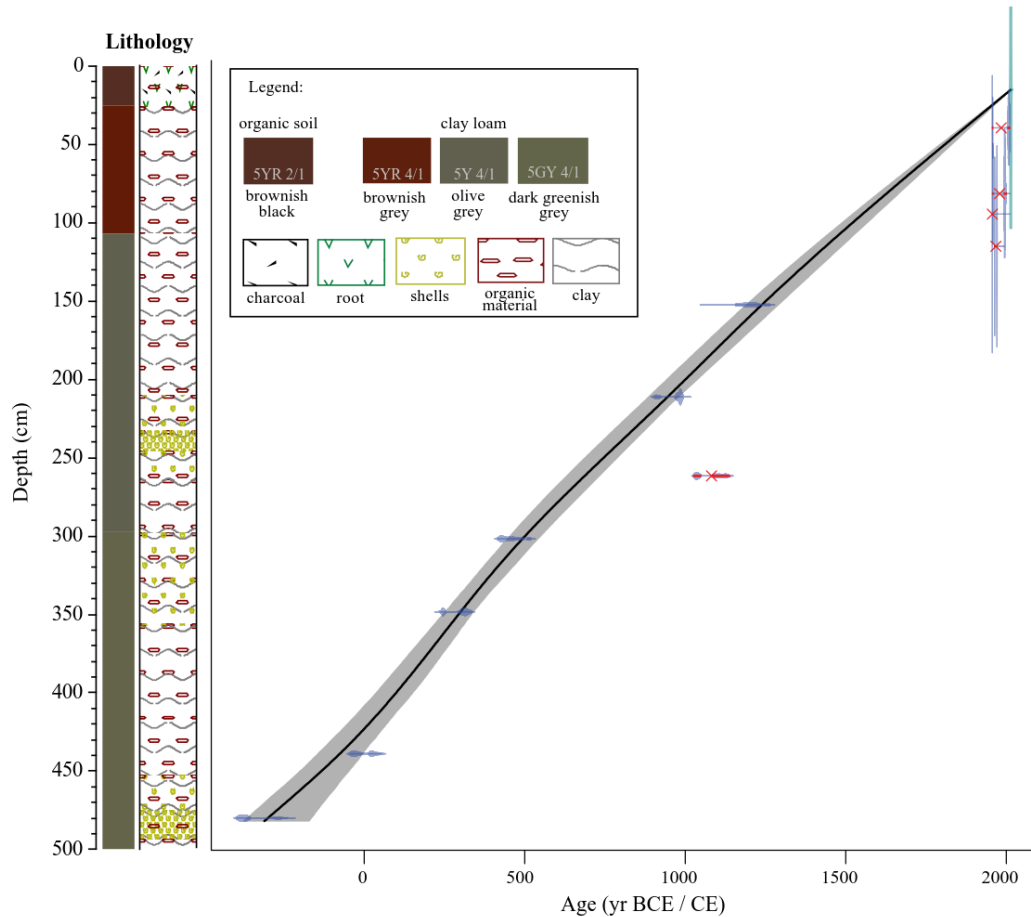


Figure 6.2 Lithological and age-depth profiles of the MI core. The age-depth model is performed using Clam 2.2 (Blaauw 2010) script in R (R Core Team 2015) using the Southern Hemisphere SHCal13.14C calibration curve (Hogg et al. 2013). A smooth spline is the best fitted model. Outlier dates are shown as red cross

Palynological results

In total, 65 pollen and 13 different spore taxa are identified in the 50 sediment subsamples (4 rare pollen and 2 spore taxa remain unknown; Table 6.4). Pollen and spore grains are well preserved and average concentration along the core is 67,000 grains/cm³. The deposits between 500 and 198 cm core depth (ca. 290 BCE–1000 CE) records average pollen concentration of ca. 50,000 grain/cm³. The pollen concentration values then increase to ca. 90,000 grains/cm³ from 198 cm to the top (ca. 1000 CE - modern).

The pollen diagram illustrates percentages of the dominant and most important taxa, which are grouped based on their ecology and habitat occurrences in the mangrove ecosystem. Mangrove community

association are divided based on tidal regimes (Watson 1928; Table 6.4). The MI record is divided into three zones according to the main changes in palynological composition based on the cluster analysis (CONISS; Figure 6.3a, b; all percentages are in average):

Zone MI-1 (500-332 cm; ca. 290 BCE - 400 CE). This zone is dominated by MM pollen (average 65%; all following percentages are in average) primarily *Rhizophora* (60%). The MA pollen are also well represented (14%) especially by *Ardisia* (10%) and by fern spores of *Nephrolepis* and *Acrostichum aureum* (1%), along with FV pollen (17%) notably by *Nauclea* (9%), *Ficus* (2%) and Moraceae (2%).

Zone MI-2 (332-125 cm; ca. 400-1350 CE). This zone is further divided into MI-2a (332–216 cm; ca. 400–950 CE) and MI-2b (216–125 cm; ca 950–1350 CE) according to the changes in vegetation composition. In subzone MI-2a, total MM pollen decreases (53%) especially *Rhizophora* (49%). The FV pollen such as *Nauclea* (10%), *Ficus* (4%) and Moraceae (6%) become more abundant. The MA pollen *Ardisia* also slightly increases (12%). In subzone MI-2b, the MS pollen start to increase (from 2% in MI-1 to 7%), represented by *Avicennia* (from 1% in MI-1 to 4%) and *Sonneratia* (from 1% in MI-1 to 3%). Total FV pollen decrease (22%) especially *Ficus* (1%) and Moraceae (3.5%), whereas *Nauclea* pollen shows an increase (13%). The MA pollen *Ardisia* also decreases (9%).

Zone MI-3 (125-0 cm; ca. 1350 CE to present). In this zone, the MS pollen remain with relatively high values (8%) especially *Avicennia* (5%) and stable representation of *Sonneratia*. The total MM and MA pollen slightly decrease (51% and 12%) particularly *Rhizophora* (46%), whilst *Bruguiera* increased (from 2% in MI-2 to 3%). The MA pollen *Ardisia* also decreases (5%). Total FV pollen are stable (24%) with a decrease of *Nauclea* (10%). Additionally, ML pollen slightly increases (from <1% in MI-2 to 2%) represent by *Lumnitzera* (1.3%) and *Nypa* (1%).

Regional sea-level change review

The available regional sea-level data show that SE Asia was experiencing a marine regression since the mid-Holocene highstand which was ca. 6 m higher at 2600 BCE (or 4550 cal yr BP; Tushingham and Peltier 1992). In particular, the data from the Malacca Strait and Singapore shown that the sea-level was estimated to be ca. 2 m higher than the present level at ca. 150 BCE (or 2100 cal yr BP). Based on this data, we can interpolate the value and estimate that the sea-level was about 2 m higher than present when the MI record started at ca. 290 BCE. The regression event continued and peaked at ca. 980 CE when the sea-level decreased below the present level of about 0.7 m (Geyh et al. 1979). Afterward, a transgression event occurred when the sea-level started to rise again up to the modern sea-level. The reconstruction from other records in SE Asia (i.e. Tjia et al. 1983; Sinsakul 1992; Somboon and Thiramongkol 1992; Horton et al. 2005; Table 6.3) shows a comparatively different trend of sea-level change with the data from Malacca Strait and Singapore. The sea-level change records a more stable and continued sea-level decrease with no recent transgression phase (Figure 6.3). The sea-level was estimated to be ca. 2 m higher at ca. 630 BCE (data from Vietnam; Tushingham and Peltier 1992) as

part of the regression since the mid-Holocene high stand. Such regression appears to have been continuous in the area north to our study site (Table 6.3; Figure 6.6).

Principal Component Analysis (PCA)

The variation of the palynological pollen and spores composition is characterized by the PCA with 32% of the total variance explained by the first (16%) and second (13%) axes (Figure 6.4). The PCA results show a link between the sea-level changes and taxa compositions as expressed in the first axis. The distribution of vegetation group follows the changes in sea-level. Subsamples within the transgression event (sea-level rates increase) score positively on the first axis, while subsamples within the regression event (sea-level rate decrease) score negatively. The result shows that the transgression phase is correlated mainly to the distribution of *Avicennia* (MS), and the regression event correlated to the distribution of *Rhizophora* (MM).

Discussion

Mangrove forest dynamics and sea-level change

The high representation of *Rhizophora* pollen indicates that mangrove forest was present close from MI site since the beginning of the record at ca. 2300 year ago. *Rhizophora* flowers are mainly pollinated by wind (Kathiresan and Bingham 2001) and its pollen is generally abundant and over-represented relative to other genera (Somboon 1990; Li et al. 2008). Abundant *Rhizophora* pollen can be interpreted as a strong local occurrence (Yulianto et al. 2005) as they generally dispersed nearby its source (Taylor et al. 2001; Kaars 2001). This also indicates that the region was strongly affected by saline tidal waters (Penny 2006), as most plants from Rhizophoraceae family prefer to grow in wet, muddy and silty sediments in the tidal zone (Lan et al. 1993).

While Rhizophoraceae were dominant at the site for the whole period, changes was more clearly in the lower represented pollen spectra. This suggests that mangrove vegetation was dynamic in this period of time. When compared to the sea-level variation which occurred close to the MI site in the Malacca Strait and Singapore, it is apparent that these dynamics were a response of the vegetation to marine regression and transgression (Figure 6.3 and 6.5). This correspondence between palynological composition and sea-level reconstruction is particularly clear in the PCA (Figure 6.4) where the highest variation can be explained by sea-level marine phases. Samples which are found in a period when sea-level was decreasing (following the mid-Holocene high stand; Hanebuth et al. 2000; Sathiamurthy and Voris 2006) were generally driven by Rhizophoraceae pollen, indicators of a tidal range. On the other hand the samples characterised by SLR, show an increased importance of mangrove taxa such as *Avicennia* in the pollen record (Figure 6.4). *Avicennia* flower is pollinated by small insect and has low pollen production (Ng and Sivasothi 2001; Rugmaia et al. 2008). Therefore, in paleo-records *Avicennia*

pollen is under-represented compared to its real floristic presence (Somboon 1990). Even the observed small increase in *Avicennia* in MI core can indicate an important expansion of MS vegetation around the site.

Mangrove belt in MI shows an adaptive response to changes in sea-level with an interesting invasion of marine belt more inland when sea-level is rising. Due to the high resolution of the record (ca. 46 years per sample), more detailed reconstructions are possible of the adaptive migration which occurred in the past ca. 2300 years (Figure 6.5).

Initial settings, mangrove-swamp forest (ca. 290 BCE): A marine regression started at ca. 5000 years ago following the mid-Holocene high stand (Hanebuth et al. 2000; Sathiamurthy and Voris 2006). The MI record started around 2300 years ago (ca. 290 BCE) when the estimated sea-level during this regression phase was ca. 2 m higher than the present level (Figure 6.5). This resulted in a coastline which was at that time located more landward compared to present-day. The pollen results indicate that the vegetation at the site was dominated by *Rhizophora* and *Bruguiera* sp. In particular, the higher relative representation of *Bruguiera*, suggests that initially the site was a mangrove swamp forest located behind the mangroves belt. A mixed open lowland/dryland forest dominated by *Nauclea*, *Ficus* and Moraceae with association of *Ardisia* and fern *Acrostichum aureum* was present further inland. The high presentation of *Nauclea* suggests a higher riverine input into the mangrove forest.

Migration of lowland forest (ca. 285 BCE – 980 CE): The sea-level regression continued up to ca. 980 CE when the coastline was estimated to be lower than the current level of ca. 0.7 m (Figure 6.3). With the coastline moving seaward, *Rhizophora* decreased in occurrence. This can be explained with the increase or migration of lowland/dryland forest into the mangrove swamp forest. While the values of lowland rainforest pollen (i.e. *Ficus*, other Moraceae and *Ilex*) is too low to indicate the local presence of dryland forest at the site (*Rhizophora* are still dominant), their relative increase suggests a background migration which was important enough to be recorded at our site. During the marine regression, sediment accumulation was relatively high compared to the following period (average 2.3 mm/yr vs. 2 mm/yr). These higher values possibly suggest a more important influence of river discharge, as also indicated by the increase of riparian taxa like *Nauclea*. This interpretation of a more freshwater influence is strengthened by the presence of *Sonneratia* (Santisuk 1983; Li et al. 2012), a pioneer in brackish water which is strongly diluted by flood water flowing out of the rivers during the rainy season (Whitten et al. 2000; Li et al. 2012).

The inland migration of mangrove-seaward vegetation (980 CE – modern): After the regression event, the sea-level started to increase from 980 CE to the present time resulting in landward coastlines movement. This transgression event might have led to a landward inundation. The mixed occurrence and increase of *Avicennia* and *Sonneratia*, which are pioneer species on tidal flat with a strong marine influence (Hong and San 1993), suggests increase in salinity in the area. Thus, it is apparent that even with the slightest increase in sea-level at the study area in MI, the MS vegetation moved more inland.

Finally, the stronger presence of the ferns *Acrostichum aureum* and Cyatheaceae at ca. 1700 CE might indicate a development of more open areas in the mangrove belt (Ellison 1989).

The palynological record captured a relatively rapid adaptation of the MI mangrove belt to sea-level change, suggesting that mangroves in the southeast coast of Sumatra island could cope with the changes in sea-level which occurred in the past ca. 2300 years.

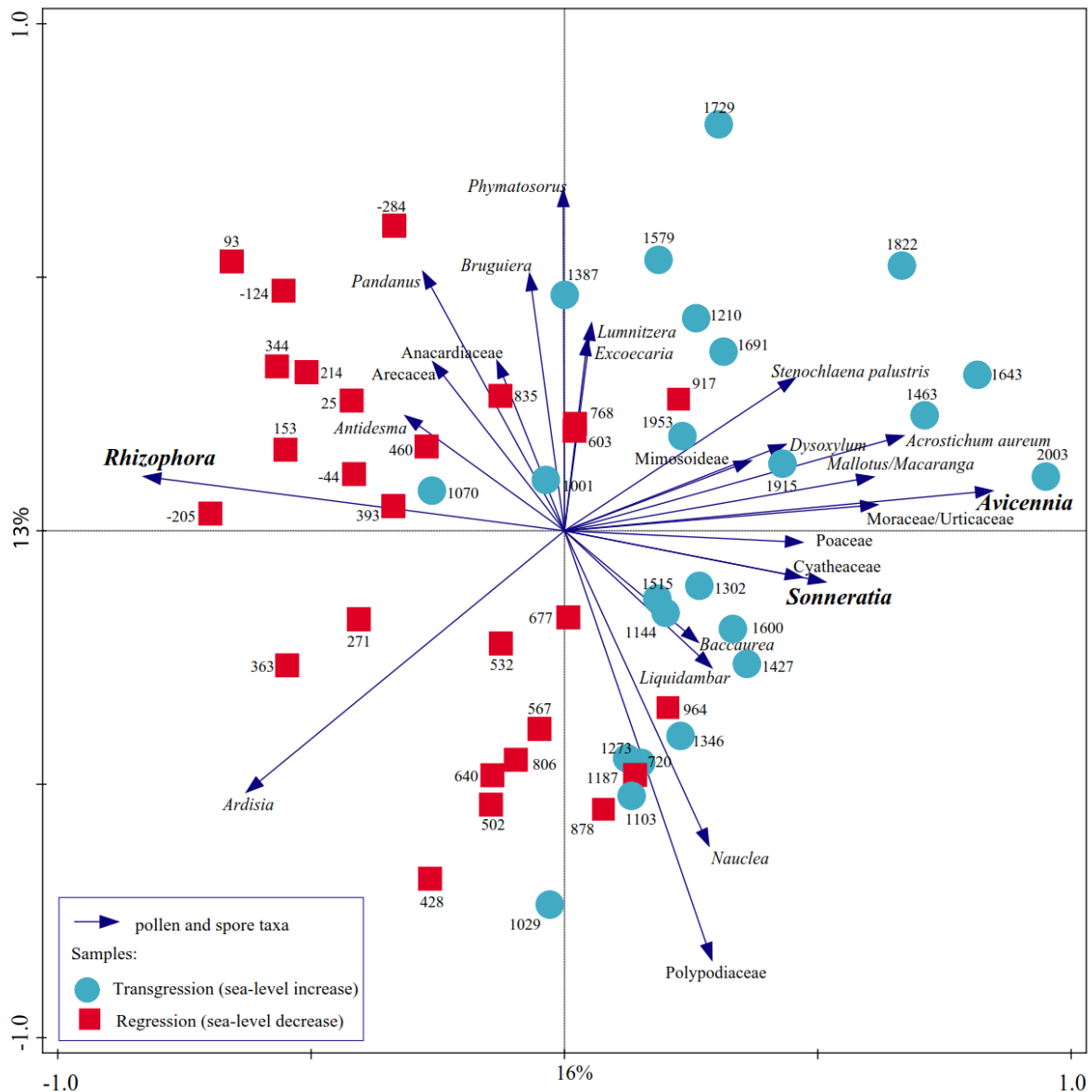


Figure 6.4 Principal Component Analysis (PCA) of all pollen and spores taxa with samples colour showing the changes in sea-level following marine transgression/regression event in the Malacca Straits and Singapore for the last 2500 years (Geyh et al. 1979; Tushingham and Peltier 1992). Age is shown in CE year, negative value shown BCE year

The sea-level data from the Malacca Strait and Singapore at the beginning of the record at ca. 2300 years ago, suggests a higher than today sea-level following marine regression since the mid-Holocene high stand (Hanebuth et al. 2000; Sathiamurthy and Voris 2006). That the initial depositional environment was influenced by marine sediment is also indicated by the intercalation of mollusc shell in the clay sediment. The marine regression continued until about 980 CE when the sea-level drop to

ca. 0.7 m below the present level. While the high representation of *Rhizophora* suggests that the mangrove swamp persisted at the MI site, forest taxa like *Nauclea*, *Ficus* and *Moraceae* increased indicating forest encroachment. These results highlight the sensitivity of mangroves species to sea-level change. When conditions are not ideal, mangroves are unable to compete successfully against freshwater vegetation (Whitten et al. 2000).

In the following period a marine transgression occurred until the present time (i.e. 1900 CE), when the sea-level reached the present level (Figure 6.5; Hanebuth et al. 2000). The rise in sea-level altered the depositional environment as the coastline moved back into landward. As a consequence, the MI site was inundated again by the sea water. This change is notable with the increase of pollen from seaward taxa such as *Avicennia* indicating a rapid migration landward of the mangrove belt. That the mangrove vegetation of MI is sensitive to sea-level changes that occurred in the past ca. 2300 years, is well highlighted in the PCA. The largest variation in pollen and spore taxa composition can be explained with sea-level change (Figure 6.4)

The impact of projected sea-level rise on mangrove forest

A period of rapid rising in sea-level started globally in the mid to late nineteenth century (Church et al. 2008), with an estimated increase of 3.2 mm/yr in the recent decades (Church and White 2011). Projections indicate this increase will continue to reach a SLR between 0.28 and 0.98 m by 2100 (IPCC 2013). These global estimates are, however of limited importance in this context, as it is clear that SLR can be very different depending on the location (e.g. Slangen et al. 2012; Perrette et al. 2013; Strassburg et al. 2015). Regional sea-level varies owing to regional processes and geographical features (e.g. Ericson et al. 2006; Parry et al. 2007) and can be altered by changes in atmospheric or oceanic circulation.

In Indonesia where thousands of island and large low elevation coastal areas are found, the current rate of SLR is much higher than the global mean (ca. 7.5 mm/yr; Nerem et al. 2010) and is predicted to accelerate in the future (Nicholls and Cazenave 2010). However, estimates vary depending on the period recorded, methodology and location. Closer to our site, in the eastern coast of North Sumatra, a study using satellite altimetry for the period 1993–2016 shows a mean SLR of 5.0 mm/yr (Lumban-Gaol et al. 2017). In general, the rise in sea-level will have a significant impact on Indonesia coastal region, specifically on the mangrove ecosystem survival ability (Duke et al. 2007; Alongi 2015).

In this context, studies on the paleo-dynamics of mangroves can be valuable to establish cut-off values and threshold beyond which mangroves loose adaptation capability. The inferred rate of sea-level changes from the study in Malacca Strait and Singapore is not very precise, due to the lack of data points for the most recent millennia, as so far scientists have been more interested in reconstructing post-glacial sea-level changes in SE Asia. Despite this limitation, the estimations so obtained can give us an understanding of the average rate which occurred in this period of time. The first interesting result

is the presence of a well-developed mangrove swamp forest at the beginning of the record, when sea-level was estimated to be 2 m higher than present (interpolated point from Malacca Strait and Singapore). Our palynological results of the MI core thus suggest that the mangroves in MI might persist under the current worst-case scenarios of SLR by 2100 (1 m projection; IPCC 2013). However, it is important to notice that when assessing adaptive capacity of mangroves, rate of changes are perhaps more important than total changes.

The period of time recorded in MI core encompass 2 major phases of sea-level change as reconstructed from Malacca Strait and Singapore: a regression phase from ca. 290 BCE (year of the start of MI record) to 980 CE and a transgression phase from ca. 980 CE to modern time (i.e. 1900 CE). The regression phase was characterized by sea-level decrease rates of 2.38 mm/yr, while the transgression was slower at average 0.68 mm/yr. Keeping in mind the limitations due to the low resolution of the sea-level reconstructions in the area, these results are very interesting, as they show the current (5.0 mm/yr; Lumban-Gaol et al. 2017) and future (7 mm/yr; Indonesian National Development Planning Agency 2009) rate of change fell well outside the range observed in our record of mangroves in MI. Additionally, the estimated rate of sediment accretion as reconstructed from the age-depth model, indicates that the capacity to accumulate sediments in MI was enough for the sea-level change rates of the past 2300 years but it will probably not be in the future (average 2.2 mm/yr accretion against a 5 mm/yr rate of sea-level increase). It is therefore clear that major concern in terms of adaptability for the mangroves ecosystems in Sumatra do not regard total sea-level change but rather the velocity at which this change will occur.

Our results from MI show adaptability to an estimated 2 m higher sea-level in MI, however the pace at which those changes occurred in the past 2300 year is much lower than the one currently ongoing and predicted in the next century. However, one study from Twin Cays, Belize show that mangroves may adapt to SLR between 1 mm/yr and 10 mm/yr (McIvor et al. 2013) and with our study we were not able to establish a threshold for mangrove collapse in Mendahara Ilir as the data indicate mangrove belt adapted to the sea level changes in the past 2300 years. More palaeoecological studies are needed in order to clearly answer the question on how much impact the rate of sea-level change predicted will have on the mangroves in Sumatra in the future.

Other driver of mangrove lost: human activities and urban coastal development

Projection of the next two decades on mangrove lost in Sumatra show that it is the third largest in Indonesia (after Kalimantan and Papua) due to land-use change (Ilman et al. 2016). This is primarily due to conversion to brackish water shrimp farm or tambak development, particularly in the last 30 years (Valiela et al. 2001; Primavera 2000) and timber exploitation at a smaller scale (Ilman et al. 2016). Other anthropogenic drivers such as agricultural and forestry activities, and urban development are considered as less essential at a regional scale (FAO 2007; Valiela et al. 2001), however, rice

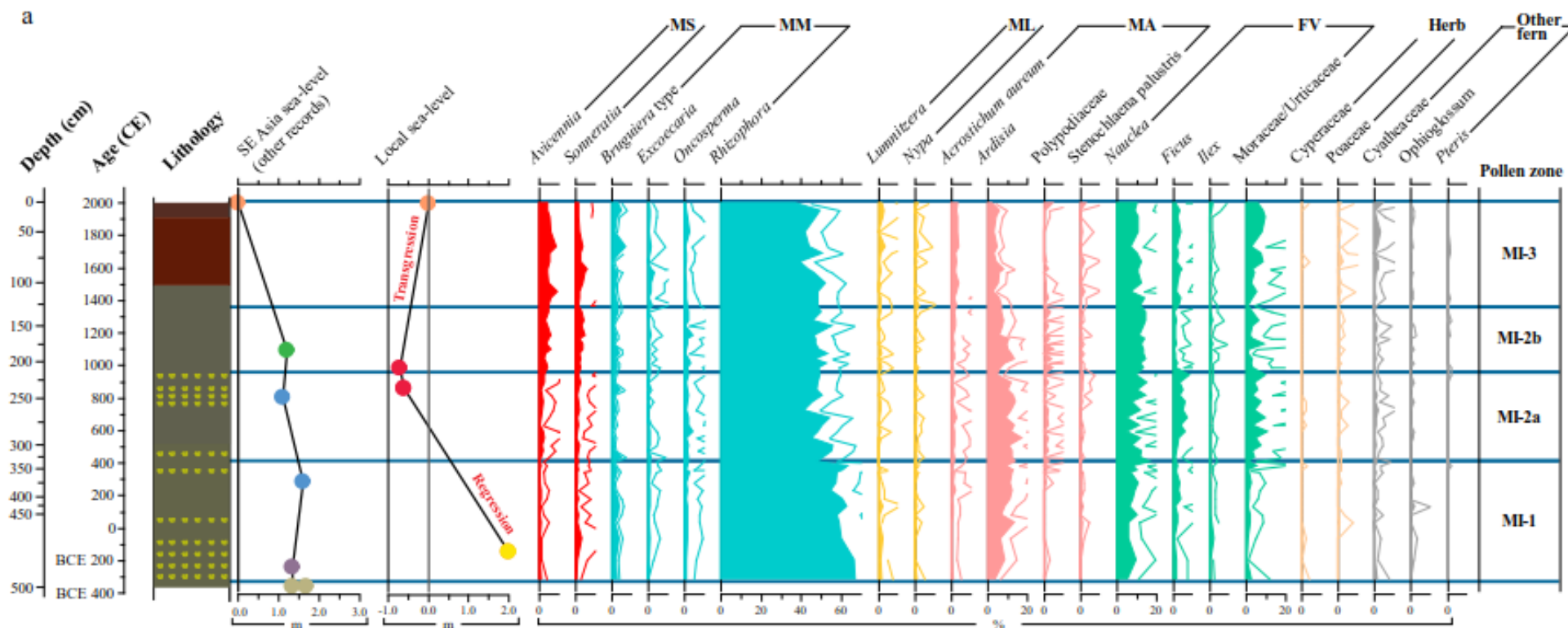
cultivation, oil palm plantation and urbanization have latterly been shown to be locally significant (Webb et al. 2014; Lai et al. 2015; Ilman et al. 2016; Richards and Friess 2016; Lee et al. 2014).

At our study site, in the MI region land-use change is mostly due to dryland agricultural field and aquaculture, and a rapid urban development. The pressures of urban development due to the large population increase in the coastal area pose the major threat to the remaining mangrove forest in the area. In particular, infrastructure such as road construction and new settlement establishment led to the clearing of the whole forest in the years following our field coring campaign. It is clear that the mangrove deforestation will increase the vulnerability of the MI coastal region to natural disaster such as flooding as the missing mangrove belt will no longer served as a natural protection against an extreme SLR. Additionally, it will largely reduce migratory path and destroy the chances of remained mangrove to migrate inland.

It is predicted that part of the southeast coast of Sumatra will be submerged by 2070 (Lovelock et al. 2015) and that the coastal area lost will be about 12 to 60 km² for 1 m and 2 m inundation (Lumban-Gaol et al. 2017). The palynological results from the MI core shows that already under a rate of sea-level change inferior to the one predicted, mangroves ecosystems were migrating seaward or landward to adapt. Even under a transgression of just about 0.68 mm/yr which occurred in the past ca. 1000 years before modern time, the relative large increase in pollen from mangroves-seaward at the MI site highlights the migratory need of these species when sea-level increases (Figure 6.5).

In the view of our results we can state that the impact of land-use change and coastal urbanization will cause large losses in the future in MI and Sumatra. This impact is direct, due to deforestation and mangrove land conversion, and indirect by impeding a much-needed migratory path with urban constructions.

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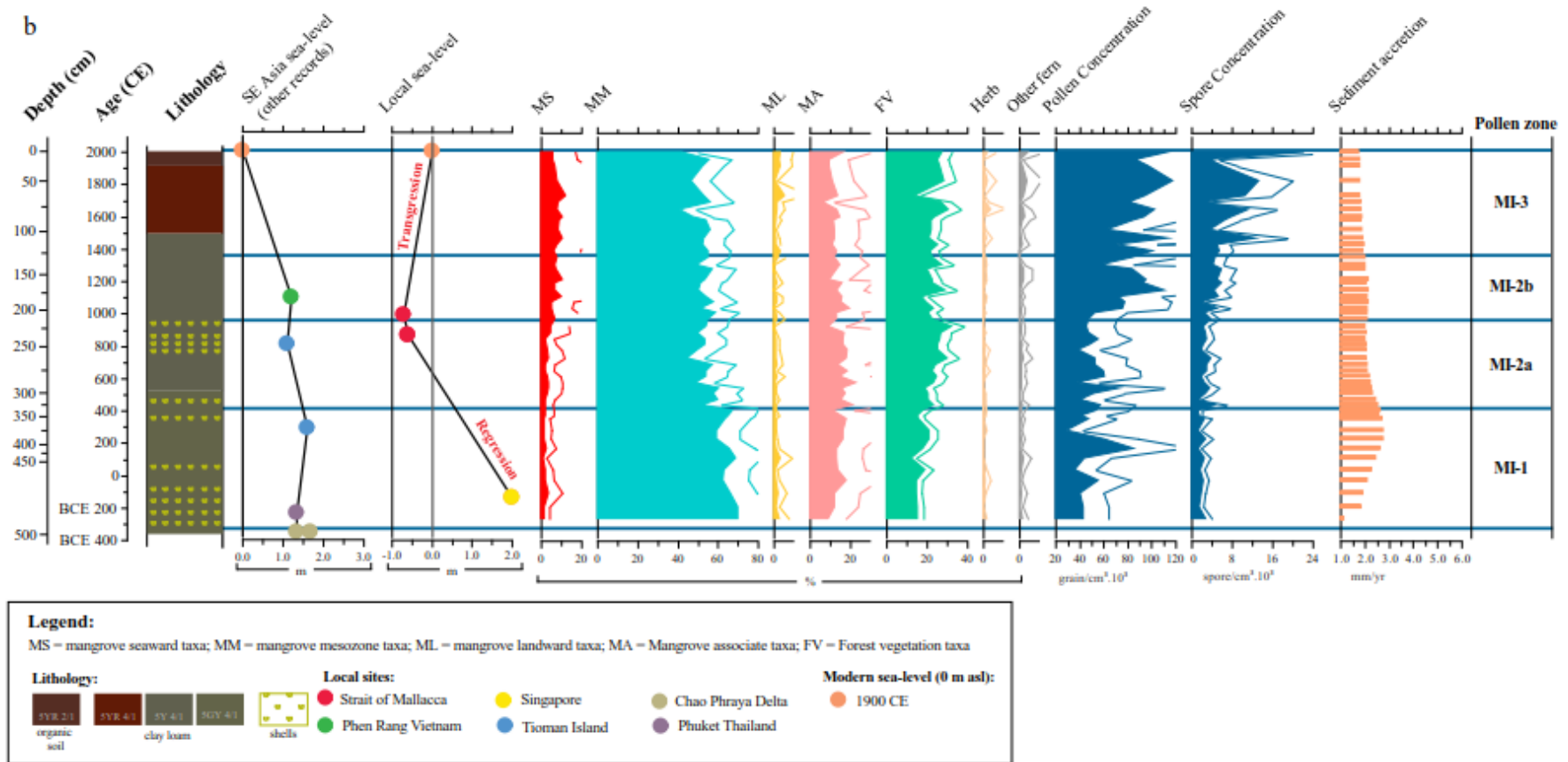


Figure 6.3 Palynological diagram of the MI-core with lithology and local sea-level change from different sites in SE Asia shown in ball symbol with different colours (see-Table 2) during the Late Holocene: (a) most important pollen and spore taxa represented as % of total sum of pollen plus spores; (b) Total sum of pollen and spores for each ecological group; pollen and spore concentration and sediment accretion rates. Current sea-level set to 0 m at 1900 CE and represented by the orange ball symbol

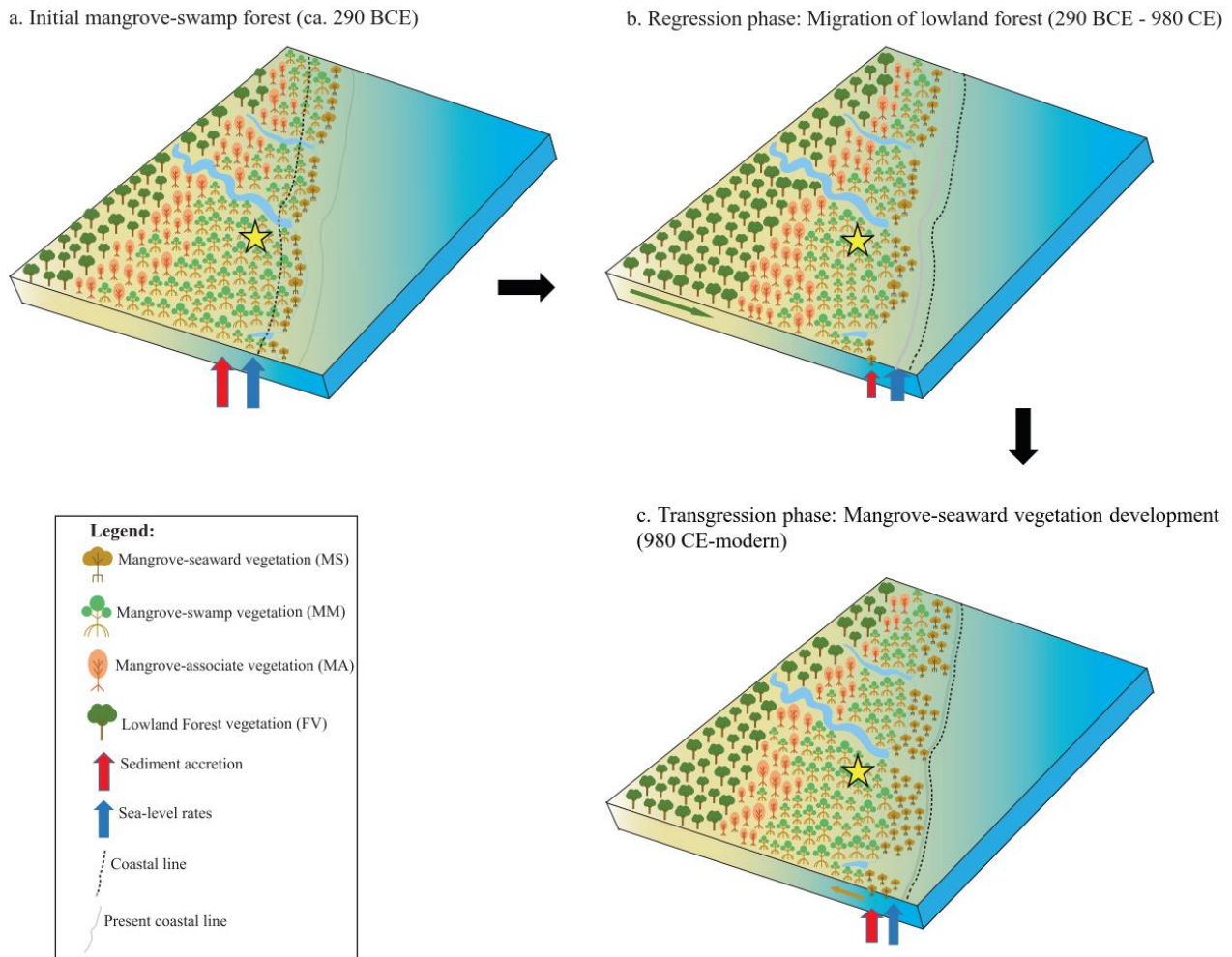


Figure 6.5 Graphical overview of vegetation dynamic based on the changes in sea-level rates following marine transgression/regression events and sediment accretion for MI site (yellow star)

Conclusions

The current and future response of mangroves to SLR projection scenario depends on the ability of mangrove to keep pace with the rising in sea-level. In order for mangroves to adapt to SLR, a sufficient increase in the surface accretion and surface elevation must be achieved through sediment accretion. Additionally, migration path landward must be available for mangroves to migrate and persist under scenario of SLR. The MI palynological record in Sumatra, Indonesia, suggests that mangroves in the southeast coast of Sumatra could adapt to the changes in sea-level which have occurred in the past 2300 years. The first interesting result is that that mangroves could persist in MI with sea-level higher than the future estimate (estimated ca. 2 m compare to the 1 m future global estimate). This suggests that no topographic barrier exists in the area that would impede the potential migration of mangroves in Mendahara Ilir in a SLR scenario or else the data would show a lower representation of mangrove pollen in this period. However, the estimated rate of sea-level change in the MI site for the past 2300 years are much lower than the current estimate and future projections. The sediment accretion estimated for the

past 2300 years also suggests a sediment accretion capacity in MI of ca. 2.2 mm/yr (min 1.82 mm/yr; max 2.80 mm/yr) much lower than the current SLR. In other words, while the MI mangroves might adapt to the absolute changes projected, the velocity at which those changes are occurring might increase the vulnerability or even cause for this adaptive capacity to cease.

The palynological results show a highly dynamic response of the mangrove forests to even these slower changes, which occurred in the past 2300 years. The forest encroached the mangrove belt during the marine regression and mangrove-seaward species migrated inland during the recent transgression. This suggests that under current and future SLR, the mangroves will need a migratory path inland to move and persist in the future. We conclude that in order to maintain the existence of mangroves forest in the MI region, mangrove reforestation along the coast and the creation of a buffer zone on the back of the current mangrove belt to allow for migratory dynamics to occur are needed to lessen adverse impact of SLR both for mangroves ecosystems and coastal populations.

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Supplementary materials

Table 6.4. List of pollen and spores with different ecological groups for mangrove ecosystem in Sumatra, Indonesia

| | |
|--|--|
| Mangrove seaward vegetation Plant Family: Acanthaceae Lythraceae | Plant taxon: <i>Avicennia</i> <i>Sonneratia</i> |
| Mangrove mesozone/swamp vegetation Plant Family: Arecaceae Euphorbiaceae Malvaceae Meliaceae Rhizophoraceae | Plant taxon: <i>Oncosperma</i> <i>Excoecaria</i> <i>Brownlowia</i> type <i>Xylocarpus</i> <i>Bruguiera</i> type <i>Rhizophora</i> |
| Mangrove landward (transition to terrestrial) Plant Family: Arecaceae Combretaceae | Plant taxon: <i>Nypa</i> <i>Lumnitzera</i> |
| Mangrove associate vegetation Plant Family: Apocynaceae Arecaceae Aspleniaceae Blechnaceae Loranthaceae Lycopodiaceae Myrsinaceae Nephrolepidaceae Phyllanthaceae Polypodiaceae Pteridaceae Sapotaceae | Plant taxon: <i>Arenga</i> <i>Stenochlaena palustris</i> <i>Lycopodium cernuum</i> <i>Ardisia</i> <i>Nephrolepis</i> <i>Glochidion</i> <i>Phymatosorus</i> <i>Acrostichum aureum</i> |
| Lowland rainforest <i>Riparian vegetation</i> Plant Family: Anacardiaceae Elaeocarpaceae Juglandaceae Leguminosae Pandanaeae Phyllanthaceae Rubiaceae <i>Dryland rainforest vegetation</i> Plant Family: Altingiaceae Aquifoliaceae Araceae Arecaceae Cannabaceae | Plant taxon: <i>Engelhardtia</i> <i>Pandanus</i> <i>Baccaurea</i> <i>Nauclea</i> <i>Randia</i> <i>Timonius</i> Plant taxon: <i>Liquidambar</i> <i>Ilex</i> <i>Colocasia</i> <i>Cocos</i> <i>Celtis</i> |

| | |
|--|---|
| <p>Casuarinaceae Celastraceae Clusiaceae Plant Family: Compositae Dipterocarpaceae Ericaceae Euphorbiaceae</p> <p>Fagaceae</p> <p>Gesneriaceae Gnetaceae Malvaceae Meliaceae Menispermaceae Moraceae Myristicaceae Myrtaceae Phyllanthaceae</p> <p>Piperaceae Proteaceae Sapindaceae Stemonuraceae</p> | <p><i>Trema</i> <i>Casuarina</i> <i>Lophopetalum</i> <i>Calophyllum</i> Plant taxon: <i>Vernonia</i></p> <p><i>Blumeodendron</i> <i>Mallotus</i> <i>Macaranga</i> <i>Lithocarpus</i> <i>Castanopsis</i> <i>Neoscoterchina</i> <i>Gnetum</i> <i>Durio</i> <i>Dysoxylum</i> <i>Stephania</i> <i>Ficus</i></p> <p><i>Antidesma</i> <i>Phyllanthus</i> <i>Peperomia</i> <i>Helicia</i> <i>Pometia</i> <i>Stemonurus</i></p> |
| <p>Herbaceous vegetation Plant Family: Cyperaceae Leguminosae Poaceae</p> | <p>Plant taxon:</p> <p>Sub. Family: Mimosoideae</p> |
| <p>Fern Plant Family: Cyatheaceae Ophioglossaceae Pteridaceae Thelypteridaceae</p> | <p>Plant taxon:</p> <p><i>Ophioglossum</i> <i>Pteris</i></p> |

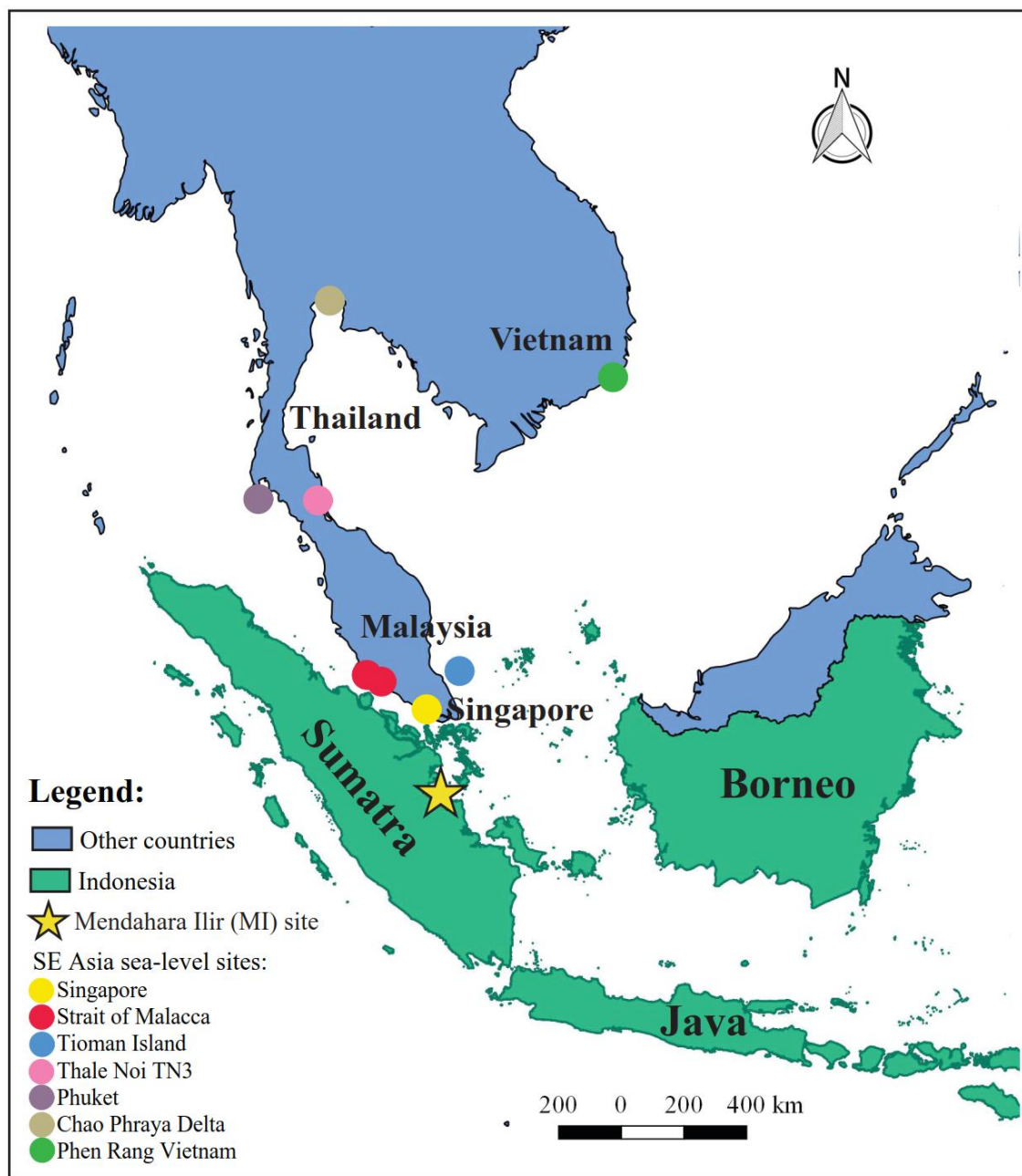


Figure 6.6 Maps of local sea-level change from different sites in SE Asia during the Late Holocene. Each site is shown in different colour

CHAPTER 7: SYNTHESIS

The results of this research contribute to improve our knowledge of the ecology and long-term dynamics of highland and coastal ecosystems in Central Sumatra. A multi-proxy palaeoecological approach was used in order to have a better understanding on how tropical mountain rainforest and coastal mangrove forest in the region have responded to different natural and anthropogenic drivers of change in time scale of thousands of years.

Synthesis of the main results on vegetation, climate, fire dynamics and human-landscape interactions

The submontane rainforest in the Kerinci Seblat National Park

Volcanism is one of the most important elements in Sumatra as the island is known as one of the most tectonically active region on earth (Salisbury et al. 2012). Therefore, volcanic processes might play an important role in the history of vegetation in Sumatra (Laumonier 1997). The Danau Njalau record is the first archive from Sumatra which provide information on how much volcanism can impact the vegetation composition in the tropical mountain of Sumatra (Chapter 4).

The vegetation dynamics reconstructed from palynological and macro-charcoal analyses reveal interaction between the volcanic deposition and vegetation for the last 5000 years. A secondary deposition of volcanic materials occurred at a slow pace (ca. 700 years) and had a strong impact on the plant composition in the area. The presence of volcanic material in the soil, gave advantage to certain species and led to the dominance of pioneer taxa like *Casuarina* and *Myrica*, which grow in deforested land and volcano slopes (volcanophile taxa). Surprisingly, when the deposition of volcanic material decreased and finally ended at ca. 4400 years ago, the presence of these volcanophile pioneer taxa remained frequent in the area. The formation of the modern forest composition took several centuries after the volcanic deposition in the soil ended (ca. 900 years at ca. 2400 cal yr BP). Such a long-time effect was likely not driven by a successional pattern, as this kind of recover pattern after volcanic eruption has been shown to have taken less than 100 years, for instance, in the island of Krakatoa in Indonesia (Whittaker et al. 1989).

Several environmental factors might have contributed to this slow increase in submontane species including soil thickness, erosion, and disturbance and human activities with soil formation play the major role in shaping plant composition. The presence of volcanic material in the soil layer where trees have their roots limited the survival and growth of most of submontane rainforests taxa rather than *Casuarina/Myrica*. Once the peaty organic soil accumulated above such a layer, species of *Casuarina* and *Myrica* could no longer outcompete against other rainforests species and rapidly decreased.

Despite the close vicinity of the site to known archaeological sites, the palynological records show no compelling evidence for prehistoric disturbance of the vegetation due to human activities such as deforestation and agriculture. The analysis of local fire history at the Danau Njalau indicates that fire never had a strong influence on the vegetation for the past 5000 years. Fire episodes were extremely rare and could not be linked to any causality (i.e. human cultural phases and climate variability), suggesting that fire occurrences were stochastic events. This result is probably due to the remote location of Danau Njalau, as archaeological evidence attest the presence of humans in Kerinci for thousands of years (Bonatz 2012).

As one of the most fertile area in the highlands of Sumatra (Miksic 2015), the Kerinci valley is a very suitable place for rice cultivation (Bonatz 2004), however there are no clear hints to when rice was first introduced in the area. In Indonesia, rice is common to be cultivating under wet-field cultivation in a bunded fields (=sawah in Bahasa Indonesia; Bellwood 2007; Maloney 1996) which is associated with tillage using the hoe or the plough (Maloney 1996). Before the introduction of machineries in SE Asia, the water buffalo (*Bubalus* sp.) was used in wet-rice cultivation to plough wet-rice field. Finding evidence of the presence of swamp buffaloes can hint important information regarding rice cultivation and its introduction in Sumatra.

Our records from Danau Bento (DB) provide the first evidence of buffaloes husbandry in the Kerinci valley since 4300 years ago based on the NPPs result. In the beginning of our record, the forest on the swamp was larger than today until ca. 3200 cal yr BP. However, grassland was already present. Due to the lack evidence of rise type Poaceae, it is likely that the swamp area was only used for the grazing of buffaloes and not for rice cultivation. Buffaloes were likely used for ploughing the wetland while agriculture was carried out elsewhere in the valley. The increase of large Poaceae from ca. 2500 cal yr BP represents the first evidence of the starting of rice cultivation in the DB swamp. At the same time, the decrease of NPPs hint to a reduction in grazing activity suggesting a change in the use of the swamp in this period. However, this rice cultivation phase only lasted for a couple of centuries (until 2100 cal yr BP). This might due to the fact that the rice cultivations in DB were not permanent but part of a shifting practice as found in other Sumatran sites such as in Danau Padang (Morley 1982) and the Toba Plateau sites (Maloney 1996). It is also possible that the swamp area of Bento resulted not productive or convenient for rice cultivations compared to other areas in the Kerinci valley and that the cultivations were simply moved somewhere else. Following the decline of rice cultivation, the swamp remained in use as grassland for buffaloes as shown by the forest not recovering, coupled with the lack of fire usage. Our records show that introduction of rice cultivation and water buffaloes in Kerinci were in line with the archaeological records of the Austronesian speaker migration to Sumatra about 4000 years ago. We also found that the rice intensification in DB swamp about 2500 cal yr BP was concurrence with the starting of rice cultivation in the Toba Plateau. Both these findings might suggest an increase in population and/or change in technology corresponding to the Bronze Age period in Sumatra.

The Mangroves forest in Jambi Province

Owning to the availability of vast coastal habitats with humid tropical climate, Indonesia has the largest mangrove area in the world (nearly 23% of the world's mangrove with ca. 3.2 million hectares; Wilkie and Fortuna 2003; Agency of Survey Coordination and National Mapping Republic of Indonesia 2009) which are widespread along the coastlines of Indonesian archipelago (Choong 1990). The present development of mangroves in Indonesia is under threat despite the ecological services and socio-economic functions they provides. Besides human activities, one of major concern for mangrove ecosystems is the effect of future sea-level rise (SLR; Krauss et al. 2014).

Our palynological record from a secondary forest in the Mendahara Ilir (MI), Jambi Province suggests that mangroves in the southeast coast of Sumatra could adapt to the changes in sea-level which have occurred in the past 2300 years (Chapter 6). The high representation of *Rhizophora* pollen indicates that mangrove forest was present at the MI site since the beginning of the record.

The initial setting of the mangroves with the dominance of *Rhizophora* started around ca. 2300 years ago. At time the sea-level was estimated to be ca. 2 m higher than the present level. Following the mid-Holocene sea-level high stand, the regression continued to ca. 0.7 m (ca. 980 CE). The lowland/dryland forest increased, suggesting a migration of dryland forest into the mangrove swamp due to seaward moving of the coastline. Afterwards a marine transgression occurred (980 CE-present), resulting in a landward coastline movement and pollen results indicate the migration of marine-seaward (MS) vegetation with *Avicennia* and *Sonneratia*. The palynological record captured a relatively rapid adaptation of the MI mangrove belt to sea-level change, suggesting that mangroves in the southeast coast of Sumatra island could cope with the changes in sea-level which occurred in the past ca. 2300 years. During the regression phase the sea-level decrease at rates 2.38 mm/yr, while the transgression was slower at average 0.68 mm/yr. Despite the limitations due to the low resolution of the sea-level reconstructions in the area, these results are very interesting, as they show the current (5.0 mm/yr; Lumban-Gaol et al. 2017) and future (7 mm/yr; Indonesian National Development Planning Agency 2009) rate of change fell well outside the range observed in our record of mangroves in MI.

Additionally, the estimated rate of sediment accretion as reconstructed from the age-depth model, indicates that the capacity to accumulate sediments in MI was enough for the sea-level change rates of the past 2300 years but it will probably not be in the future (average 2.2 mm/yr accretion against a 5 mm/yr rate of sea-level increase). Our result suggests that under current and future SLR, mangroves will need a migratory path inland to move and persist in the future. Therefore, in order to maintain the existence of mangroves forest in the MI region, mangrove reforestation along the coast and the creation of a buffer zone on the back of the current mangrove belt to allow for migratory dynamics to occur are needed to lessen adverse impact of SLR both for mangroves ecosystems and coastal populations.

Concluding remarks, open questions and recommendations

As shown in the introduction to my thesis, Sumatra supports a wide range type of ecosystems from the coastal forest to mountain rainforests. Despite this extensive landscape diversity and biodiversity, limited studies (Biagioni et al. 2015; Hapsari et al. 2017) have been conducted using palaeoecological methods to test drivers of change, resilience and dynamic of these ecosystems. With my research I could start finding first evidence of the importance of certain factors such as volcanism, herbivores grazing, rice cultivation and sea-level change.

Our record from Danau Njalau provides a new insight on vegetation and volcanic deposition association in Sumatra. While this record suggests that the effect of volcanism on the western side of Sumatra might be spatially and temporally important in shaping the composition and structure of this diverse rainforests, it should be noted this is a single case study and more records are needed to confirm these results. The good news is that Kerinci Seblat National Park provides many locations where such studies could be conducted.

We know from the archaeological records that cultivators were present in Sumatra for thousands of years (Morley 1982; Maloney 1996). However, physical evidence of the impact of humans on the landscape were certainly lacking. Our record from Danau Bento, while showing an early use of the grassland for buffaloes grazing also seems to indicate and increase in human use of the landscape in the Bronze Age period (ca. 3000 cal yr BP). During this phase in Kerinci rice cultivation expanded also in the less suitable areas like the Bento swamp. Similar results were found in the North of Sumatra, in the Toba region (Maloney 1996). Why did that happened? Was a consequence of population expansion or technological advancement? These are all open questions currently missing an answer. Interestingly, in Danau Bento we found that human were constantly managing the vegetation in this area since 4500 years, and intensified after 2500 years ago. It turned out that the protected swamp forest today present at the site is just a remnant of a much larger swamp forest, which is not there now for thousands of years due to human activities.

It has been long debated how we could protect mangroves forests in the face of the increase in sea-level currently occurring and projected in the next future due to climate change. An important part of this discussion should be on how sensitive the mangroves are to estimated rate of change and how much they can adapt. Using palaeoecological methods we can improve our understanding of the sensibilities of these important ecosystems, and help manage them in a more realistic way. Our results from the Mendahara Ilir mangroves show that this mangrove were easily adapting to the changes in sea-level which occurred in the past 2300 years. They were moving inland and outward depending on the sea-level tendency and the sediment accretion was high enough to cope with sea-level rise. Despite this could be seen as a good news, we also found that the rate at which these changes were occurring are much lower than the one projected (average 2.2 mm/yr accretion against a 5 mm/yr rate of sea-level increase). Even with a lower rate the mangroves needed space to move inland. Currently this is impeded

in Mendahara Ilir due to urbanization and agricultural practices which favour the coastal regions. Based on our results we can infer that land use will have to change in the area, if mangroves are to be preserved under future scenarios of change. The greatest limitation of our study was the lack of solid data on the sea level change in the past two millennia. While it is useful to study Quaternary and early Holocene changes, these are conditions which is not realistic for future scenarios in Indonesia. More effort should be put on obtaining high resolution records of sea level change for the past 2000 years.

With my research I hope I could show the value that can be obtaining from investigating the Palaeoecology of tropical ecosystems. More should be done however, if we are to gain a deep understanding of the dynamics, characteristic and stability of these diverse tropical ecosystems.

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Appendix A

Identified pollen, spores and non-pollen palynomorphs (NPP) of the records – complete list and photos of selected taxa

Appendix A1: Table of identified pollen, spores and NPP taxa

Abbreviations for palynological records:

DN: Danau Njalau (Chapter 4)

DB: Danau Bento (Chapter 5)

MI: Mendahara Ilir (Chapter 6)

Pollen

| Family | Pollen type | Photo no. | Records |
|-------------------------------|------------------------------|-----------|------------|
| Acanthaceae | Acanthaceae | 1 | DB |
| | <i>Avicennia</i> | 2 | MI |
| Actinidiaceae | <i>Saurauia</i> | 3 | DN, DB |
| Altingiaceae | <i>Liquidambar</i> | | MI |
| Amaranthaceae | Amaranthaceae | 4 | DB |
| Anacardiaceae | Anacardiaceae | | DB |
| | <i>Campnosperma</i> | 5 | DB |
| Annonaceae | Annonaceae | 6 | DN, DB |
| Apocynaceae | Apocynaceae | | MI |
| Aquifoliaceae | <i>Ilex</i> | 7 | DN, DB, MI |
| Araceae | <i>Colocasia</i> | | MI |
| Arecaceae | Arecaceae | 8 | MI |
| | <i>Arenga</i> | 9 | DN, MI |
| | <i>Calamus</i> | | DN |
| | <i>Cocos</i> | | MI |
| | <i>Livistona</i> | | DN |
| | <i>Nypa</i> | | MI |
| | <i>Oncosperma</i> | 10 | DN, MI |
| Asteraceae | Asteraceae | 11 | DN, DB, MI |
| Burseraceae | <i>Canarium</i> | 12 | DN |
| Cannabaceae | <i>Celtis</i> | 13 | DN, DB, MI |
| | <i>Trema</i> | 14 | DN, DB, MI |
| Caprifoliaceae | Caprifoliaceae | 15 | DB |
| Casuarinaceae/Myricaceae | <i>Casuarina/Myrica</i> | 16 | DN, DB, MI |
| Celastraceae | Celastraceae | 17 | DN, DB |
| | <i>Lophopetalum</i> | | MI |
| Clusiaceae | <i>Calophyllum</i> | | DN, MI |
| Combretaceae | <i>Lumnitzera</i> | 18 | MI |
| Combretaceae /Melastomataceae | Combretaceae/Melastomataceae | 19 | DN, DB |
| Compositae | <i>Ambrosia</i> | | DN |
| | <i>Vernonia</i> | 20 | DN, DB, MI |
| Cyperaceae | Cyperaceae | 21 | DN, DB,MI |
| Dipterocarpaceae | Dipterocarpaceae | 22 | DN, MI |

| Family | Pollen type | Photo no. | Records |
|-----------------------------|--------------------------------|-----------|------------|
| Dipterocarpaceae | <i>Dipterocarpus</i> | | DN, MI |
| | <i>Shorea</i> | | DB |
| Ebenaceae | <i>Diospyros</i> | 23 | DN, DB |
| Elaeocarpaceae | <i>Elaeocarpus</i> | 24 | DN, DB, MI |
| Ericaceae | Ericaceae | 25 | DN, MI |
| | <i>Vaccinium</i> | | DB |
| Euphorbiaceae | <i>Acalypha</i> | 26 | DN |
| | <i>Blumeodendron</i> | | DN, MI |
| | Euphorbiaceae | | DB |
| | <i>Excoecaria</i> | 27 | MI |
| | <i>Homalanthus</i> | 27 | DN, DB |
| | <i>Mallotus/Macaranga</i> | 27 | DN, DB, MI |
| Fabaceae | Fabaceae | 27 | DN, DB |
| | <i>Mimosoideae</i> | | DN, MI |
| | <i>Lithocarpus/Castanopsis</i> | 31 | DN, DB, MI |
| | <i>Quercus</i> | | DB |
| Flacourtiaceae | Flacourtiaceae | 32 | DN |
| Gnetaceae | <i>Gnetum</i> | 33 | DN, DB |
| Hamamelidaceae | Hamamelidaceae | | DN |
| Juglandaceae | <i>Engelhardia</i> | 34 | DN, DB, MI |
| Lauraceae | <i>Lauraceae</i> | | DN |
| Leguminosae | <i>Acacia</i> | | DN |
| | Leguminosae | | MI |
| Liliaceae/Iridaceae | Liliaceae/Iridaceae | | DN |
| Loranthaceae | Loranthaceae | 35 | DN, DB, MI |
| Lythraceae | <i>Sonneratia</i> | 36 | MI |
| Malpighiaceae | Malpighiaceae | | DN |
| Malvaceae | Malvaceae | 37 | DN |
| | Tilioideae | 38 | DN, DB |
| Malvaceae (Bombacoideae) | <i>Durio</i> | | DB |
| Malvaceae (Brownlowioideae) | <i>Brownlowia</i> type | | DB |
| Melastomataceae | Melastomataceae | | DN |
| Meliaceae | <i>Aglaia</i> | 39 | DN |
| | <i>Dysoxylum</i> | 40 | DN, DB, MI |
| | <i>Xylocarpus</i> | 41 | MI |
| Menispermaceae | Menispermaceae | | DN |
| | <i>Stephania</i> | | MI |
| Moraceae | <i>Ficus</i> | 43 | DN, DB, MI |
| Moraceae/Urticaceae | Moraceae/Urticaceae | 42 | DN, DB, MI |
| Myristicaceae | Myristicaceae | 44 | DN, DB, MI |
| Myrsinaceae | Myrsinaceae | | DB |
| | <i>cf. Aegiceras</i> | 45 | DN |
| Myrtaceae | Myrtaceae | 46 | DN, DB, MI |

| Family | Pollen type | Photo no. | Records |
|------------------|--------------------|-----------|------------|
| Oleaceae | <i>Ligustrum</i> | 48 | DB |
| | Oleaceae | 47 | DN |
| Pandanaceae | <i>Pandanus</i> | 49 | DN, DB, MI |
| Pentaphylacaceae | <i>Eurya</i> | 50 | DB |
| Phyllanthaceae | <i>Antidesma</i> | 51 | DN, DB, MI |
| | <i>Baccaurea</i> | 52 | DN, MI |
| | <i>Bischofia</i> | 53 | DN |
| | <i>Glochidion</i> | 54 | DN, DB, MI |
| | <i>Phyllanthus</i> | 55 | DN, MI |
| Pinaceae | <i>Pinus</i> | 56 | DN |
| Piperaceae | <i>Peperomia</i> | | MI |
| Plantaginaceae | <i>Plantago</i> | | DB |
| Poaceae | Poaceae (large) | 57 | DN, DB, MI |
| | Poaceae (small) | 58 | DN, DB, MI |
| Podocarpaceae | <i>Dacrydium</i> | 59 | DN, DB |
| | <i>Podocarpus</i> | 60 | DN, DB |
| Potamogetonaceae | <i>Potamogeton</i> | | DB |
| Primulaceae | <i>Maesa</i> type | | MI |
| | <i>Myrsine</i> | 61 | DB |
| Proteaceae | <i>Helicia</i> | | MI |
| Rhizophoraceae | <i>Bruguiera</i> | 62 | MI |
| | <i>Rhizophora</i> | 63 | MI |
| Rosaceae | <i>Prunus</i> | 64 | DN, DB |
| | Rosaceae | | DN |
| Rubiaceae | <i>Canthium</i> | 65 | DB |
| Rubiaceae | <i>Gardenia</i> | | DN |
| | <i>Nauclea</i> | 66 | DN, MI |
| | <i>Randia</i> | 67 | DN, MI |
| | Rubiaceae | 68 | DN, DB |
| | <i>Timonius</i> | 69 | DB, MI |
| Rutaceae | <i>Melicope</i> | 70 | DB |
| | Rutaceae | 71 | DN, MI |
| | <i>Zanthoxylum</i> | 72 | DN, DB |
| Sapindaceae | <i>Filicium</i> | 73 | DB |
| | <i>Pometia</i> | 74 | DN, MI |
| | Sapindaceae | 75 | DN |
| Sapotaceae | Sapotaceae | 76 | DN, MI |
| Stemonuraceae | <i>Stemonurus</i> | 77 | MI |
| Typhaceae | <i>Typha</i> | | DB |
| Verbenaceae | Verbenaceae | 78 | DN |
| Vitaceae | <i>Leea</i> | 79 | DN |
| Winteraceae | <i>Drymis</i> | 80 | DB |

Spores




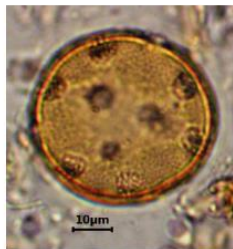
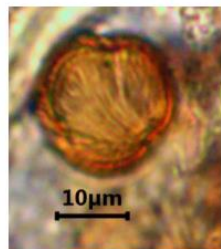

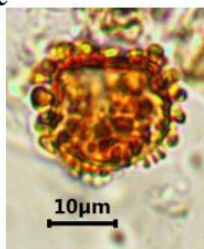


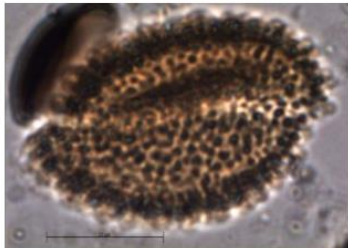
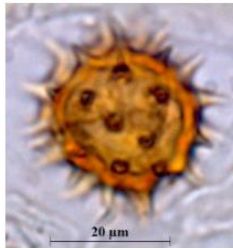

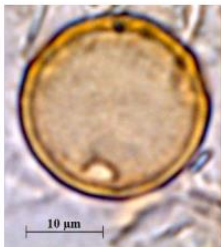
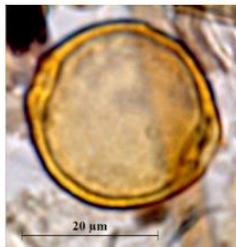

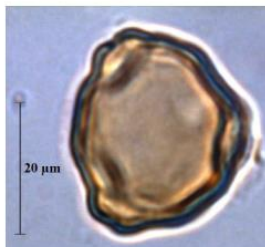
| Family | Spore type | Photo no. | Records |
|------------------|-------------------------------|-----------|------------|
| Aspleniaceae | Aspleniaceae | | MI |
| Blechnaceae | <i>cf. Blechnum</i> | 81 | DB |
| | <i>Stenochlaena palustris</i> | 82 | DN, DB |
| Cyatheaceae | <i>Cyathea</i> | 83 | DN, DB, MI |
| Davalliaceae | <i>Davalia</i> | 84 | DN, DB |
| Dicksoniaceae | <i>Dicksonia</i> | 85 | DB |
| Dryopteridaceae | <i>Arachniodes</i> | 86 | DB |
| | <i>Ctenitis</i> | 87 | DB |
| Hypodematiaceae | <i>Leucostegia</i> | 88 | DB |
| Lindsaeaceae | <i>Lindsaea</i> | 89 | DB |
| Lycopodiaceae | <i>Huperzia</i> | 90 | DB |
| | <i>Lycopodiella cernua</i> | 91 | DB |
| | <i>Lycopodium</i> | 92 | DN, DB, MI |
| Lygodiaceae | <i>Lygodium</i> | 93 | DB |
| Marattiaceae | <i>Angiopteris</i> | 94 | DB |
| | Marattiaceae | 95 | DN |
| Nephrolepidaceae | <i>Nephrolepis</i> | 96 | MI |
| Ophioglossaceae | <i>Ophioglossum</i> | 97 | DN, DB |
| Polypodiaceae | <i>Phymatosorus</i> | 98 | DN, DB, MI |
| | Polypodiaceae | | DN, DB, MI |
| | <i>Polypodium</i> | | DB |
| Pteridaceae | <i>Acrostichum aureum</i> | 99 | MI |
| | <i>cf. Adiantum</i> | 100 | DB |
| | <i>Pteris</i> | | DN, DB |
| Schizaeaceae | <i>Schizaea</i> | 101 | DN |
| Selaginellaceae | <i>Selaginella</i> | 102 | DN, DB |
| Thelypteridaceae | <i>Thelypteris</i> | 103 | DN, MI |



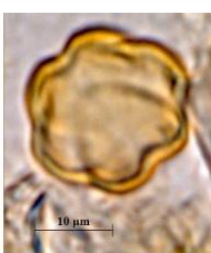
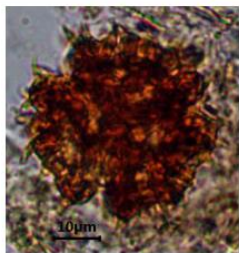

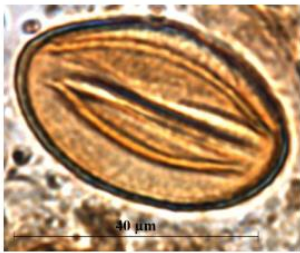
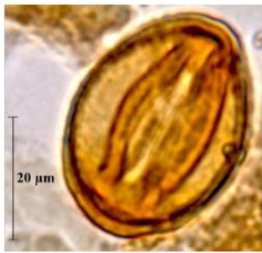
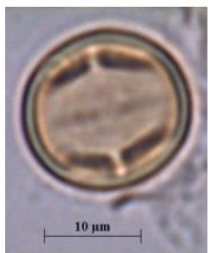


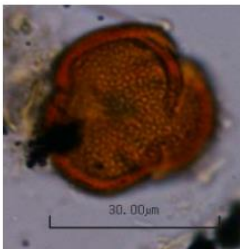
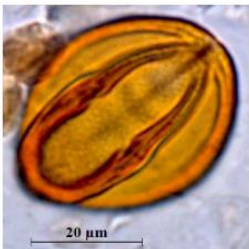
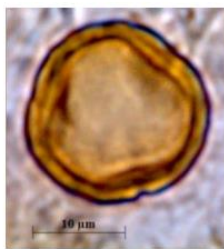
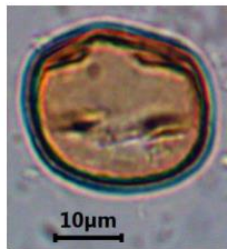
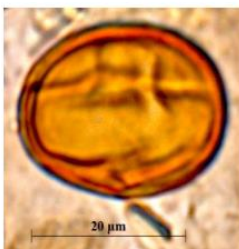
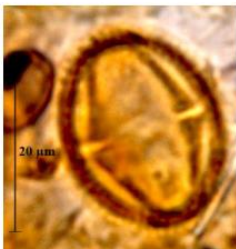
Non-pollen palynomorphs


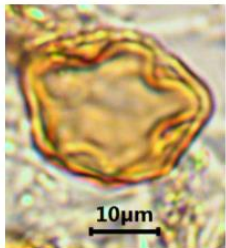
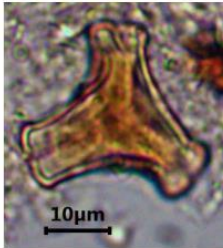



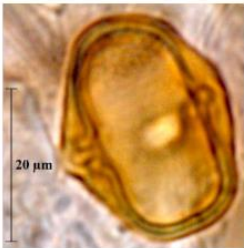
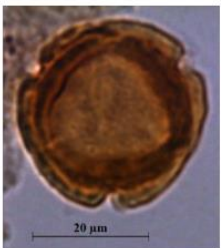
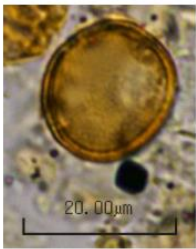
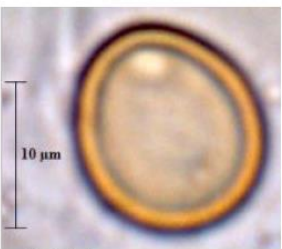
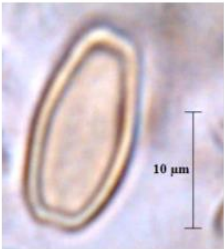
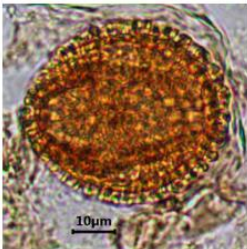
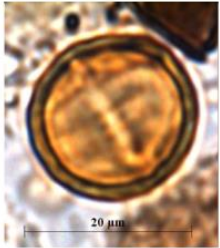
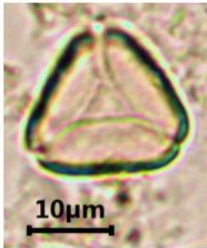
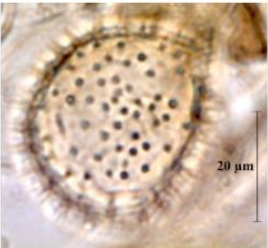
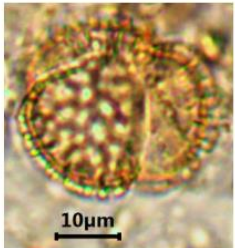
| Family | NPPs type | Photo no. | Records |
|----------------------|---------------------------------|-----------|---------|
| Aliquandostipitaceae | <i>Megalohypha aqua-dulces</i> | 104 | DB |
| Botryococcaceae | <i>Botryococcus</i> | 105 | DN |
| Dothideomycetidae | <i>Potamomyces</i> | 106 | DB |
| Glomeraceae | <i>Glomus</i> | 107 | DN, DB |
| Lasiochaeraceae | <i>Cercophora</i> | 108 | DB |
| Phaeotrichaceae | <i>cf. Trichodelitchia</i> | 109 | DB |
| Sordariaceae | <i>Sordaria</i> | 110 | DB |
| Teichosporaceae | <i>Byssothecium</i> | 111 | DB |
| Xylariaceae | <i>Xylariaceae</i> | 112 | DB |
| | <i>cf. Kretzschmaria clavus</i> | 113 | DB |
| Unknown type | <i>Ustilina deusta</i> | 114 | DB |
| | Type HdV-1010 | 115 | DB |
| | Type UG-1095 | 116 | DB |
| | Type UG-1085 | 117 | DB |
| | Type UG-1311 | 118 | DB |
| | Type UG-1307 | 119 | DB |
| | Type UG-1320 | 120 | DB |

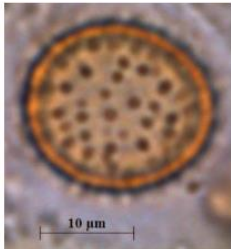
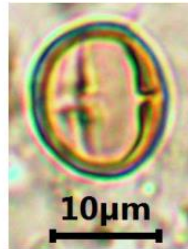



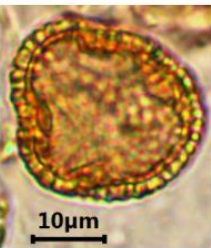
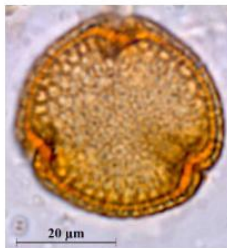

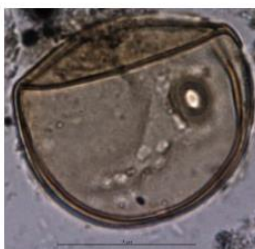


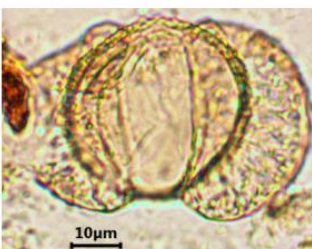
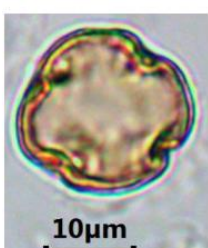


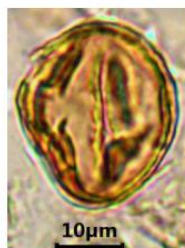
Appendix A2: Plates of selected pollen, spores and NPP taxa

Pollen

| | | | |
|---|---|--|---|
| Acanthaceae | | Actinidiaceae | Amaranthaceae |
|  |  |  |  |
| 1) Acanthaceae | | 2) <i>Avicennia</i> | 3) <i>Saurauia</i> |
| Anacardiaceae | | Annonaceae | Aquifoliaceae |
|  |  |  |  |
| 5) <i>Camptosperma</i> | | 6) Annonaceae | 7) <i>Ilex</i> |
| Arecaceae | | Asteraceae | Burseraceae |
|  |  |  |  |
| 9) <i>Arenga</i> | | 10) <i>Oncosperma</i> | 11) Asteraceae |
| Cannabaceae | | Caprifoliaceae | Casuarinaceae |
|  |  |  |  |
| 13) <i>Celtis</i> | | 14) <i>Trema</i> | 15) Caprifoliaceae |
| | | | 16) <i>Casuarina</i> |

| | | | |
|---|---|--|---|
| Celastraceae | Combretaceae | Combretaceae/ Melastomataceae | Compositae |
|  |  |  |  |
| 17) Celastraceae | 18) <i>Lumnitzera</i> | 19) Melastomataceae | 20) <i>Vernonia</i> |
| Cyperaceae | Dipterocarpaceae | Ebenaceae | Elaeocarpaceae |
|  |  |  |  |
| 21) Cyperaceae | 22) Dipterocarpaceae | 23) <i>Diospyros</i> | 24) <i>Elaeocarpus</i> |
| Ericaceae | Euphorbiaceae | | |
|  |  |  |  |
| 25) Ericaceae | 26) <i>Acalypha</i> | 27) <i>Excoecaria</i> | 28) <i>Homalanthus</i> |
| Euphorbiaceae | Fabaceae | Fagaceae | Flacourtiaceae |
|  |  |  |  |
| 29) <i>Mallotus/Macaranga</i> | 30) Fabaceae | 31) <i>Lithocarpus</i> | 32) Flacourtiaceae |




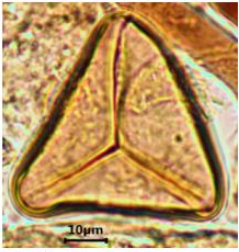
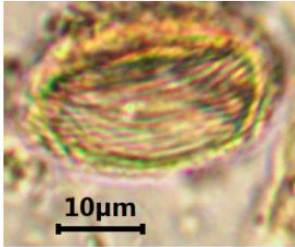
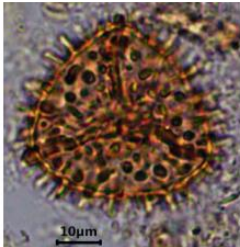

| | | | |
|---|---|--|---|
| Gnetaceae | Juglandaceae | Loranthaceae | Lythraceae |
|  |  |  |  |
| 33) <i>Gnetum</i> | 34) <i>Engelhardia</i> | 35) Loranthaceae | 36) <i>Sonneratia</i> |
| Malvaceae | | Meliaceae | |
|  |  |  |  |
| 37) Malvaceae | 38) Tilioideae | 39) <i>Aglaia</i> | 40) <i>Dysoxylum</i> |
| Meliaceae | Moraceae/Urticaceae | Moraceae | Myristicaceae |
|  |  |  |  |
| 41) <i>Xylocarpus</i> | 42) Moraceae | 43) <i>Ficus</i> | 44) Myristicaceae |
| Myrsinaceae | Myrtaceae | Oleaceae | |
|  |  |  |  |
| 45) <i>cf. Aegiceras</i> | 46) Myrtaceae | 47) Oleaceae | 48) <i>Ligustrum</i> |

| | | | |
|--|---|---|--|
| Pandanaceae | Pentaphylacaceae | Phyllanthaceae | |
|  49) <i>Pandanus</i> |  50) <i>Eurya</i> |  51) <i>Antidesma</i> |  52) <i>Baccaurea</i> |
| Phyllanthaceae | | Pinnaceae | |
|  53) <i>Bischofia</i> |  54) <i>Glochidion</i> |  55) <i>Phyllanthus</i> |  56) <i>Pinus</i> |
| Poaceae | | Podocarpaceae | |
|  57) Poaceae (Large) |  58) Poaceae (Small) |  59) <i>Dacrydium</i> |  60) <i>Podocarpus</i> |
| Primulaceae | Rhizophoraceae | | Rosaceae |
|  61) <i>Myrsine</i> |  62) <i>Bruguiera</i> |  63) <i>Rhizophora</i> |  64) <i>Prunus</i> |

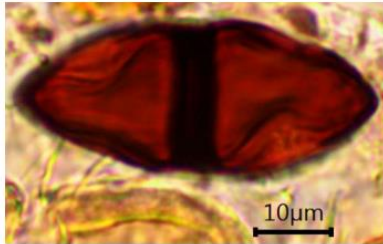
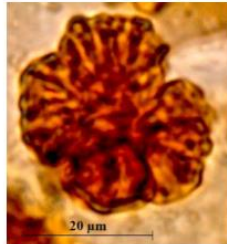
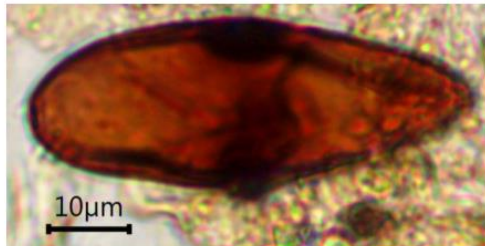

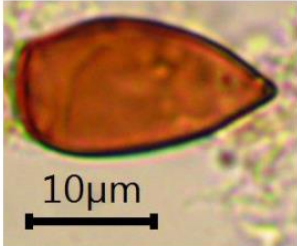
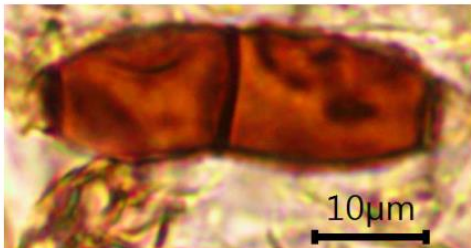
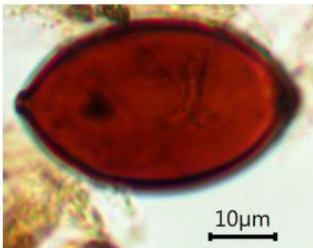
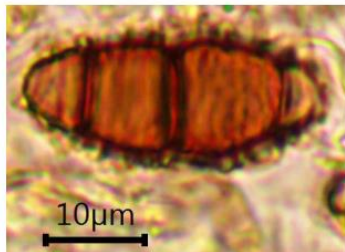
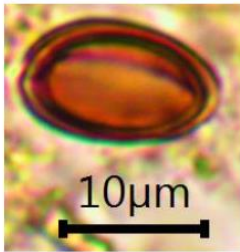
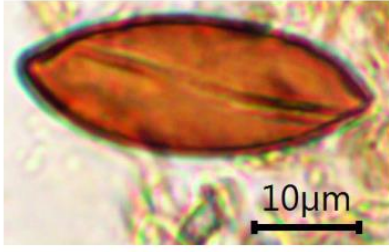
| | | | |
|--|---|--|--|
| Rubiaceae | | | |
|  65) <i>Canthium</i> |  66) <i>Nauclea</i> |  67) <i>Randia</i> |  68) <i>Rubiaceae</i> |
| Rubiaceae | Rutaceae | | |
|  69) <i>Timonius</i> |  70) <i>Melicope</i> |  71) <i>Rutaceae</i> |  72) <i>Zanthoxylum</i> |
| Sapindaceae | | | Sapotaceae |
|  73) <i>Filicium</i> |  74) <i>Pometia</i> |  75) <i>Sapindaceae</i> |  76) <i>Sapotaceae</i> |
| Stemonuraceae | Verbenaceae | Vitaceae | Winteraceae |
|  77) <i>Stemonurus</i> |  78) <i>Verbenaceae</i> |  79) <i>Leea</i> |  80) <i>Drymis</i> |

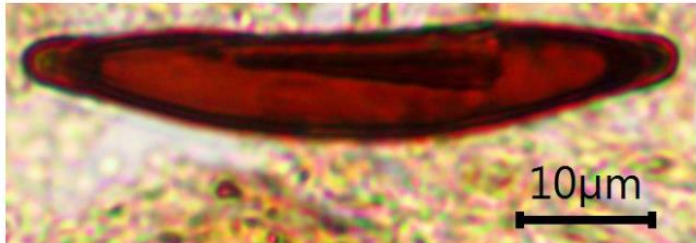
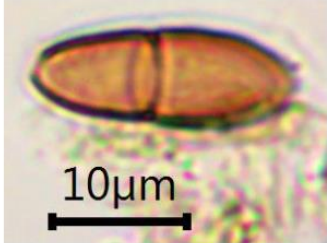
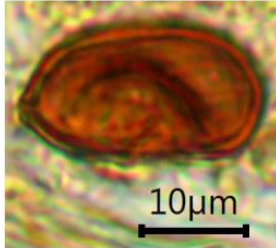
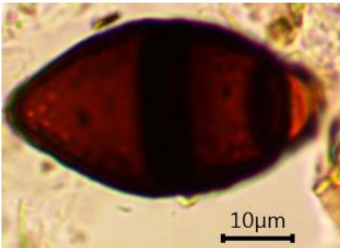
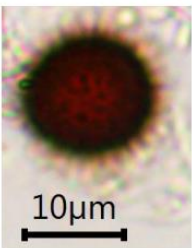
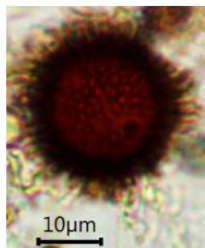
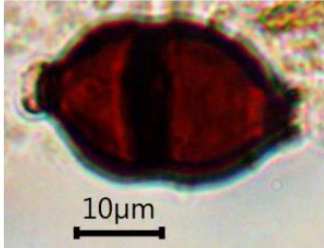
Spores

| | | | |
|--|--|--|---|
| Blechnaceae 81) <i>Blechnum</i> | | Cyatheaceae 83) <i>Cyathea</i> | Davalliaceae 84) <i>Davallia</i> |
| Dicksoniaceae 85) <i>Dicksonia</i> | Dryopteridaceae 86) <i>Arachniodes</i> | | Hypodematiaceae 88) <i>Leucostegia</i> |
| Lindsaeaceae 89) <i>Lindsaea</i> | Lycopodiaceae 90) <i>Huperzia</i> | | |
| | 91) <i>Lycopodiella cernua</i> | 92) <i>Lycopodium</i> | |
| Lygodiaceae 93) <i>Lygodium</i> | Marattiaceae 94) <i>Angiopteris</i> | | Nephrolepidaceae 96) <i>Nephrolepis</i> |
| | 95) <i>Marattiaceae</i> | | |

| Ophioglossaceae | Polypodiaceae | Pteridaceae | |
|--|---|---|---|
|  <p>97) <i>Ophioglossum</i></p> |  <p>98) <i>Phymatosorus</i></p> |  <p>99) <i>Acrostichum aureum</i></p> |  <p>100) cf. <i>Adiantum</i></p> |
| Schizaeaceae | Selaginellaceae | Thelypteridaceae | |
|  <p>101) <i>Schizaea</i></p> |  <p>102) <i>Selaginella</i></p> |  <p>103) <i>Thelypteris</i></p> | |

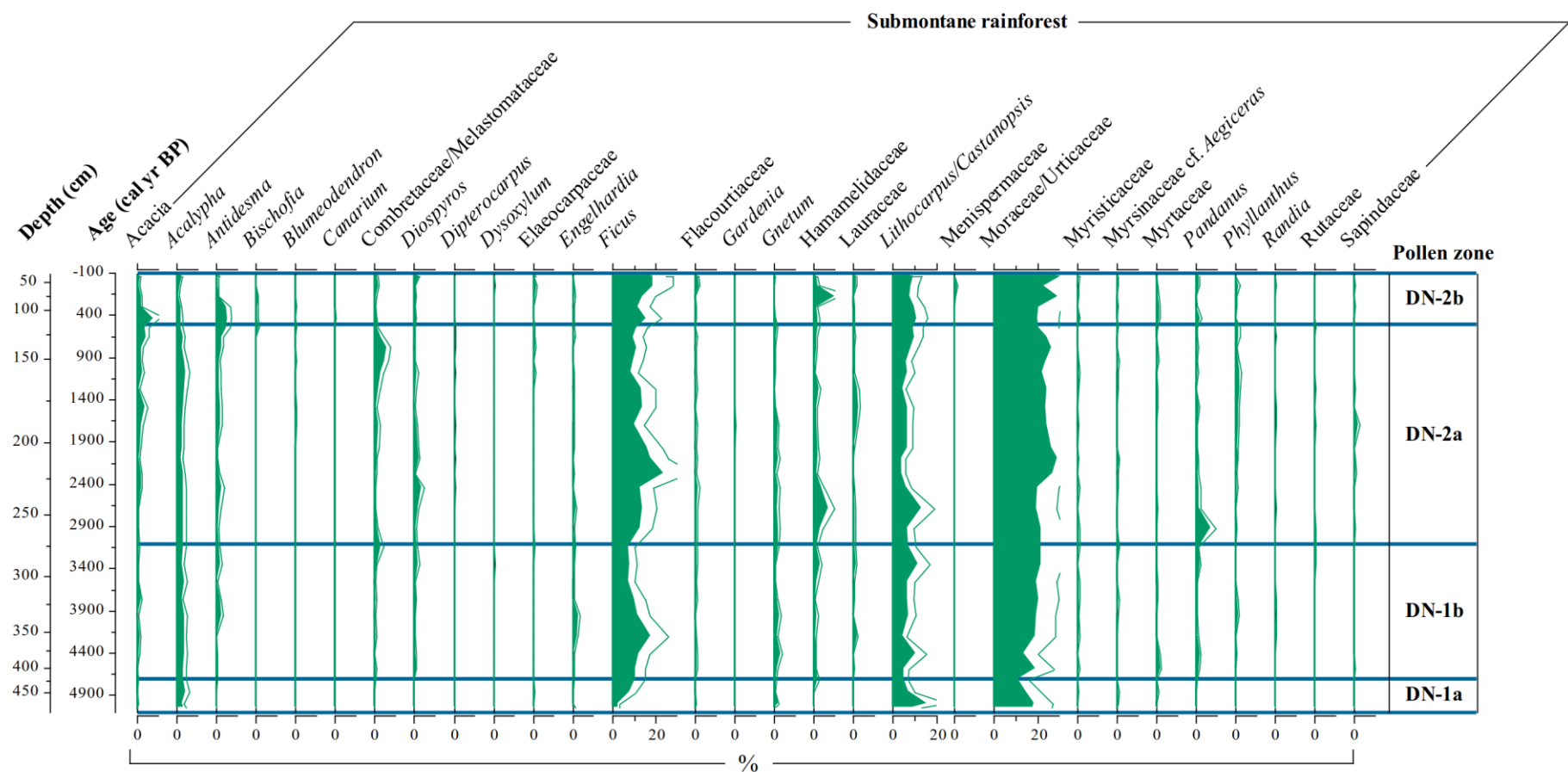
Non-pollen palynomorphs

| | | | |
|---|---|--|--|
| Aliquandostipitaceae | | Botryococcaceae | |
|  | |  | |
| 104) <i>Megalohypha aqua-dulces</i> | | 105) <i>Botryococcus</i> | |
| Dothideomycetidae | | Glomeraceae | Lasiosphaeriaceae |
|  | |  |  |
| 106) <i>Potamomyces</i> | | 107) <i>Glomus</i> | 108) <i>Cercophora</i> |
| Phaeotrichaceae | | Sordariaceae | |
|  | |  | |
| 109) cf. <i>Trichodelitschia</i> | | 110) <i>Sordaria</i> | |
| Teichosporaceae | Xylariaceae | | |
|  |  |  | |
| 111) <i>Byssothecium</i> | 112) Xylariaceae | 113) <i>Kretzschmaria clavus</i> | |

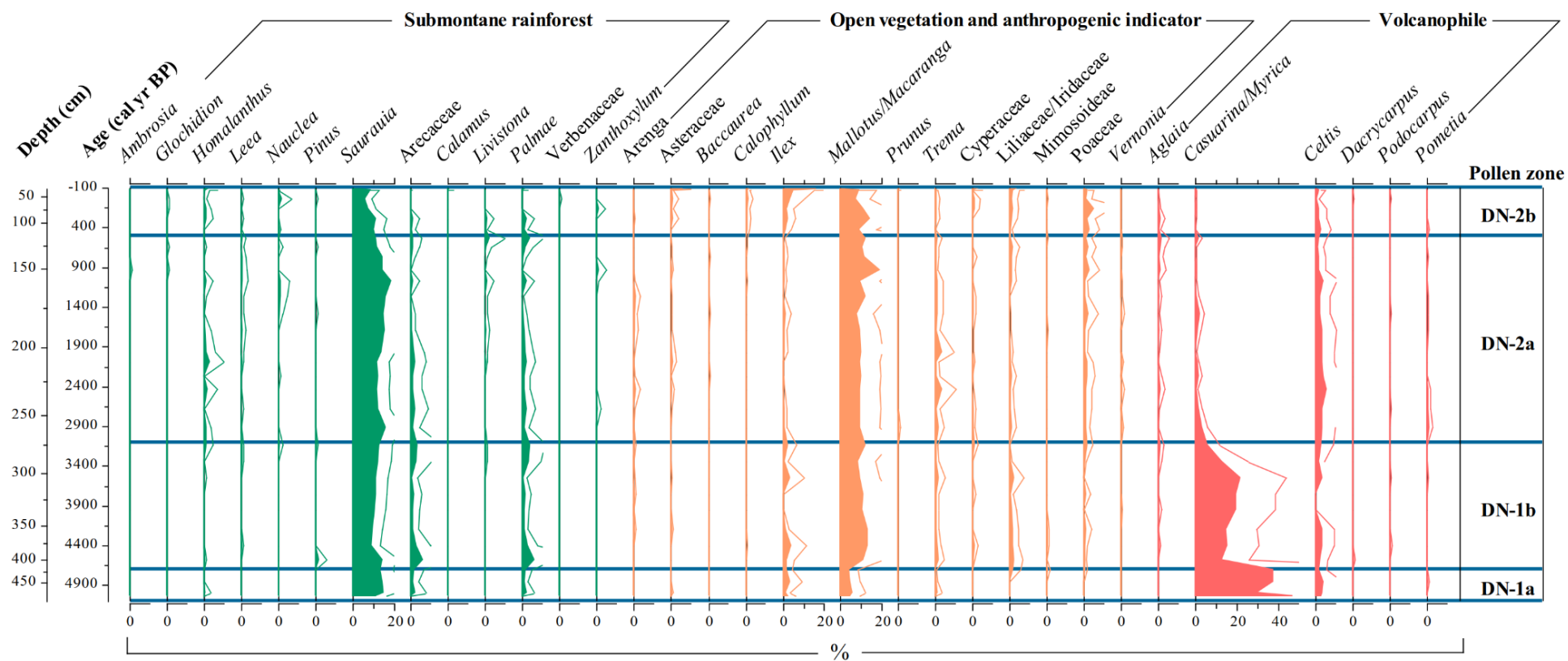
| | |
|--|---|
| Xylariaceae | Unknown type |
|  114) <i>Ustulina deusta</i> |  115) Type Hdv-1010 |
| Unknown type | |
|  116) Type UG-1095 |  117) Type UG-1085 |
|  118) Type UG-1311 |  119) Type UG-1307 |
| Unknown type | |
|  120) Type UG-1320 | |

Appendix B

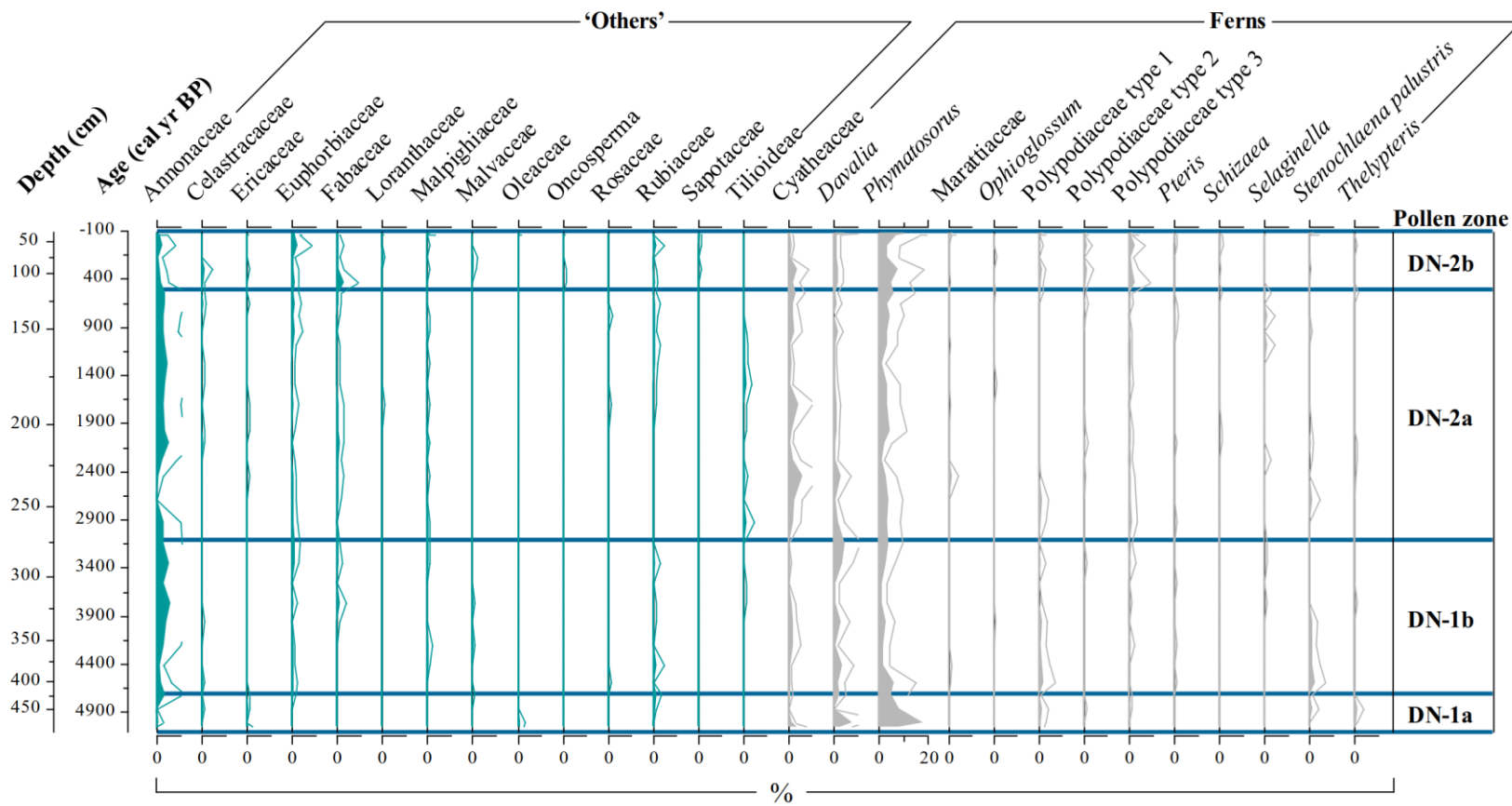
Complete pollen, spores, non-pollen palynomorphs and charcoal records



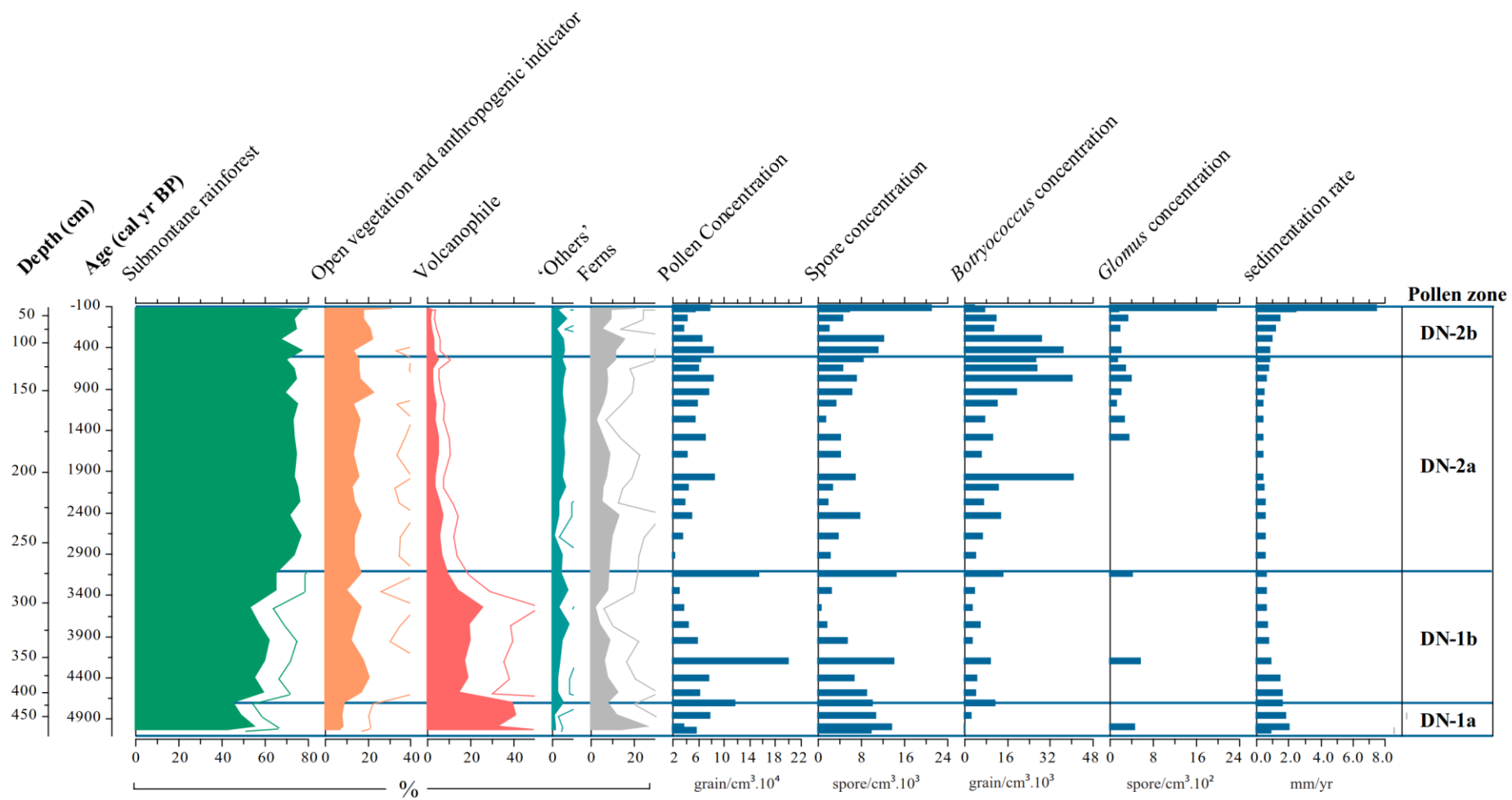
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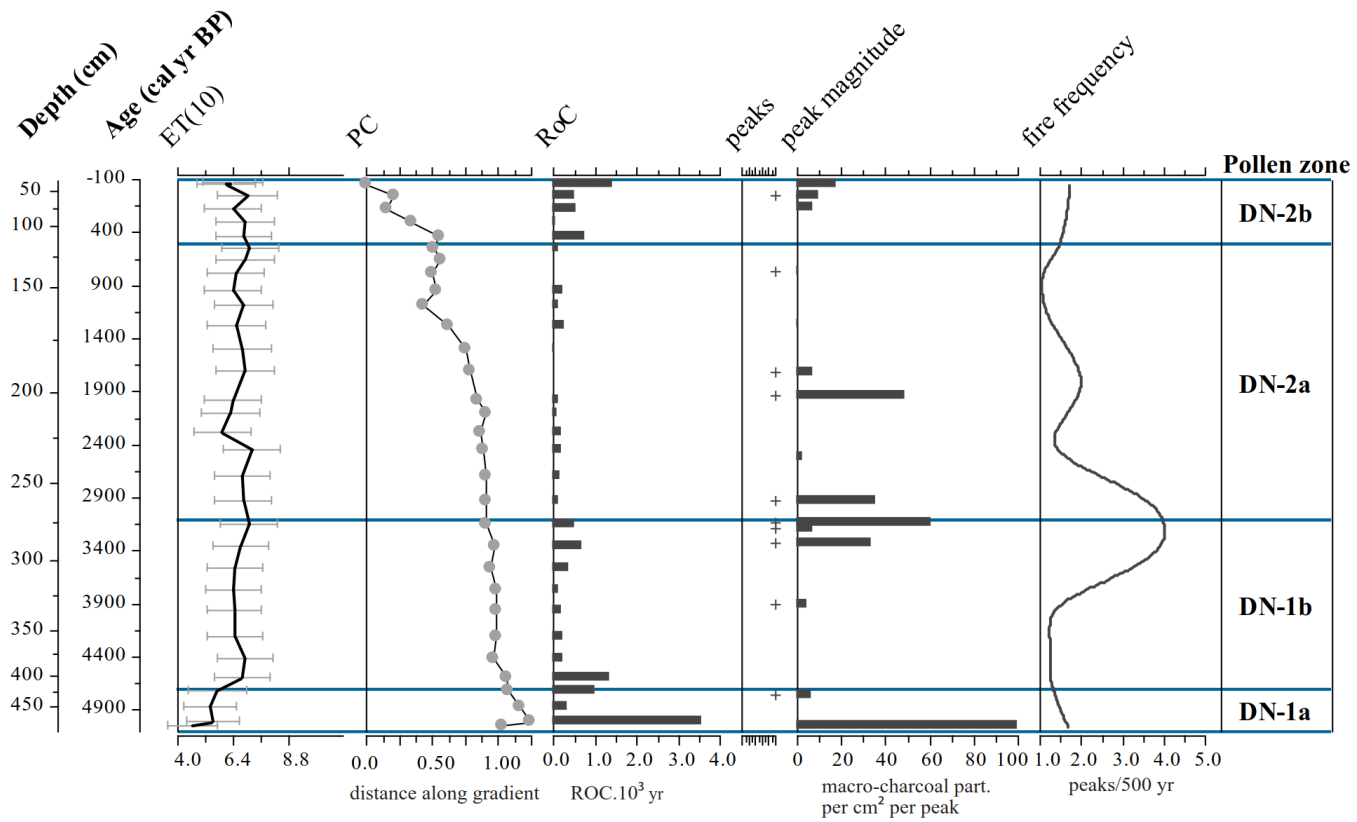


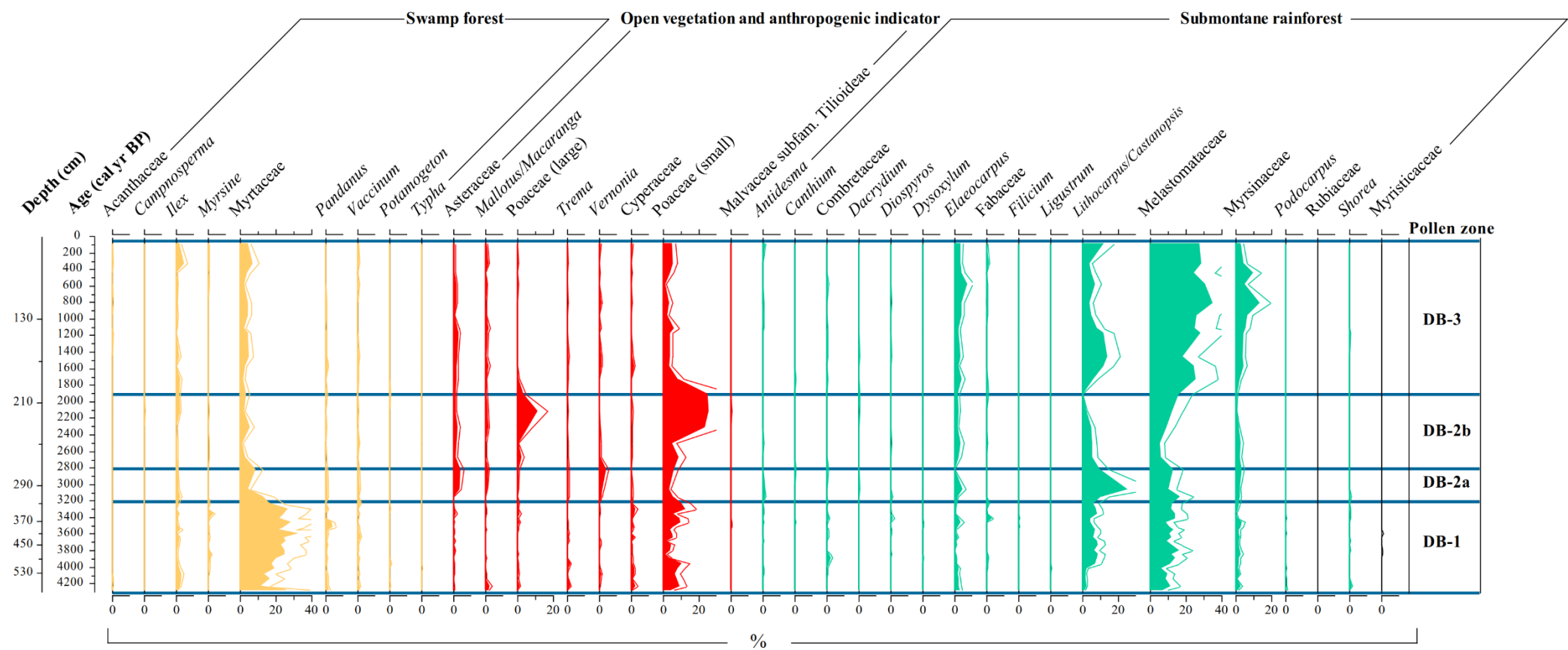
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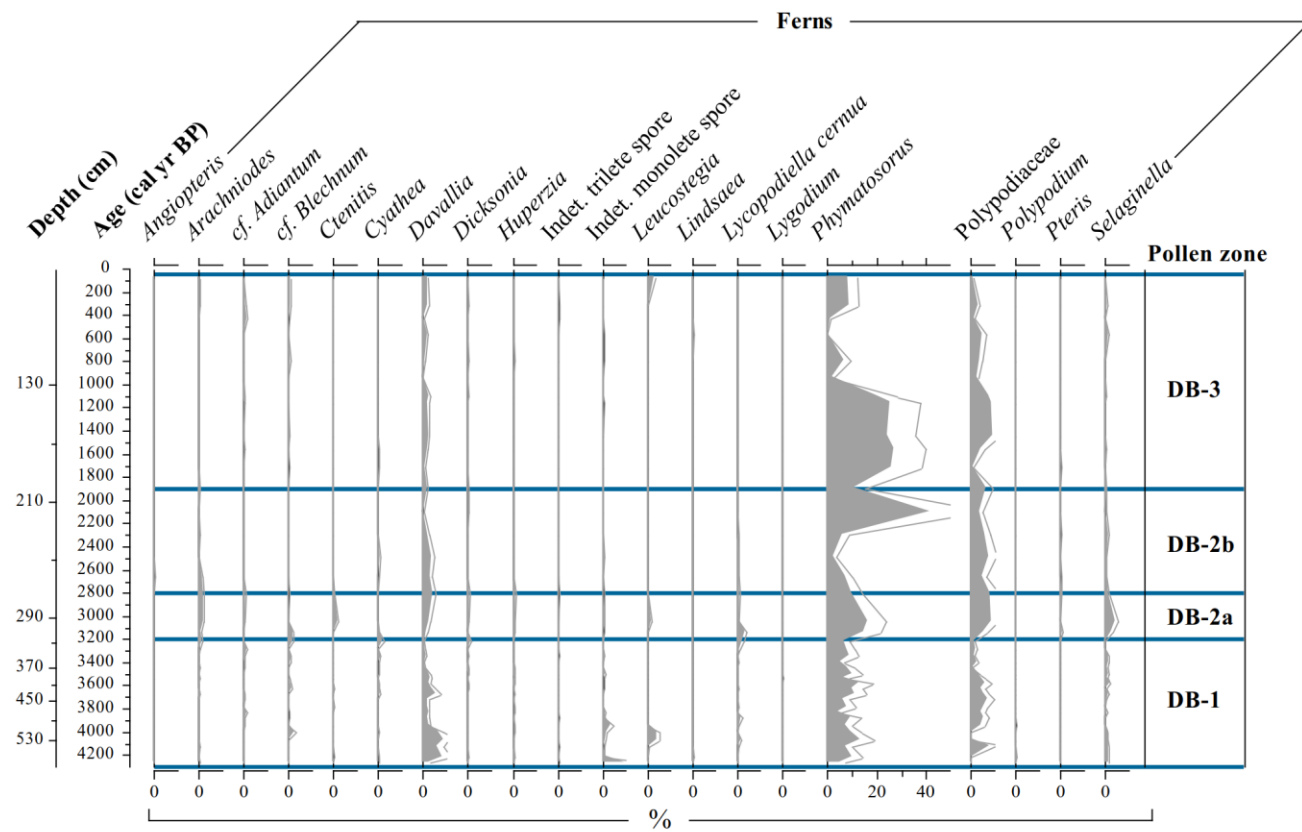
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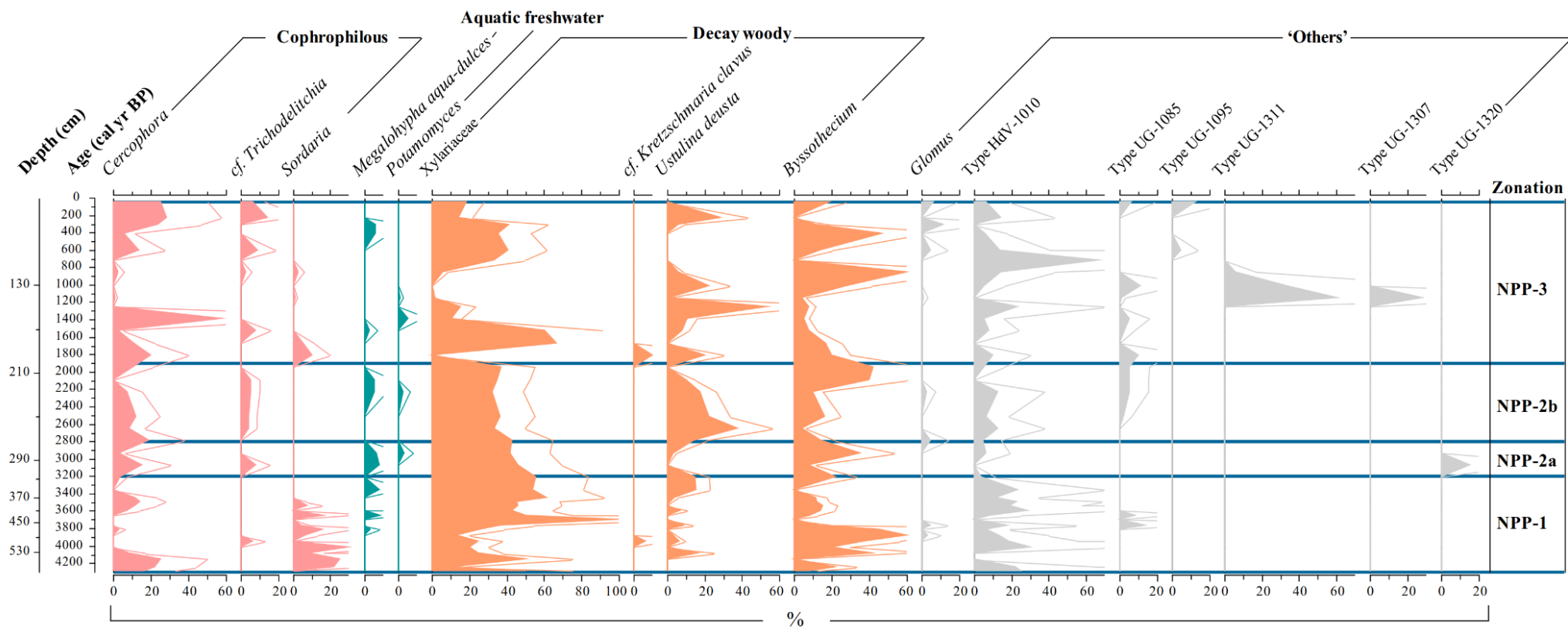


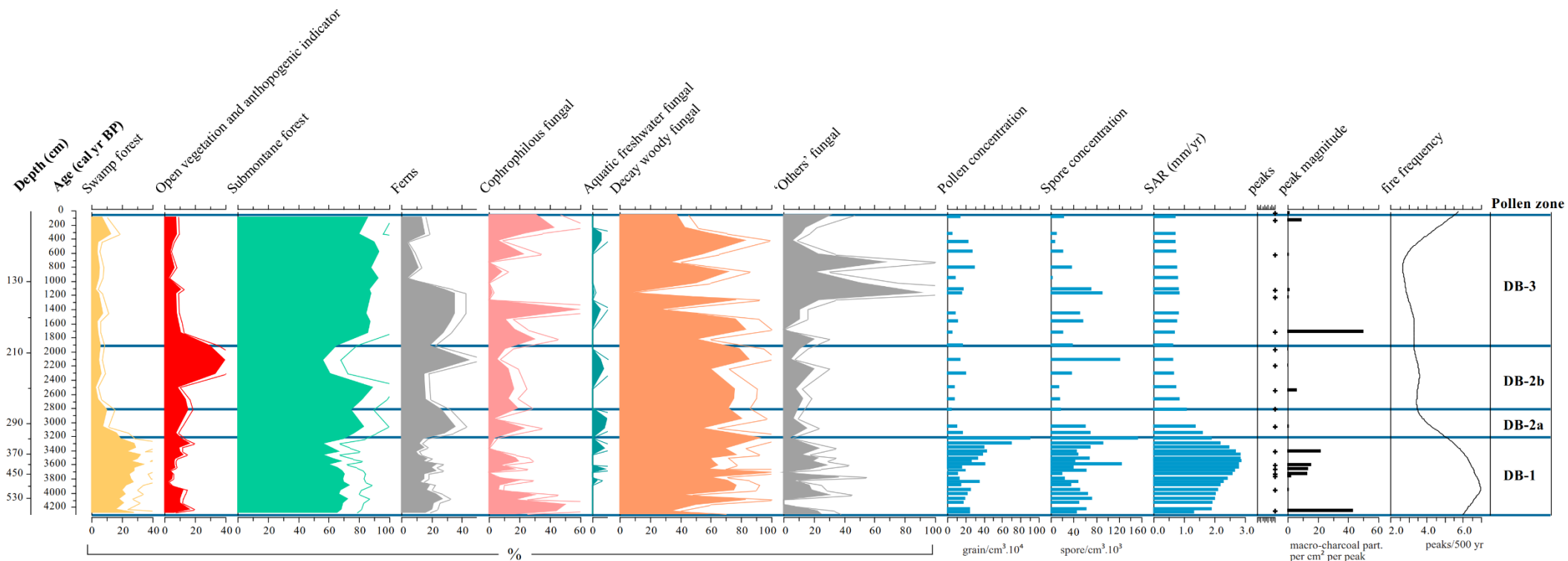


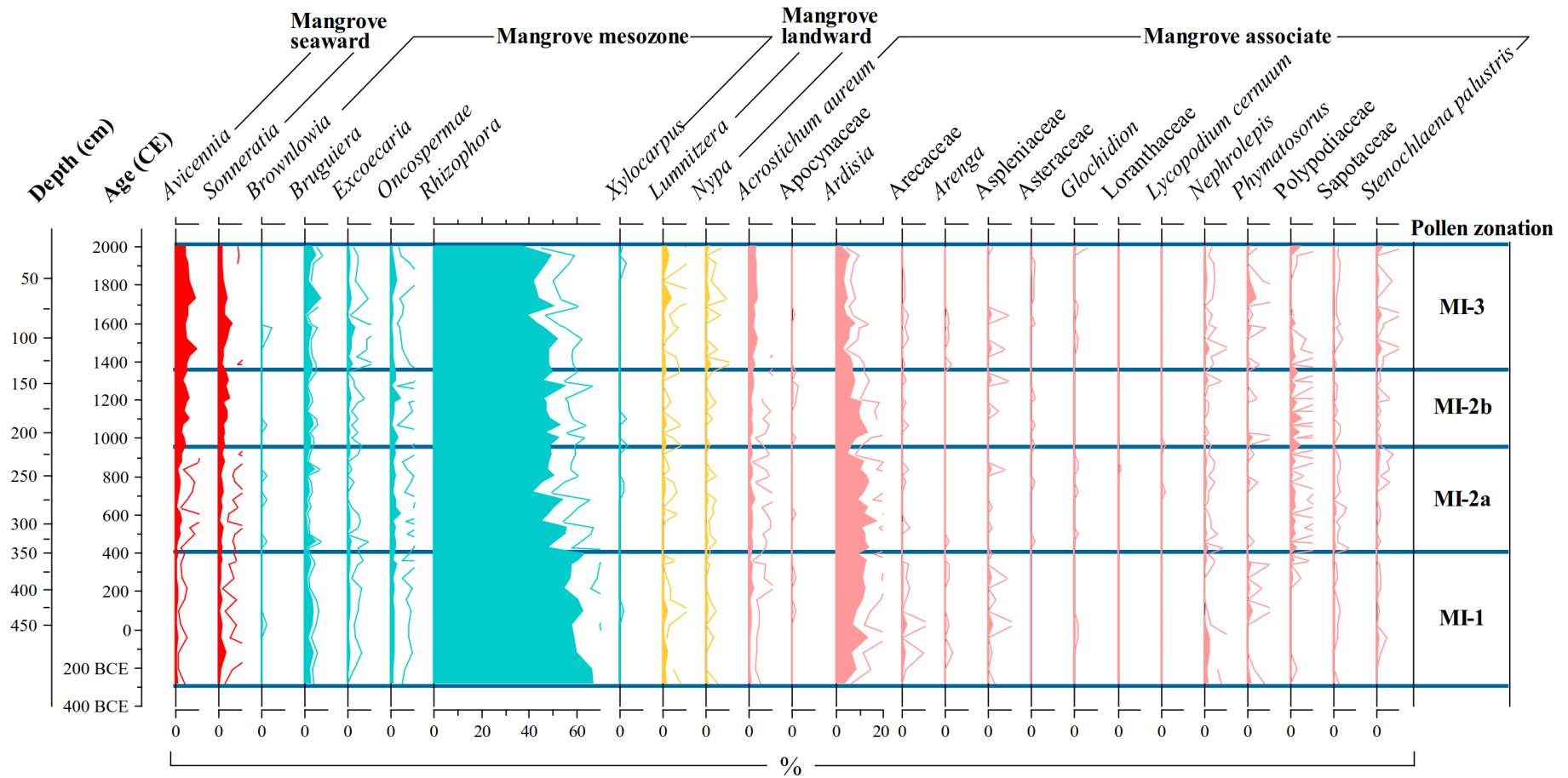


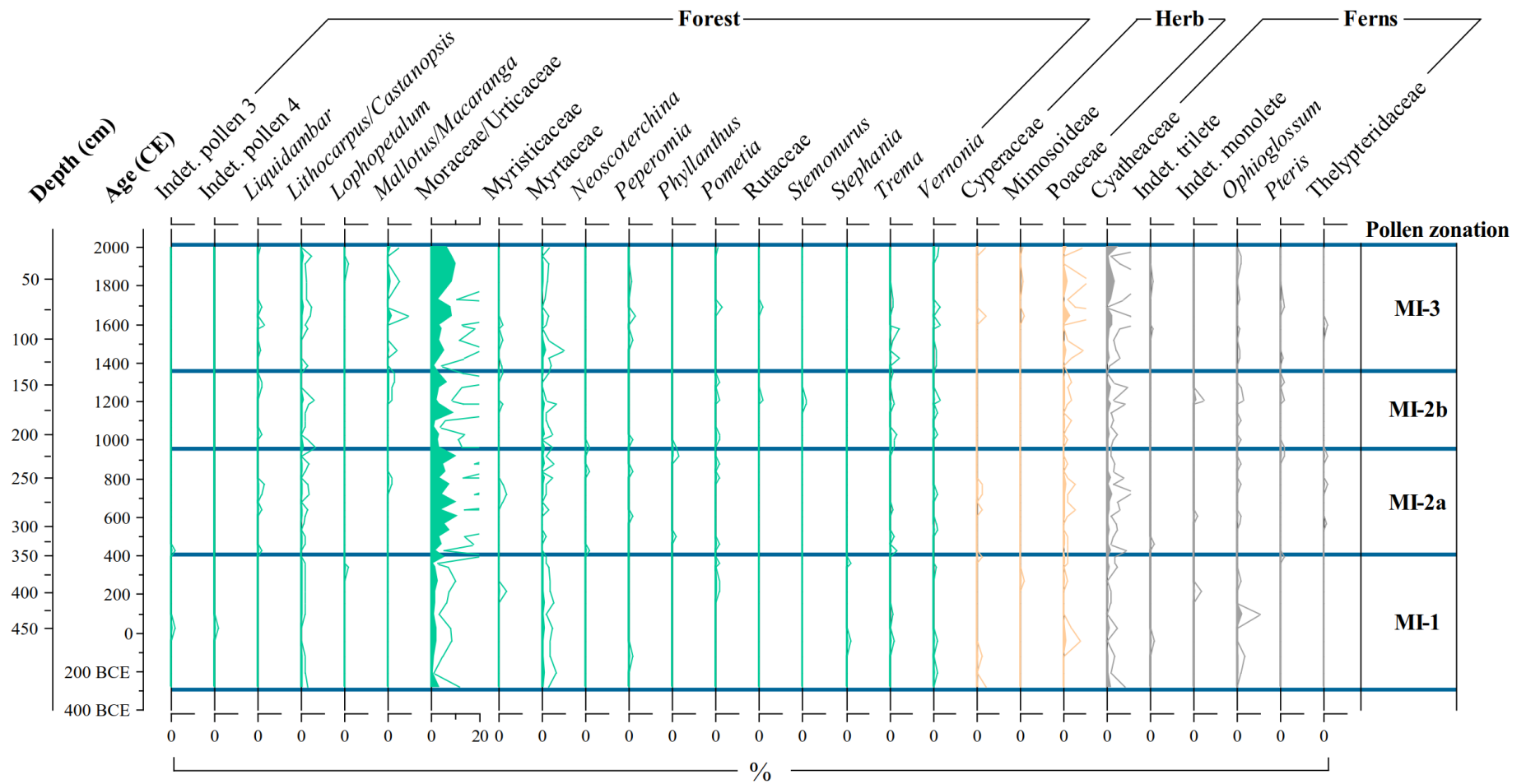
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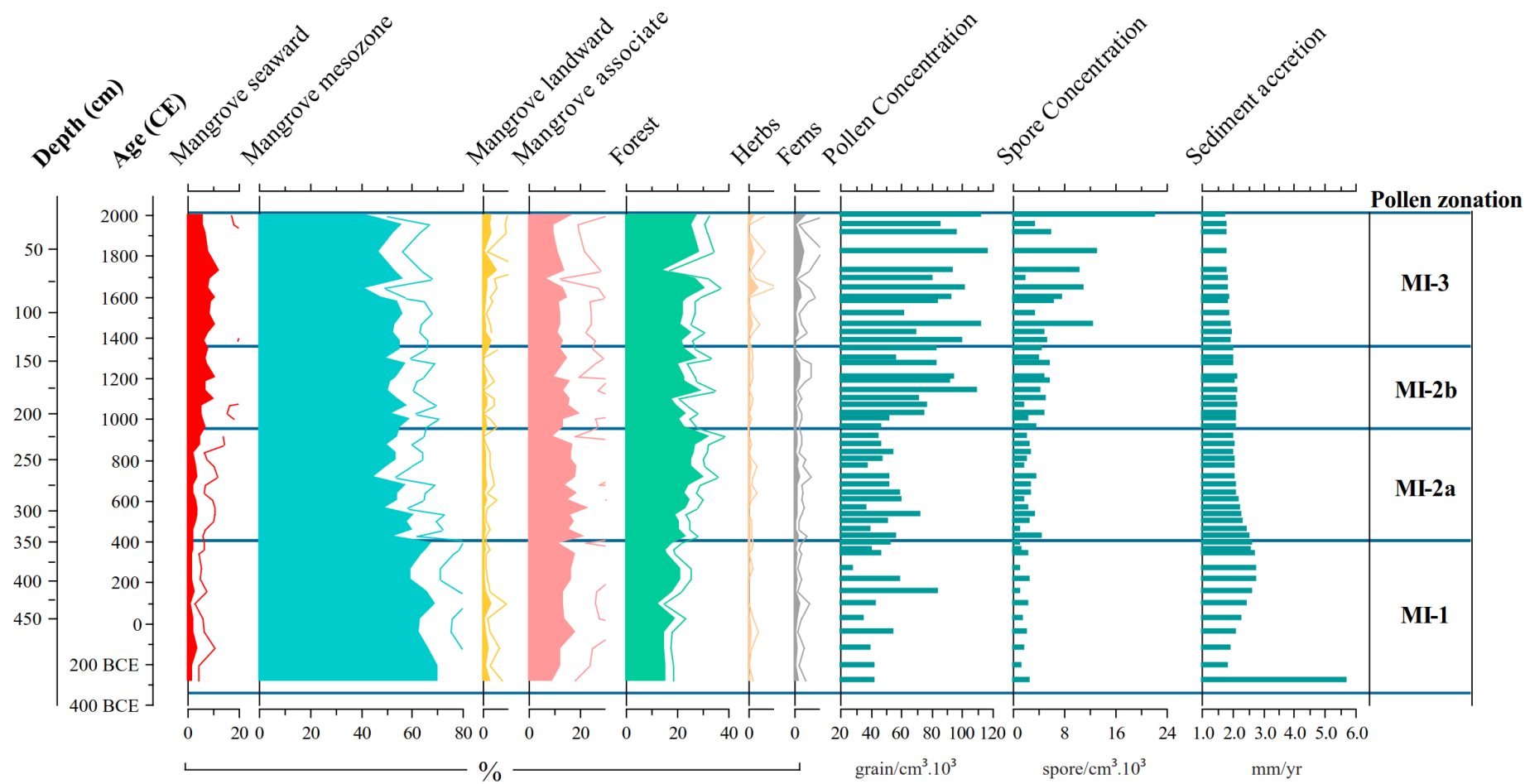












Declaration of Academic Integrity

I hereby confirm that the present dissertation is solely the work of myself. All scientific collaborators appear as co-authors of the manuscripts. If any passages or figures/diagrams from books, papers, the Web or other sources have been copied or in any other way used, all references, including those found in electronic media, have been acknowledged and fully cited.

Christina Ani Setyaningsih

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