ECOLOGICAL RESPONSES OF A PHILIPPINE DIPTEROCARP RAINFOREST TO LATE HOLOCENE CLIMATIC CHANGES

Thesis submitted for the Degree of Doctor of Philosophy, University of Oxford

Word Count c. 40,000

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Trinity Term 2016

THESIS ABSTRACT

Ecological responses of a Philippine Dipterocarp rainforest to late Holocene climatic changes

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Thesis submitted for the degree of Doctor of Philosophy (DPhil), Trinity term 2016.

Tropical rainforests comprise the world's oldest and most biodiverse biome, covering over 10% of Earth surface and providing livelihoods for over 300 million people. The upcoming consequences of anthropogenic climate change on tropical rainforests remain poorly understood. This is particularly true of the lowland tropical rainforests of Southeast Asia, aka Dipterocarp rainforests, in relation to the projected changes in El Niño/Southern Oscillation dynamics (ENSO). To address this important knowledge gap, this thesis aims to elucidate the ecological responses of Dipterocarp rainforests to past ENSO changes using a sediment-based multiproxy palaeoecological approach.

A suite of fossil proxies (e.g. lipid biomarkers, pollen, charcoal) from a Philippine lacustrine sequence spanning the last 1,400 years were used to generate records of precipitation, fire, nutrient availability and plant dynamics. These records were used to explore the effects of major environmental drivers on the structure and functioning of Dipterocarp rainforests, specifically their dominant tree family, Dipterocarpaceae, and their pioneer plant taxa.

The results suggest that Dipterocarp rainforests have been exposed to a prolonged period of enhanced ENSO regime during the second half of the Little Ice Age (~AD 1650-1900), yet there was no apparent effect of this climatic variability on the biomass of Dipterocarp trees. In contrast, the findings indicate that major fluctuations in phosphorus availability at the study site have had a significant influence on the biomass of Dipterocarp trees, though it remains uncertain which aspect of their biomass was primarily affected. Finally, my results propose that changes in ENSO conditions can significantly affect the abundance of pioneer taxa, with the nature and magnitude of that effect depending heavily on the level of fire activity.

This thesis examined for the first time the vegetation responses of Dipterocarp rainforests to large-scale climatic changes in the past. The findings presented here provide new insights into the likely structure and functioning of this globally important ecosystem in a warming world, and provide a context for understanding its resilience to current and future environmental change.

ACKNOWLEDGEMENTS

My DPhil journey was long and bumpy to say the least, but it made me grow as a researcher and as an individual more than I thought possible. Much of it is due to my supervisor Prof Kathy Willis. Kathy, thank you for everything – I would not be where I am now if it weren't for you.

Big thanks to my co-supervisor, Dr Alistair Seddon for his help with data analysis and interpretation – his critical thinking and attention to detail contributed greatly to the quality of this thesis.

Many thanks to Dr Dirk Sachse for his continuous mentorship, and logistical and financial support in undertaking the research on lipid biomarkers – he opened up a whole new fascinating field to me.

My gratitude also goes out to Prof Keith Bennet for his kind support in the field, as well as for finding time to address my many questions that followed with much thought and care.

I am also very grateful to Prof Marc Macias Fauria for stimulating scientific discussions throughout my DPhil studies.

Special thanks to Dr Emily Coffey – your DPhil experience and unbreakable spirit taught me a lot about what to expect from my own DPhil and how to best deal with unpredictable difficulties.

Big thanks to my OxLEL palaeo-colleagues – Dr Sandra Nogue Bosch, Dr Carolina Tovar, Dr Lydia Cole and Dr Elizabeth Jeffers - for their helpful assistance at various stages of my DPhil studies, and for finding time to discuss my research ideas.

To the amazing OxLEL 2012 student crew – Henrik Hanemmann, Herizo Andrianandrasana, Hsiao Hang Tao and Jessica Thorn – it has been a pleasure and a privilege to share this journey with you, thank you for all the good times.

Many thanks to Dr Bernd Hoffmann, Mr Philip Bartilet, Prof Peter Ashton, Dr Steven Moreton, Prof Stephen Harris, Dr Malin Kylander, Prof Jaboury Ghazoul, Dr Jake Snaddon, Dr Lawrence Heaney, Ms Iris Van der Veen, Dr Sandra Yap, Dr Christine Lane and so many others who have helped with different aspects of the DPhil project, from grant proposal writing, to fieldwork to data analysis and interpretation.

I am deeply thankful to my examiners, Prof Hermann Behling and Prof Yadvinder Malhi for their thorough comments and insightful suggestions.

My DPhil studies would not have been possible without the Clarendon Scholarship given to me by the Clarendon Fund - I am deeply grateful for this support. My sincere gratitude also goes to many of the organisations whose financial assistance made my DPhil fieldwork possible - Royal Geographical Society (Monica Cole Research Grant and Paddy Coker Postgraduate Research Award), Quaternary Research Association (New Research Worker's Award), Department of Zoology at the University of Oxford (Postgraduate Research and Training Grant), and Merton College (several of the Graduate Research Expenses and Supplementary Travel Grants). I would also like to offer my sincere gratitude to the NERC for awarding funds for radiocarbon dating analysis, and to the staff at the NERC Radiocarbon Facility, East Kilbride, for undertaking the analysis.

Many thanks to my Croatian friends for their emotional support, especially to Danijel Kovačević who always found time to listen about my DPhil challenges and offer brilliant solutions.

To my lab room-mate Dr Carla Romeu-Dalmau - you have been a true friend and a big support during the most challenging times - your contagious optimism and positive energy helped me immensely in completing this work and moving onto 'better things', thank you so much.

To my family for their love and patience, and for understanding the long periods of my absence. Special thanks to my grandfather Vladimir for teaching me the value of discipline and hard work, and to my brother Ivan, for reminding me about the importance of having fun even at the busiest of times.

My biggest thanks goes to my two favourite people in the world – my mother Vesna and my partner Marwan.

Mum, everything good about me I owe it to you – you have shown me how to follow my dreams and fight for things I believe in against all odds. This thesis would not be completed without your unconditional love and support.

Marwan, you have been my rock throughout this endeavour, keeping me sane to the end. I'll never forget all the sacrifices you have made to be there for me, from our trips to the Philippines, to helping make my graphs look professional to reading the 101st version of my thesis, you have my eternal gratitude.

PREFACE

This thesis is structured around four research papers which have been prepared as manuscripts for submission to the scientific journals detailed below. Thus, the length and formatting of these manuscripts follow broadly the journals' requirements. References and Supplementary Material can be found at the end of each chapter.

PAPER 1: Prohaska A., Seddon A. W. R., Hoffmann B., Willis K. J. and D. Sachse. (In prep.) Enhanced El Niño/ Southern Oscillation dynamics in the tropical Pacific during the Little Ice Age. Manuscript in preparation for *Nature Geoscience*.

PAPER 2: Prohaska A., Seddon A. W. R, Sachse, D. and K. J. Willis. (In prep.) Effects of ENSO Changes on Tree Biomass Dynamics in Dipterocarp Rainforests. Manuscript in preparation for *Proceedings of the National Academy of Sciences*.

PAPER 3: Prohaska A., Seddon A. W. R, Sachse, D. and K. J. Willis. (In prep.) The Effect of Phosphorus Availability on Tree Biomass Dynamics in Dipterocarp Rainforests. Manuscript in preparation for *Nature Ecology and Evolution*.

PAPER 4: Prohaska A., Seddon A. W. R., Sachse, D. and K. J. Willis. (In prep.) Effects of ENSO Changes on Pioneer Taxa and Gap Dynamics in Dipterocarp Rainforests. Manuscript in preparation for *Ecology Letters*.

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CHAPTER 1: INTRODUCTION

Tropical rainforests are the oldest and most biodiverse extant biome on the planet. They originated sometime after 100 million years ago and though they presently cover only 7% of the Earth's surface, they harbour approximately 50% of all living species (Ghazoul and Sheil 2010). On geological scales, tropical rainforests have repeatedly experienced large-scale climatic changes and yet the consequences of these changes on their biodiversity and ecological processes are poorly understood (Bush *et al.* 2011). This is largely due to a general scarcity of the studies on tropical rainforests that span hundreds to thousands of years and can thus capture biotic responses to major climatic changes. Consequently, robust predictions on the structure and functioning of this important biome in a warming world remain beyond our reach.

The overarching aim of this thesis is to advance the understanding of the sensitivity of tropical rainforest vegetation to large-scale precipitation changes, from the perspective of pioneer and climax taxa, and in comparison to other relevant drivers of change, namely fire activity and nutrient availability.

In this thesis I focus on the lowland rainforests of Southeast Asia, known as the Dipterocarp rainforest. These forests constitute the largest expanse of aseasonal tropical rainforest on the planet and cover much of peninsular Malaysia, Sumatra, Java, Borneo and the Philippines (Appanah 1985) (Figure 1). Though aseasonal forests can be found sporadically in other tropical regions, it is only in Southeast Asia that they form the predominant vegetation cover stretching continuously over nearly 80% of the region (Appanah and Turnbull 1998).

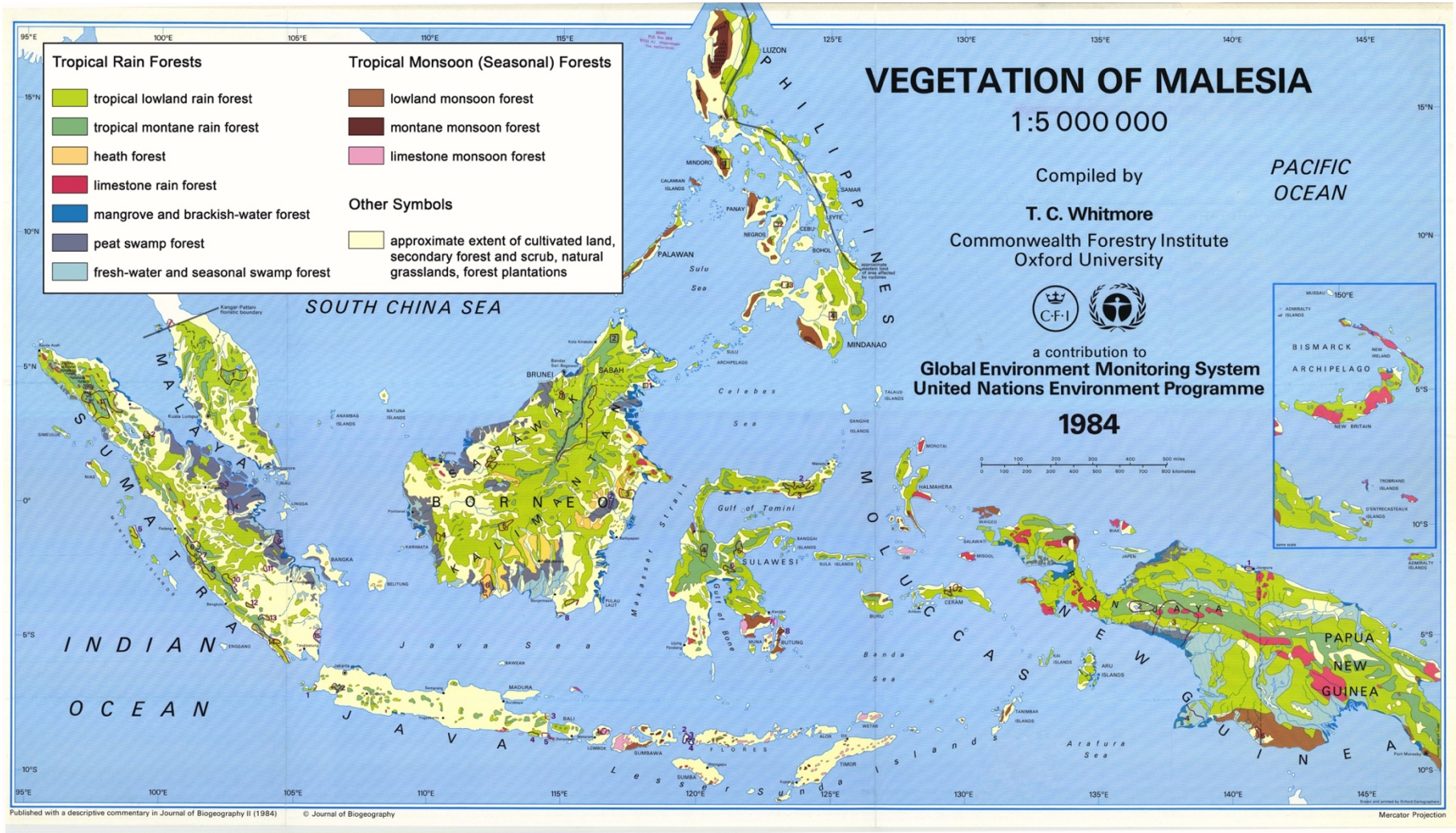


Figure 1 | Vegetation map of Southeast Asia (modified from Whitmore 1984). The map shows the distribution of main vegetation types in the region, including the forest type this thesis focuses on - the lowland tropical rainforests of Southeast Asia, aka the Dipterocarp rainforests, which are shown as the light green coloured areas in Malaysia, Sumatra, Borneo, Java and the Philippines.

Moreover, the biodiversity of Dipterocarp rainforests is only second to its Amazonian counterparts, and represents the main forest type in two global biodiversity hotspots (Myers *et al.* 2000).

Over the last few decades, Dipterocarp rainforests have been experiencing some of the highest rates of deforestation and forest degradation globally, and it is estimated that today they occupy less than 50% of their original range (Sodhi *et al.* 2004). Two principle drivers of this forest loss have been logging and agricultural expansion. Specifically, wood of the dominant tree family, Dipterocarpaceae, holds a preeminent place in the international tropical timber trade and in the economies of the hosting countries, while the habitat provides favourable conditions for growing oil palm, the fastest growing agricultural crop in the region. Numerous studies have recorded the effects of these two drivers on the biodiversity and ecological processes in Dipterocarp rainforests (Styring and Ickes 2001; Sodhi *et al.* 2004; Fayle *et al.* 2010; Sodhi *et al.* 2010; Kronseder *et al.* 2012; Kenzo *et al.* 2015). In contrast, how upcoming climate change will affect this already highly endangered ecosystem remains an understudied question.

Dipterocarp rainforests & ENSO

Most future climate projections indicate marked changes in the El Niño/ Southern Pacific Oscillation (ENSO), particularly an increase in the frequency of extreme El Niño events (Latif and Keenlyside 2009; Collins *et al.* 2010). Previous studies have shown that ENSO dynamics shape precipitation patterns across the Southeast Asian region and, subsequently, exert a large influence on species and ecological processes in Dipterocarp rainforests (Van Nieuwstadt and Sheil 2005, Sakai *et al.* 2006). For instance, severe droughts induced by El Niño episodes increase mortality rates for the majority of tree species, and large trees (i.e. >80 cm diameter at breast height, d.b.h.) seem to be particularly susceptible (Itoh *et al.* 2012). It has been therefore postulated that a regime of more frequent and intense droughts, as expected under the enhanced ENSO regime projected for the 21st century, will result in a forest with uneven structure, lower stature, more opened canopy and reduced above ground biomass, as well as an increased proportion of drought-tolerant and early successional taxa (Newbery *et al.* 1999). However, empirical evidence needed to test these hypotheses is very limited due to the temporal nature of ENSO variability. Specifically, instrumental records show that ENSO activity has been relatively stable over the last few decades (Cobb *et al.* 2003). While observational studies have

provided a wealth of knowledge on the structure and functioning of Dipterocarp rainforests under present climatic conditions, they have limited capacity to investigate the impacts of major ENSO changes on Dipterocarp rainforest dynamics as such changes normally take place on centennial to millennial scales. The palaeosciences offer a valuable alternative as they can provide both long-term records of ENSO variability and corresponding records of vegetation dynamics (Birks and Birks 2004). Combined, these records can be used to directly measure the nature and rate of Dipterocarp rainforest responses to marked ENSO changes.

Past changes in ENSO dynamics

ENSO is a powerful inter-annual climate mode that shapes temperature and precipitation patterns across the globe, though its impacts are particularly prominent in the tropics (Cobb *et al.* 2013). Despite the considerable research efforts invested into understanding the ENSO phenomenon, many aspects of its cycle remain unknown, including its sensitivity to continued anthropogenic greenhouse forcing (Latif and Keenlyside 2009; Collins *et al.* 2010). This directly contributes to large uncertainties in regional precipitation projections for the tropics, which are urgently needed to develop effective climate change adaptation strategies for the 70% of the world's population threatened by extreme poverty (Cobb *et al.* 2013). Any further improvements in these projections will require knowledge of the full range of natural ENSO variability.

Robust estimates of past ENSO variability have been hindered by the scarcity of palaeorecords in which ENSO driven changes can be distinguished from those caused by other climatic drivers (Atwood and Sachs 2014; Nelson and Sachs 2016). This is particularly true for the Common Era, which is marked by major shifts in the Intertropical Convergence Zone (ITCZ) position, particularly during the Little Ice Age, LIA (i.e. ~AD 1300-1850) (Sachs *et al.* 2009; Yan *et al.* 2015). Consequently, there has been a long-standing debate about the strength of the El Niño/ Southern Oscillation system during the LIA with conflicting evidence coming from sea surface temperature (SST) reconstructions and hydrological records. Whereas SST reconstructions show relative warming in the eastern (Conroy *et al.* 2008; Conroy *et al.* 2010) and central tropical Pacific (Cobb *et al.* 2003) and significant cooling in the western equatorial Pacific (Newton *et al.* 2006; Oppo *et al.* 2009), indicating an El Niño-like state, the majority of hydrological records show wetter conditions in the Indo-Pacific (Tierney *et al.* 2010; Yan *et al.*

2011; Rodysill *et al.* 2011; Zeng *et al.* 2012), and drier conditions in the central (Sachs *et al.* 2009) and the eastern equatorial Pacific (Moy *et al.* 2002; Conroy *et al.* 2008), suggesting enhanced PWC and a La Niña-like phase. The cause of this conflict may at least partly be related to the existence of two prominent sources of precipitation in the tropical Pacific; in addition to the ENSO-associated Pacific Walker Circulation (PWC), hydrological conditions in many parts of the region are strongly influenced by the position of the ITCZ. Therefore, more records from the tropical Pacific are needed to tease apart the ENSO signal from the ITCZ signal, either by offering independent proxies for each of these two phenomena, or by selecting sites that are largely influenced by one or the other.

Past dynamics of Dipterocarp rainforests

A large number of palaeoecological studies have been undertaken in Southeast Asia to date. These studies have predominately focused on the peat swamp forests (Morley 1981; Taylor *et al.* 2001; Wust and Bustin 2004; Biagioni *et al.* 2015; Cole *et al.* 2015; Dommain *et al.* 2015), fresh swamp forests (Anshari *et al.* 2001; van der Kaars *et al.* 2001) and montane forests (Stuijts *et al.* 1988; Maloney and McCormac 1995), revealing valuable insights into the ecology of these ecosystems, from their ontogenesis and succession, to their compositional and structural changes during the glacial periods, to their sensitivity to natural fire and anthropogenic burning. Surprisingly, considerably less work has been done on the long-term ecology of Dipterocarp rainforests, with virtually all of the information coming from marine sediments (van der Kaars 1991; van der Kaars and Dam 1995; Wang *et al.* 1999; Sun *et al.* 2000; van der Kaars *et al.* 2000). Marine sediments normally have a much larger pollen source area than lake and peat sediments; the majority of pollen in lake and peat sediment comes from tens to hundreds of meters from the coring site (Prentice 1985; Sugita 1994), in comparison marine sediments pick up pollen signal from tens to hundreds of kilometres. The dynamic influence of wind and sea currents also introduce additional changes in pollen source area over time (Poliakova *et al.* 2014). Hence, while marine sediments offer valuable information on the distribution of biomes in the region (Wang *et al.* 1999; Sun *et al.* 2000; van der Kaars *et al.* 2000), they have limited capacity for examining the dynamics of individual ecosystems. In contrast, small to medium size lakes can provide excellent control over the pollen source area (Sugita 1993), ensuring that the majority of pollen in the record comes from the surrounding vegetation and, thus, providing a reliable account of its compositional changes over time. Consequently, lake sediments are

well suited for reconstructing past vegetation dynamics of Dipterocarp rainforests. To the best of our knowledge, however, no lacustrine records of vegetation dynamics have been obtained from Dipterocarp rainforests to date, mainly due to general scarcity of suitable coring sites.

Present structure and functioning of Dipterocarp rainforests

Dipterocarp rainforests are unique among the world's tropical rainforests in that they are dominated by a single tree family, Dipterocarpaceae. Not only does this family make up the largest size class of trees in Dipterocarp rainforests (i.e. genera *Shorea* and *Dipterocarpus*, with d.b.h. ca.100-200 cm), it also usually comprises up to 10% of total tree diversity, over 50% of the basal area and nearly 80% of all emergent individuals (Appanah 1985). Furthermore, members of this family play a key role in the reproduction of Dipterocarp rainforests. A large number of Dipterocarpaceae species can only reproduce during mass flowering events - gregarious, community-wide masting events that are most often triggered by El Niño-induced drought events (Sakai *et al.* 2006). Mass flowering of Dipterocarps is accompanied by heavy flowering of many other plant species, including members of Anacardiaceae, Euphorbiaceae, Annonaceae, Fabaceae, Burseraceae, Moraceae and Myristicaceae, though for the majority of these it seems to be an opportunistic rather than obligatory behaviour (Appanah 1985). Therefore, it is the Dipterocarp species that shape the flowering patterns in these forests. Moreover, unlike most other tree taxa in Dipterocarp rainforests, Dipterocarps are predominately ectomycorrhizal trees (Appanah and Turnbull 1998) and producers of potent triterpene resins (Diaz and Ourisson 1966); as such, they have a decisive influence on the composition of soil fungi, herbivorous insect and plant pathogen communities. Given the overwhelming dominance of Dipterocarp trees, any significant changes in their biomass are likely to bring about significant changes in the overall structure and functioning of Dipterocarp rainforests. Hence, a meaningful evaluation of the resilience of Dipterocarp rainforests to ENSO changes requires the reconstruction of Dipterocarp tree responses to such conditions.

Pioneer taxa comprise another distinct group of plants that can offer a window into the effects of ENSO changes on Dipterocarp rainforests. Pioneer taxa can only be established in forest gaps and therefore their abundance is directly linked to the frequency and size of forest gaps (Ashton 2014, page 81). However, gaps also allow seedlings and saplings of climax taxa to gain enough height to reach the canopy (Whitmore 1988; Ashton 2014; Ghazoul 2016). Whether a

forest gap will be dominated by pioneer taxa or climax taxa seems to depend on many factors, including gap size, the time since its creation and the level of disturbance (Ghazoul and Sheil 2010). Though gaps are a natural part of the growth cycle in tropical rainforests, Dipterocarp rainforests have some of the lowest recorded gap frequencies; at Lambir Hills National Park in Sarawak, Borneo, gaps form ~0.1% of the total area per year, which is an order of magnitude lower than in Neotropical rainforests where annual gap formation occupies 0.7-2.9% of the forest (Ghazoul 2016). This has been linked to relatively low mortality rates of large trees due to benign environmental conditions (e.g. favourable climates, low wind speeds, few large-scale disturbances) (Ghazoul 2016). Enhanced ENSO conditions are expected to increase mortality rates of large trees and, thereby, increase gap occurrence, but what remains unknown is whether such climatic conditions will favour pioneer or climax taxa dominated regeneration in the new gaps. Given the marked differences in life-history traits between pioneer and climax taxa (Ashton 2014, page 79), the nature of vegetation regeneration in forest gaps under enhanced ENSO conditions will have notable influence the structure and functioning of Dipterocarp rainforests.

Secondary drivers of change in Dipterocarp rainforests

Examining the impacts of other relevant environmental drivers in Dipterocarp rainforests, such as fire and nutrient availability, can help evaluate the relative severity of ENSO effects, as well as distinguish between their individual and synergistic effects.

While fire is a relatively rare disturbance in Dipterocarp rainforests, a single severe episode can lead to near complete mortality of smaller stems (i.e. <10 cm d.b.h) (Van Nieuwstadt and Sheil 2005). While El Niño droughts increase the likelihood of forest fires, they are not the main cause of fire in Dipterocarp rainforests today (Field and Shen 2008; Langner and Siegert 2009). The increasing frequency and magnitude of this disturbance in Dipterocarp rainforests documented during the last two decades (Salafsky 1994; Folkins *et al.* 1997; Salafsky 1998; Siegert *et al.* 2001; Huijnen *et al.* 2016) has been actually linked to anthropogenic activities such as forest fragmentation and degradation (Curran *et al.* 1999). For instance, at least 80% of the 1997– 1998 ENSO-associated fires across Indonesia (primarily Kalimantan) were caused by logging and plantation firms (Curran *et al.* 1999). It is therefore highly likely that the projected intensification of ENSO coupled with continuous anthropogenic activities will be

accompanied by heightened fire activity in the region. Such a combination of drought and fire can be particularly destructive to Dipterocarp rainforests as it causes mortality of both larger and smaller trees (Van Nieuwstadt and Sheil 2005). On the other hand, the positive effects of fire on the establishment and growth of pioneer plants, including pioneer trees, ferns and grasses has also been recorded, indicating that fire frequency can significantly influence gap dynamics (Woods 1955; Schulte and Schöne 1996; Whitmore 1998). Therefore, fire is an important component if we are to understand the past and future effects of enhanced ENSO regime on Dipterocarp rainforests.

Nutrient availability is another potentially important driver of change in tropical rainforests. Phosphorus is assumed to be the main limiting nutrient for the productivity of lowland tropical rainforests (Vitousek 1984), being a primary plant macronutrient with particularly low concentrations in tropical soils. Yet the evidence of this claim is limited and mixed for Dipterocarp rainforests, and based primarily on fertilization experiments and observations across nutrient gradients. Experimental studies indicate that phosphorus addition has little to no effect on the growth of Dipterocarp seedlings (Turner *et al.* 1993; Burslem *et al.* 1995; Gunatilleke *et al.* 1997; Palmiotto *et al.* 2004; Brearley *et al.* 2007) or the growth of adult individuals (Mirmanto *et al.* 1999) while observational studies looking at the biomass production in Dipterocarp rainforest plots (Paoli *et al.* 2005; Paoli and Curran 2007; Paoli *et al.* 2008) suggest that tree biomass increment is positively related to phosphorus, and that this increment is more strongly related for large trees than for small trees (Dipterocarp trees were not assessed separately in these studies, but grouped together with other trees species). Given the relatively short duration of both environmental and observational studies (<50 years), they have limited ability to measure the effects of phosphorus availability the reproduction and growth of large tree species, such as Dipterocarps. For instance, the regeneration time of Dipterocarps ranges from 20 to 50 years, and their life span extends several hundred years (Ng 1966; Appanah and Turnbull 1998). Hence, a clear pattern of phosphorus influence on such long-lived and slow producing trees is likely to emerge over centennial to millennial time scales. This could explain the lack of conclusive evidence from short-term analyses, and highlights the value of including nutrient considerations into long-term ecological studies.

Given the above discussed knowledge gaps, the main focus of this thesis is to investigate the responses of Dipterocarp rainforests to changes in ENSO dynamics in the past, both

individually and in combination with changes in fire activity and nutrient availability. The four central research questions addressed here, each comprising a separate chapter, are as follows:

i) What was the nature and extent of past ENSO changes in the tropical Pacific? (Prohaska *et al.* In prep., see Chapter 3),

ii) What were the effects of the past ENSO changes on the biomass dynamics of Dipterocarpaceae taxa, and does the direction and magnitude of these effects depend on fire activity? (Prohaska *et al.* In prep., see Chapter 4),

iii) Has phosphorus availability played an important role in the biomass dynamics of Dipterocarpaceae taxa over longer time scales (Prohaska *et al.* In prep., see Chapter 5),

iv) What were the responses of pioneer taxa to the past changes in ENSO dynamics and fire activity, and how did these responses influence gap dynamics in Dipterocarp rainforests? (Prohaska *et al.* In prep., see Chapter 5)?

To answer the above stated questions, I employ a multi-disciplinary and multi-proxy approach that includes a range of field, laboratory and statistical techniques. Various proxies (e.g. lipid biomarkers, fossil pollen, charcoal) were extracted from sediment cores collected from Bulusan Lake in south-east Luzon, Philippines, and used to reconstruct the long-term dynamics of precipitation, fire, nutrient availability and vegetation dynamics. Statistical analyses were carried out on the resultant data in order to make inference about the relationships between the reconstructed environmental and ecological variables. The thesis focuses on the last 1,400 years (late Holocene) because large-scale changes in the ENSO dynamics have been reported for this time period (Cobb *et al.* 2003; Conroy *et al.* 2010).

Thesis Outline

Chapter 2 gives a detailed account of the study area, study site and study organisms, as well as the field, laboratory and statistical methods used to extract, process and analyse data.

The first study, presented in **Chapter 3**, uses the isotopic analysis of higher plant leaf waxes from the collected sediments to reconstruct precipitation dynamics at the Bulusan Lake over the last 1,400 years and make inference about ENSO variability during this time period. The novelty of this work involves the generation of the ENSO record from an understudied region and at a location that is only marginally influenced by ITCZ dynamics.

Chapter 4 investigates the effects of ENSO-induced changes in precipitation recorded in the Bulusan record over the last 1,400 years on the biomass of the dominant tree family Dipterocarpaceae. The drought effects are examined individually and in interaction with fire activity to test for any synergy between the two drivers of change. Fossil pollen and macrocharcoal are used as proxies of Dipterocarp biomass dynamics and local fire activity, respectively. The originality of this study lies in the provision of the first palaeovegetation record from Dipterocarp rainforests and a first empirical assessment of the sensitivity of Dipterocarpaceae taxa to major ENSO changes.

Chapter 5 examines the extent to which phosphorus availability limits the productivity of Dipterocarp rainforests through the lenses of Dipterocarpaceae family responses to the volcano-induced reductions in phosphorus supply, as recorded in the geochemical profile of the Bulusan core. This is the first study to assess the sensitivity of large tropical trees to the reduction in phosphorus supply on a centennial scale, thereby accounting for their relatively slow growth and reproduction rates.

In **Chapter 6**, I analyse fossil pollen of some of the key pioneer taxa in Dipterocarp rainforests in order to reconstruct their responses to the ENSO-induced precipitation changes, and test if the direction and magnitude of these responses depend on the level of fire activity, and whether this varies among different pioneer taxa. This paper pioneers the use of palaeoecological proxies to evaluate the impact of changing ENSO regimes on gap dynamics in Dipterocarp rainforests.

Chapter 7 synthesises the main findings of Chapters 3 to 6, offers concluding remarks and discusses future research directions.

Appendix A presents the newly built Dipterocarpaceae pollen reference collection using herbarium samples from the Kew Royal Botanic Gardens, while **Appendix B** includes complete pollen diagrams for the Bulusan sedimentary sequence.

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CHAPTER 2: MATERIALS AND METHODS

Study Area

The Philippine Archipelago (11° N, 124° E) is located in the Western Pacific, 700 km from mainland Asia. The archipelago consists of more than 7000 oceanic islands with a total land area of 298,170 km^2, the largest of which is Luzon (Government of the Philippines 2016). The Philippine islands started to emerge from the ocean floor in the early Oligocene without dry-land connections, with most of the extant islands having been formed by the late Miocene and Pliocene (Hall 1998). During the Pleistocene's glacial periods, the sea level was on average 120 m below the current levels and land bridges connected neighbouring islands into four larger islands known as the Pleistocene aggregate island complexes: Greater Luzon, Greater Mindanao, Greater Negros-Panay and Greater Palawan (Heaney 1985; Heaney 1986; Brown and Diesmos 2002). This repeated formation and breakup of the land bridges during glacial cycles is considered a key driver of diversification in the Philippine archipelago (Heaney, 1985, 1986; Brown and Diesmos 2002).

High species diversity coupled with high proportions of endemics make the Philippine archipelago one of the most important biodiversity hotspots (Myers *et al.* 2000). Specifically, 50% of plant species (Merrill 1922; Myers *et al.* 2000), 64% of land mammals, 44% of breeding land birds, 68% of the reptiles, and 78% of amphibians in the Philippines are considered endemic (Heaney and Regalado 1998). At the same time, with only 3% of primary forest remaining, the Philippines are one of the most deforested countries globally (Myers *et al.* 2000). The main contributors include logging, shifting cultivation and transformation into settlements or agricultural fields (ESSC 1999; Langenberger 2006). Despite the high endemism and widespread deforestation in the country, Philippine vegetation remains largely understudied, and Dipterocarp rainforests are no exception. Much of the current knowledge on Philippine Dipterocarp rainforests is based on studies undertaken in the early 20th century (Whitford 1906; Whitford 1911; Brown and Mathews 1914), though several more recent studies have built on this knowledge, namely with respect to the forests' non-economic plant species, disturbance

ecology, rehabilitation practices and conservation (Margraf and Milan 1996; Langenberger *et al.* 2006; Langenberger 2006; Yap *et al.* 2016).

At the beginning of the 20th century Dipterocarp rainforests covered much of the Philippines (Whitford 1911). Today, remnants of these forests can only be found in localities where large-scale logging was not profitable, e.g. due to difficult terrain (Langenberger 2006).

There are several different types of Dipterocarp rainforests in the Philippine archipelago depending on the climatic conditions, elevation and slope, and these forest types are named according to their dominant Dipterocarp species: 1) Lauan-Apitong Dipterocarp forest, dominated by *Dipterocarpus grandiflorus*, in areas with a more pronounced dry season, 2) Yakla-Lauan Dipterocarp forest dominated by *Hopea malibato*, on low hills of volcanic origin along rivers, 3) Tanguile-Oak Dipterocarp forest dominated by *Shorea polysperma* and *Lithocarpus pruinosa*, on higher hills and steep slopes, 4) Lauan-Hagakhak Dipterocarp forest dominated by *Dipterocarpus warburgii*, on low lying areas up to 100 m, and 5) Lauan Dipterocarp forest dominated by *Shorea contorta* (Margraf and Milan 1996). Other notable large tree genera include *Nephelium*, *Dysoxylum*, *Drypetes*, *Chisocheton*, *Strombosia*, *Pinanga, Leptonychia* and *Ficus* (Co *et al.* 2006). Species of *Litsea, Aglaia, Xanthophyllum* and *Syzygium* dominate in the lower canopy, while *Leea, Praravinia, Lepisanthes, Cyrtandra, Psychotria* and *Maesa* are prominent subcanopy trees.

Interestingly, Dipterocarp rainforests in the Philippines extend to a considerably higher northward position (i.e. 18°N) than their counterparts on the mainland (i.e. 8°N). The ecological and evolutionary factors underpinning this biogeographical paradox remain poorly understood. Another interesting feature of Philippine Dipterocarp rainforests is their regular exposure to typhoons. Yap *et al.* (2016) quantified the impacts of a powerful typhoon from 2003 on Dipterocarp rainforests in a permanent plot in Palanan, north-eastern Luzon using a complete census of 100 000 trees from 1998-2010. They found that while tree mortality was significantly higher during the typhoon interval, above-ground biomass loss was minimal and biomass surpassed pre-typhoon levels after only six years. Additionally, the recruitment rates during the typhoon interval were nearly four times higher than the rates in the subsequent non-typhoon interval, which was attributed to the increased growth of seeds and seedlings of pioneer species due to the open, defoliated canopy. The relatively low mortality and fast recovery rates

recorded in the Palanan plot indicate high resilience of Dipterocarp rainforests to intense typhoon disturbance.

Study site

Bulusan Lake (12°45' N, 124°6' E) is located in south-east Luzon, Philippines. It is a 0.28-km^2 oval shaped lake of volcanic origin situated at 360 m.a.s.l. The lake consists of two basins: a round basin, and a larger narrow basin, which are 12 and 24 m deep respectively (Figure 1). Without any inlets or outlets present, the two basins comprise a closed system fed primarily by precipitation and ground water. Lake Bulusan features clear, bright green waters and no floating or submerged vegetation has been recorded at the lake.

Bulusan Lake sits within the Philippine climatic belt Type II (PAGASA 2016), which covers the eastern side of the Philippines from north Luzon to south Mindanao (Figure 2A). This climate type is characterized by the lack of a dry season (i.e. mean monthly rainfall >100 mm) and very pronounced rainfall from November to April caused by the north-eastern monsoon (Indo-Australian monsoon) (Fisheries and Aquaculture Department 1983). Inter-annually, the precipitation is strongly linked to ENSO variability, with most El Niño/ La Niña events taking place during the boreal winter (November-February) (Philippine Atmospheric, Geophysical and Astronomical Services Administration 2016). Northern migration of the Intertropical Convergence Zone (ITCZ) during the boreal summer (June to September) brings additional rainfall to the study area, however, its contribution is relatively small compared to that of the north-eastern monsoon. Annual temperature and precipitation in the area over the last 60 years has ranged between 25-28°C and 2000-4800 mm, respectively (Legaspi weather station - Menne *et al.* 2012a; Menne *et al.* 2012b). The Philippines are positioned across the typhoon belt, featuring typhoons and strong storms from July through to October, and these are especially hazardous for northern and eastern Luzon, including the Bulusan area (PAGASA 2016) (Figure 2B). For instance, there have been 4-6 tropical storm landfalls per year in the Philippines in the period between 1902 and 2005 (Kubota and Chan 2009).

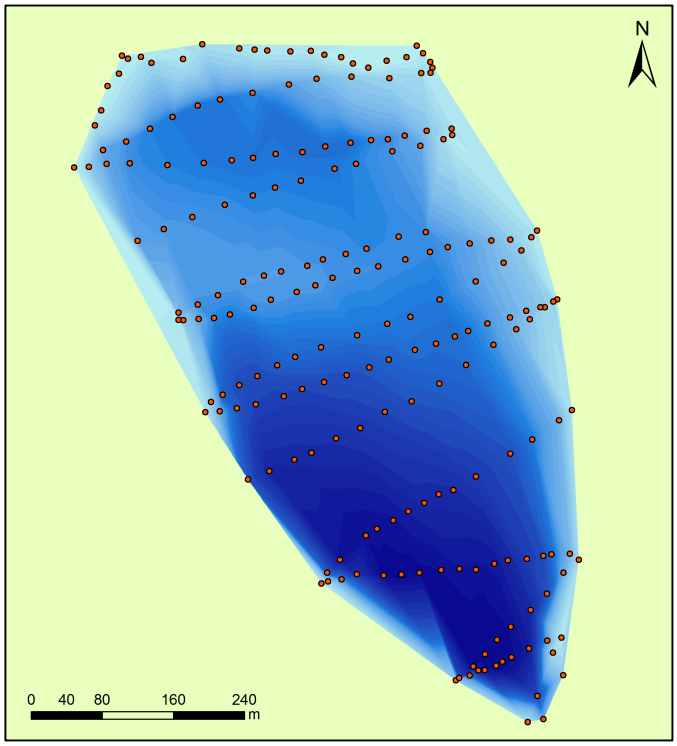


Figure 1 | Map showing the bathymetry of Bulusan Lake. The lake consists of two basins - a round basin 12 m deep and a larger narrow basin 24 m deep. The bathymetry values were extrapolated from the depth points measurements (red circles) using the Natural Breaks (Jenks) classification method in ArcGIS 9.3 (ESRI 2008).

Bulusan Lake lies at the foot-slopes of Mt Bulusan, an active stratovolcano at the southeast end of the Bicol Volcanic Arc (Delfin *et al.* 1993). The volcano undergoes regular eruptions, the latest of which was in June 2016. Its wider area comprises the Bulusan Volcano National Park, a nature reserve that was first established in 1935 (Abada Gatumbato *et al.* 2011). The park covers an area of 36,72 km^2 which mainly consists of rugged terrain with steep slopes and features numerous springs, rivers and waterfalls. There are two other lakes in the park in addition to Bulusan Lake, Aguingay Lake at 410 m.a.s.l and Blackbird Lake at 1,560 m.a.s.l. Aguingay Lake is a seasonal lake produced on a volcanic plain by heavy rains from November to April, while Blackbird Lake is one of the four craters at the Mt Bulusan summit. The soils in the park are classified as loamy clay and as such are well drained with a rapid basic infiltration rate and medium to high water-holding capacity (Abada Gatumbato *et al.* 2011). In addition, the pyroclastic materials, particularly volcanic ash, deposited during the volcano's eruptions act as an additional source of nutrients. Consequently, the soils around Bulusan volcano are

more fertile than most other soils in the Southeast Asian region.

The dominant forest type in the Bulusan Volcano National Park, including the area around Bulusan Lake, is primary Dipterocarp rainforests of Lauan type dominated by *Shorea contorta* and *Parashorea malanonaan*. Other notable types include secondary forests towards the edge of the park, and mossy forests above 1,000 m. While most of the park is forested, there are several localities covered by monoculture of the grass species *Imperata cylindrica*. In the park, there are 241 recorded plant species belonging to 152 genera and 72 families, and 14 of these are considered threatened. There is also a total of 72 species of terrestrial animals belonging to 58 genera and 37 families, 31 of which are Philippine endemic. Four animal species have been listed as high conservation priority based on their global status under the IUCN's 2010 Red List: Golden-crowned flying fox (*Acerodon jubatus*), Southern Luzon giant cloud rat (*Phloeomys cumingii*), Philippine warty pig (*Sus philippensis*) and the Luzon tarictic hornbill (*Penelopides manillae*). Limited and strongly regulated logging, hunting and agricultural activities are allowed in certain, mostly marginal, areas of the park.

Study Organisms

Dipterocarps of Southeast Asia

The Dipterocarpaceae family includes three subfamilies: Dipterocarpoideae in Asia, Pakaraimoideae in South America and Monotoideae in Africa and South America. Depending on classification system, the family contains 15 to 19 genera and 470 to 580 species, of which the overwhelming majority belongs to Dipterocarpoideae (Appanah and Turnbull 1998).

Most Asian Dipterocarps remain in evergreen forests (some in seasonal regions, most in aseasonal areas), but there are few species of *Dipterocarpus* and *Shorea* which live in fire-climax savanna woodlands (Ashton 1979). In aseasonal regions, Dipterocarps constitute the dominant element of the lowland rain forest (Whitmore 1988). As a family they dominate the canopy and emergent layer, but are also well represented in the understorey. Most belong to the mature phase of primary forest, and though some can colonise secondary forests during the later stages of succession, none seems presently confined to secondary formations (Appanah and Turnbull 1998). Dipterocarps occupy a large variety of habitats within the 0-1200 m elevation range (Symington *et al.* 2004), from coastal to inland, riverine and swampy to dry land, flat to

undulating terrain, ridges and slopes to valley bottoms, and well-drained to poorly drained soils both rich and poor in nutrients.

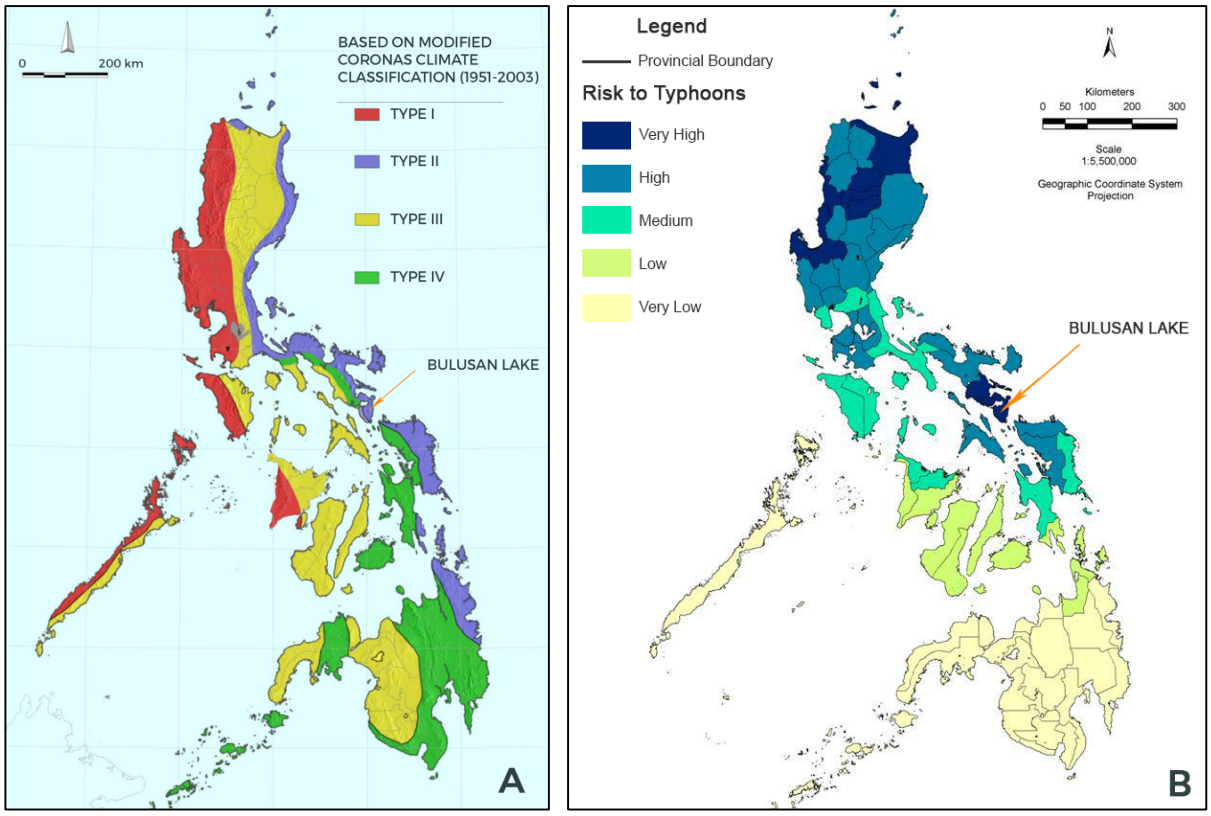


Figure 2 | A, Map of the Philippines showing the distribution of the four climate types. Type I - two pronounced seasons, dry conditions from November to April and wet conditions from May to October, Type II - no dry season and very pronounced rainfall from November to April, Type III - seasons are not very pronounced, drier from November to April, and Type IV - rainfall is relatively evenly distributed through the year. Map source: (PAGASA 2016). **B, Map of the Philippines showing the risk of typhoon landfalls across the country.** Data from the Joint Typhoon Warning Centre and National Statistics Office, Philippines. Map source: (The Manila Observatory, Ateneo de Manila University 2016).

Gregarious mass flowerings of aseasonal Dipterocarps takes place every 2-7 years (Ashton 1988; Ashton 1989) and is normally caused by ENSO-induced droughts. The gregarious flowerings are synchronous within populations and occur over several months for the whole family (Ashton 1969; Chan 1980; Chan 1981; Appanah 1993). Dipterocarps are pollinated by a wide variety of insects, but mostly thrips and bees (Appanah and Chan 1981; Dayanandan *et al.* 1990). Among the pollinators recorded so far, all except thrips are capable of moving pollen over long distances.

The majority of Asian species have developed wind-dispersed fruits where sepals are modified into wing-like structures that allow them to gyrate towards the ground (Ashton 1982). In closed forests these winged fruits usually have limited possibilities for dispersal, however storms and very strong winds may transport them over the canopy for several hundred metres and sometimes over one kilometre. Dipterocarp seeds usually germinate quickly under moist, warm conditions with the time to 50% germination between 2 and 13 days (Tompsett and Kemp 1996; Appanah and Turnbull 1998).

Unlike most other trees in the Southeast Asian region, Dipterocarps are predominantly ectomycorrhizal (particularly with Basidiomycete genera) but a few species have been reported to form both ectomycorrhizas and arbuscular mycorrhizas (Appanah and Turnbull 1998). The presence of wood resin canals and the production of triterpenes constitute another familial feature of the Asian Dipterocarps.

Pests and diseases affect seeds, seedlings, saplings and trees of Dipterocarp species. Seed predation can be very high, and the crop can be completely wiped out. While insects are the major seed pests (~80 species, mostly Curculionidae, Lepidoptera) (Daljeet-Singh 1974; Atmowidi *et al.* 1996), there is also destruction by birds and mammals such as wild pigs (*Sus scrofa*), squirrels (*Callosciurus prevostii* and *C. notatus*) and monkeys (*Presbytis rubicunda*) (Appanah and Turnbull 1998). Wild pigs (*Sus scrofa*), rodents and deer are significant as pests of seedlings and saplings (Appanah and Turnbull 1998). Shoot and root borers species (Daljeet-Singh 1974; Smits *et al.* 1991), and galls producing leaf damage (Anthony 1977), were also recorded on various Dipterocarps.

Based on differences in the frequency of recruitment and rate of seedling mortality, Asian Dipterocarp species can be broadly categorised as shade-tolerant or light-demanding. Shade-tolerant Dipterocarps can have seedlings established beneath closed canopied forest for long periods of time (>10 years). However, both groups of Dipterocarps have cohorts of seedlings that continually replenish the seedling bank from successful mast years (Ashton 2014; Ghazoul 2016). Natural disturbances that stimulate the release of existing Dipterocarp seedlings include lightning strikes, insect defoliation of canopy trees, tree falls, and tropical cyclones as these allow the groundstorey vegetation to remain largely unharmed. Disturbances such as landslides, flooding and fire generally destroy groundstorey vegetation and hinder Dipterocarp

regeneration (Appanah and Turnbull 1998).

Many species of Dipterocarps are threatened by deforestation and forest degradation (Ghazoul 2016). Consequently, many in-situ and ex-situ conservation strategies are now being implemented across the region to conserve the existing genetic diversity, including Dipterocarp plantations, nature reserves and community-based conservation programmes.

There are 45 known species of Dipterocarps in the Philippines with the most common ones being *Shorea squamata, Shorea negrosensis, Shorea polysperma, Shorea almon, Shorea palosapis, Shorea contorta, Dipterocarpus grandifloras, Dipterocarpus validus,* and *Vatica mangachapoi* (Margraf and Milan 1996; Co *et al.* 2006).

Pioneer plants of Dipterocarp rainforests

Pioneer plants are defined as species whose successful establishment is limited to forest gaps (Ashton 2014, page 81). Given that forest gaps cover only up to 1% of total area in Dipterocarp rainforests (Ghazoul 2016), pioneer plants comprise only a small fraction of the vegetation community. However, a unique set of life-history traits and a ubiquitous role in vegetation regeneration (Whitmore 1988; Ashton 2014) make pioneer plants a functionally distinct and integral part of Dipterocarp rainforests. Trees are the dominant pioneer growth form in Dipterocarp rainforests today, but many species of tropical grasses and ferns depend on open habitats and are therefore also limited to gaps in forested regions.

Pioneer trees have short to medium longevity and relatively high growth rates in comparison to climax species (Whitmore 1998; Ashton 2014, page 79). They are characterised by a low root to shoot ratio and a low leaf area index, and produce flowers and seeds frequently and in large quantities from an early age. Their small seeds are dispersed over large distanced by wind and animals, and their dormancy capacity ensures an abundant soil seed bank. Germination is usually caused by direct sunlight by means of temperature and/ or light, and seedlings require bare soil for successful establishment. Pioneer trees can rapidly form a new canopy under which their seedlings and seedlings of other pioneer species are unable to regenerate. This leads to their gradual replacement by shade-tolerant seedlings. Important pioneer trees and shrubs in Dipterocarp rainforests include species of *Macaranga, Trema, Melastoma, Dillenia, Alstonia,* and *Eupatorim* (Woods 1989; Davies and Ashton 1999; Co *et al.* 2006; Ashton 2014).

Previous studies have suggested that it is the severity of the disturbance that shapes the composition of pioneer communities. In Southeast Asia, for instance, communities regenerating on land deforested and cultivated for less than two years tend to be dominated by species of *Trema, Macaranga* and *Mallotus* (Kochummen and Ng 1966), whereas communities regenerating on deforested and severely degraded land are initially dominated by species of *Melastoma, Chromolaena* and *Dicranopteris* (Kochummen and Ng 1977), and later by species of *Adinandra, Ploiarium* and *Rhodamnia* (Sim *et al.* 1992). Furthermore, previous work indicates that fire in logged forests leads to severe canopy loss and generates gaps dominated by grasses (e.g. *Imperata cylindrica*), while burnt primary forest experiences less severe canopy damage and thus the abundance of grasses remains low (Woods 1989).

Methodology

Field techniques

Collection of lake sediments

Two overlapping sedimentary sequences were collected as 1-m segments in March 2013 from the smaller basin of Bulusan Lake with a Livingstone Piston corer from an anchored platform. The sediments were sealed in aluminium foil and protective plastic containers, shipped to the University of Oxford and stored at 5°C. The two sedimentary sequences were used to create a continuous, undisturbed composite core that was the focus of the following laboratory analyses.

Laboratory techniques

Age-Depth Modelling

A high-resolution age-depth model for the Bulusan sequence was established using AMS^{14}C dates. The radiocarbon analysis was carried out on identified terrestrial plant macrofossils (e.g. leaves, twigs) to avoid reservoir effects and minimize age uncertainty. AMS samples were measured at the NERC Radiocarbon Facility, East Kilbride. The age–depth modelling of the Bulusan core was performed at 1-cm resolution with the *Bacon 2.2* package (Blaauw and Christen 2011; Blaauw and Christen 2015) using the R version 3.2.4 (R Core Team 2013) and the IntCal13 radiocarbon calibration curve for the Northern Hemisphere (Reimer 2013).

Analysis of terrestrial lipid biomarkers

Terrestrial lipid biomarkers from Bulusan sediments were used to generate a record of past precipitation variability at the site. Hydrogen-isotopic analysis of lipid biomarkers is a recently developed and increasingly important method for studying ancient environments (Sachse *et al.* 2012). Early studies have established that the composition of hydrogen isotopes in individual lipids from aquatic and terrestrial organisms can be correlated with the composition of the environmental water used in their growth (Sauer *et al.* 2001; Huang *et al.* 2002; Huang *et al.* 2004; Sachse *et al.* 2004; Engelbrecht and Sachs 2005). Consequently, compound-specific deuterium/ hydrogen ratios of lipid biomarkers from sedimentary sequences, expressed as δD values, are now widely used as palaeohydrological proxies over a range of geological timescales (Schefuß *et al.* 2005; Pagani *et al.* 2006; Tierney *et al.* 2008; Sachs *et al.* 2009; Rach *et al.* 2014). More recent studies have reported that isotopic fractionation between hydrogen in environmental water and hydrogen in terrestrial and aquatic lipids can be influenced by a range of biochemical, physiological, and environmental factors, highlighting the need to consider these additional effects when selecting particular lipid biomarkers as well as when interpreting palaeohydrological conditions using their δD values (Sachse *et al.* 2012).

In this thesis, I focused on the $nC_{27\text{-}31}$ alkanes because these are the most widely used leaf wax biomarkers, and their hydrogen isotopic composition has been shown as a robust recorder of plant source water δD along extraordinarily steep climatic gradients (Eglinton and Hamilton 1967).

The *n*-alkanes ($nC_{23\text{-}31}$ homologues) from the aliphatic fraction were identified and quantified using a gas chromatograph (GC 7890-A) equipped with a mass selective detector-mass and a flame ionisation detector (FID) (MS 5975-C). Sulphur and unsaturated hydrocarbons were removed from the aliphatic fraction by elution through a pipette column of activated copper powder and a pipette column of an activated mix of silver nitrate and silica gel, respectively. Compound-specific hydrogen isotope ratios of the aliphatic fraction were measured using a ThermoFisher Delta-V-Plus Isotope Ratio Mass Spectrometer coupled to a ThermoFisher TraceGC 1310 gas chromatograph at the University of Potsdam.

Fossil Pollen Analysis

Fossil pollen from the Bulusan sedimentary sequence was used to reconstruct the dynamics of key plant taxa in the landscape surrounding Bulusan Lake. Fossil pollen is a powerful proxy for reconstructing ancient vegetation dynamics for three main reasons: i) the number of pollen grains of a particular plant species is strongly linked to its quantity on a landscape, and ii) fossil pollen are the most abundant and accessible fossils of the Quaternary due to their small size (ca. 10-100 μm), high production rates and good preservation capacity, and iii) the shape and pattern of the outer layer of pollen wall varies across different plant taxa, allowing taxonomic identification of pollen grains upon microscopic examination (Bennett and Willis 2001). Consequently, fossil pollen morphology has been the most commonly used method for reconstructing long-term records of plant dynamics for almost a century.

Fossil pollen counts can be used to estimate both the relative and absolute abundance of plant taxa. In ecology, **relative abundance** is a concept referring to the relative representation of a species in a particular community/ecosystem, while **absolute abundance** is the number of individuals in a given area. In palaeoecology, the relative abundance of a particular taxon is calculated as the proportion of the taxon in the total pollen counts, expressed in percentages. Since proportion of one taxon in the community is influenced by the proportion of other taxa, these measurements are inter-dependent. Absolute abundance of a plant taxon, on the other hand, is approximated using pollen accumulation rates (PARs) which provide independent data points for each taxon. While pollen percentages are used primarily for evaluating community level dynamics (e.g. diversity, dominance), PARs have been used to track the dynamics of individual taxa over time, including their population size (primarily at species level, e.g. Magyari *et al.* 2011; Jeffers *et al.* 2012), abundance (normally for higher level taxa, e.g. Davis 1969; Bjune and Birks 2008), and biomass (e.g. Mazier *et al.* 2012; Jeffers *et al.* 2015).

A comprehensive interpretation of the PARs of a particular taxon requires the consideration of its life history traits. When the size of a plant taxon at the age of first flowering is close to the maximum size of that taxon, then the sizes of flowering individuals across the population is similar. In that case, PARs can be approximated to the number of flowering individuals on a landscape and the use of the term (absolute) abundance is appropriate. However, when the size of a plant taxon at the age of first flowering is considerably smaller than the maximum size of

that taxon, e.g. for large tree species, then PARs are unlikely to provide reliable estimates of absolute abundances because larger trees tend to produce more flowers and, thereby, more pollen. In that case, a more suitable term is biomass. Biomass in ecology is defined as the mass of living organisms in a given area or ecosystem at a given time. As such, it does not depend on the number of individuals, but their total size and/ or weight. Hence, it is usually applied at the population level, growth form level (e.g. tree biomass) or production type (e.g. flower biomass, fruit biomass, woody biomass etc.). Due to scarcity of reliable pollen-biomass calibrations, it is often difficult to translate PARs into absolute unit-based biomass estimates (but see Seppä *et al.* 2009; Mazier *et al.* 2012), and in those cases, relative biomass estimates are more fitting (e.g. Jeffers *et al.* 2015).

Both abundance and biomass estimates from fossil pollen are potentially confounded by changes in pollen productivity over time. Specifically, even the best modern estimates of pollen productivity-plant abundance relationship cannot remove the possibility that this relationship has changed in the past due to internal (i.e. genetics) or external drivers (e.g. climate). Hence, this bias needs to be considered whenever interpreting past plant dynamics from fossil pollen counts. For taxa with regular (e.g. sub-annual to annual) flowering, the fluctuations in pollen productivity have a significant influence on pollen deposition primarily on shorter time scales (1-5 years) while on longer time scales (50s-100s years) it is the changes in taxon density, age and size that exert a dominant effect (Mazier *et al.* 2012). However, for taxa with irregular flowering and/or taxa that (mass) flower on an environmental cue (e.g. Dipterocarp species, some temperate and boreal tree species (Koenig and Knops 1998; Houle 1999; Roland *et al.* 2013), potential changes in pollen productivity can also influence fossil pollen counts on longer time scales.

The terms and processes discussed above have been applied in my thesis in the following manner.

Pioneer plants are short-lived, fast growing and regular flowering species whose size at the age of first flowering is relatively similar to their maximum size (Ashton 2014, page 79). Therefore, on longer time scales, their PARs are likely to reflect their absolute abundances (i.e. number of flowering individuals on a landscape). Therefore, when interpreting pioneer taxa PARs (Chapter 6), I use the term ‘abundance’. In contrast, **Dipterocarp trees** are long lived

and slow growing species whose size at first flowering is normally considerably smaller than their maximum size. Therefore, their PARs may reflect not only the number of Dipterocarps on a landscape, but also their varying sizes. Thus, in this thesis, I interpret Dipterocarp pollen numbers in terms of their relative biomass. Furthermore, since Dipterocarps also have irregular flowering patterns in response to an environmental cue (i.e. drought every 2-7 years), the influence of potential changes in pollen productivity on their PARs also needs to be considered on longer time scales. The production of pollen is directly related to the production of flowers, and the latter falls under reproductive biomass. Consequently, Dipterocarp PARs are likely to capture both woody and reproductive biomass dynamics. This is the approach I used in interpreting the Dipterocarp PARs in Chapters 4 and 5.

In addition to plant abundance/ biomass and pollen productivity, taphonomy can also influence pollen numbers in the fossil record. For instance, changes in the lake level can influence its size and shape, and subsequently, change pollen deposition rates (K. Bennett and Buck 2016). Similarly, changes in the sedimentation rates, due to changes in the biotic activity or soil erosion rates, can alter the concentration of pollen in the sediments (Giesecke and Fontana 2008). Finally, changes in the preservation conditions due to alternating sediment types, drying of the sediments or large time span of the core, can all affect pollen counts along the core. Careful choice of the coring site (e.g. deep anoxic lakes) and use of additional proxies can ensure that these taphonomic factors are avoided and/ or adequately addressed. A robust age-depth model is particularly important for reconstructing and interpreting PARs values because it accounts for changing sedimentation rates and helps to minimize the errors around the time span of the individual samples and time intervals between them (Bennett 1994).

Standardised protocols were employed for the extraction and counting of fossil pollen from Bulusan sediments (Bennett and Willis 2001) from 4 cm long slices of 1 cm^3 volume. Pollen identification was performed using a the newly built reference collection of Dipterocarpaceae pollen (see the following section for more details) as well as previously published material, namely Australasian Pollen and Spore Atlas Online Database (APSA Members 2007), Pollen flora of the Philippines (Bulalacao 1997), and Pollen Flora of Taiwan (Huang 1972). In each sediment sample, 500 terrestrial grains were counted and identified. PARs were calculated as the number of pollen grains accumulated in a particular area size per unit of time (i.e. grains $cm^{-2}yr^{-1}$) according to the standard procedures (Stockmarr 1971; Birks and Birks 2004).

Pollen Reference Collection Building

The Dipterocarp pollen reference collection developed for this study consists of 75 images for identification of 18 Dipterocarp species, 12 of which are present in the Philippines today. The accurate identification of fossil pollen is vital for a valid reconstruction of past plant dynamics, and morphological identification of pollen is heavily reliant on the comparison with modern material (Faegri and Iversen 1964). Consequently, large number of atlases for pollen identification have been produced from virtually every region of the world (e.g. Beug 1961; Faegri and Iversen 1964; Huang 1972; Webb *et al.* 1991; Roubik and Moreno Patiño 1991; Colinvaux *et al.* 2003; Reille 1995). With the advent of computerization and internet, there has been also proliferation of online pollen databases (e.g. Lezine 2005; APSA Members 2007; Bush and Weng 2007; QPG 2008; Gosling *et al.* 2013). However, modern pollen flora from tropical regions remains largely understudied, and the access to the images for tropical pollen identification is patchy (Gosling *et al.* 2013). This is particularly true for Dipterocarpaceae family; whereas there are more than 370 species of Asian Dipterocarps, pollen identification images are provided for only a handful of species. Given the dominance of this family in the Southeast Asian region and their importance for answering the questions posed in this thesis, it was important to build a more elaborate reference collection of Dipterocarpaceae pollen.

Herbarium samples of Dipterocarp species flowers were taken from the Southeast Asian Dipterocarp Collection at the Kew Royal Botanical Gardens. Fully formed but still closed flowers were sampled to minimise the introduction of foreign pollen into the sample. Each sample was treated with a mix of 4 ml of NaOH (10%) and 15 ml of distilled water and left to disaggregate in a water bath at 90 °C for 2-4 mins. Samples were sieved using a mesh size of 150 µm with distilled water to collect fresh pollen. The collected pollen was treated with a acetolysis mixture (9 parts acetic anhydride: 1 part sulphuric acid) in order to remove cellulose and other organic material, and coloured with 0.2% aqueous safranin to make pollen shape and pattern more visible. The pollen samples were then mounted on glass slides and photographed on the Leica MC170 HD microscope camera at 40x magnification. The images are presented in the Appendix A, showing both polar and equatorial views of the grain where it was possible to obtain images. Species are organised by genera and alphabetically.

Fossil charcoal analysis

Macroscopic and microscopic fossil charcoal from the Bulusan sediments were used to create a record of local and regional fire activity, respectively (Clark 1988). Previous research has established that most macrocharcoal particles are deposited within the first km of a fire in forested areas (Peters and Higuera 2007; Duffin *et al.* 2008), and sometimes only within the first 100 m (Lynch *et al.* 2004). Dipterocarp rainforest extends several km in each direction from Bulusan Lake, which ensures that the macrocharcoal source area is within this forest type. While studies in temperate and boreal forests have suggested that further dispersal of macrocharcoal can occur (Whitlock and Millspaugh 1996; Tinner *et al.* 2006; Peters and Higuera 2007), this is unlikely to be the case in tropical forests, where high humidity and absence of strong winds hinders long-distance transport of macrocharcoal particles (McMichael *et al.* 2012). Thus, macrocharcoal particles are standardly used as a proxy for local fire. Microcharcoal particles on the other hand can be lofted to great heights and travel long distances (e.g. 10s of km) (Clark and Patterson 1997). Consequently, this size class of charcoal particles can be deposited from considerably larger distances and is normally used as a proxy for regional or 'background' fire activity (Whitlock and Larsen 2002).

There are several potential drivers of fire activity in an ecosystem, including climate, humans, storms and volcanic eruptions (Bowman *et al.* 2009). Given that fire events caused by different drivers can generate charcoal particles of similar size and shape it is challenging to identify the main drivers of fire activity at a particular site from fossil charcoal analysis alone. In humid environments where natural fire is a rare occurrence (e.g. tropical rainforest) (Scott 2000), high charcoal influx rates in absence of enhanced drought conditions are usually linked to humans (e.g. Bush *et al.* 2008). This is particularly the case where high charcoal rates are coupled with archaeological evidence (e.g. settlement remains, artefacts). Furthermore, previous studies have shown that poor spatial and temporal autocorrelation between charcoal values from the different sites, indicative of discontinuous and asynchronous fires, can also be linked to isolated human-made fires (Bennett *et al.* 1990). This is a particularly useful approach in understudied regions such as the tropics where archaeological evidence is sparse. However, storms and volcanic eruptions can also generate frequent yet isolated fire events (Wilmshurst and McGlone 1996; Beckage *et al.* 2008; Zhao *et al.* 2015). Subsequently, in areas with a high occurrence of storms

and/ or volcanic eruptions, such as the Philippines, the link between discontinuous and asynchronous fire patterns and human activities in the sediment record is less straightforward.

For building the macro- and micro-charcoal records, 4 cm long slices of 1 cm^3 volume were taken from the sediment cores in a continuous fashion. Each sample was treated with a mix of 4 ml of NaOH (10%) and 15 ml of distilled water and left to disaggregate in a water bath at 90˚ C for 7 mins. Samples were then sieved using a mesh size of 150 μm with distilled water to collect macroscopic charcoal (particle size >150 μm). The extracted macroscopic charcoal was then counted on a Nikon stereoscope at 18x magnification. Macrocharcoal influx rates were calculated by dividing the total number of macrocharcoal particles counted in each sample with the corresponding sediment accumulation rate (Clark 1988; Mooney and Tinner 2010). Influx rates of microcharcoal particles (particle size <150 μm) were measured by counting the total number of microcharcoal particles in each sample, calculating its concentration using known marker concentrations and then dividing it with the corresponding sediment accumulation rate.

Textural and geochemical analysis of sediments

X-ray fluorescence (XRF) spectroscopy analysis of the Bulusan sedimentary sequence was undertaken using the ITRAX Core Scanner (Croudace *et al.* 2006) at Arhus University, Denmark, in order to obtain detailed optical, radiographic and geochemical profiles of the Bulusan sequence. Itrax XRF spectroscopy is a non-destructive, semi-quantitative method used to provide high-resolution data on the geochemical variations in a sediment core. Optical and radiographic profiling is used for analysing the textural stratigraphy of sediment cores, including sediment laminations (i.e. sequences of fine sediment layers differing in colour and density, often of annual resolution) (O'Sullivan 1983) and sediment deformations (e.g. slumping) (Bennett 1986). Full details of the methods and radiometric limitations of the machine are given in Croudace *et al.* (2006).

Bulusan core sections were scanned at a step-size of 0.2 mm to obtain the ED-XRF spectrum at each step. A digital continuous-strip X-radiograph, 22 mm in width and of the same scanning resolution, was collected immediately prior to the XRF scan using a charge-coupled (CCD) line camera. The count time for each measurement was 30 seconds to ensure that minor elements were well detected. The X-ray beam used to irradiate the core was generated using a 3 kW Mo

X-ray tube run at 55 kV and 50 ma for x-radiography and 30 kV and 50 ma for the XRF scan. The recorded spectra were deconvolved in live time to construct profiles of peak area integrals for individual elements. The element peak area, presented in counts per second, reflects element abundances within the sediment. We calculated the mean average of the peak areas for each element of interest for 4 cm long slices to align the data with the sample resolution of other fossil proxies (e.g. pollen, charcoal).

Magnetic susceptibility analysis

Magnetic susceptibility analysis was performed on the Bulusan sequence in order to detect any tephra layers and changes in soil erosion rates. Magnetic susceptibility readings measure the relative abundance of iron oxides in the sediment (Gubbins and Bervera 2008), and as such can be used as a proxy of soil-water content, erosion events and sediment regimes (Balsam *et al.* 2011). In general, smaller and more negative values indicate higher proportion of diamagnetic compounds (Hunt and Premathilake 2012) such as soil moisture (Grimley *et al.* 2008) and organic matter (Hamilton *et al.* 1986). Magnetic susceptibility has been shown to be particularly useful for detecting the presence of tephra layers in lacustrine sequences because tephra is usually rich in ferromagnetic material, which shows up as positive peaks in a magnetic susceptibility record (Oldfield *et al.* 1983a; Oldfield *et al.* 1983b; Oldfield 1988; Lozano-García *et al.* 1993).

Magnetic susceptibility was measured on intact Bulusan cores using the Barrington MS2 Magnetic Susceptibility System made of a magnetic susceptibility meter coupled with a core logging sensor. The analysis was done at 2 cm spatial resolution and a measurement period of 11s SI (9s CGS).

Statistical techniques

Generalised Linear Least Squares

The relationship between ecological and environmental variables in the Bulusan sediments was assessed using the Generalised Linear Least Squares (GLS). This is a linear fixed-effects model that permits errors to be correlated and/ or have unequal variance (Pinheiro and Bates 2009).

I applied several GLS models using different combinations of temporal correlation and variance

structures imposed on the error components to allow unequal variance of the errors. Errors were specified to follow an autoregressive and moving average (ARMA) process and variance structure was defined with explanatory variables as variance covariates. Several mean model structures were examined including different combination of relevant explanatory variables and their interactions, starting with the most complicated model and consecutively removing insignificant variables. The validity of individual models was then evaluated using diagnostic tests (Galecki and Burzykowski 2013). The best fitting model with satisfying diagnostics was selected based on the lowest Akaike Information Criterion (AIC) coefficients with a simpler model selected whenever the difference in AIC coefficients between two models was smaller than 2. Models were considered significant at the 95 % level of confidence. Positive and negative slopes are indicated as (+) or (−), respectively. Where appropriate, we compared models with different response lags to determine the most likely rate of response. Prior to the final model running, we removed any points with zero pollen counts as well as any strong outliers.

Sequential T-test Analysis of Regime-Shifts algorithm

The Sequential T-test Analysis of Regime-Shifts algorithm (STARS) algorithm (Rodionov 2004; Rodionov 2006) was used to detect significant changes in the mean of PARs and of the different environmental proxies (e.g. Seddon *et al.* 2014). STARS enables detection of a regime shift in a variable's mean and subsequent monitoring of temporal changes in its magnitude. Unlike most other methods for an automatic detection of discontinuities in a time series, the performance of the STARS algorithm does not diminish drastically at the ends of the series, and thus, shifts in these parts of the record can also be readily detected. Additionally, the algorithm can be easily used for an automatic calculation of multiple regime shifts in large sets of variables. The method also allows flexibility in choosing the size of time window, sensitivity to outliers and p-value cut off.

To address uneven spacing of the Bulusan samples, each time series was sorted into the smallest bins that still generated a continuous record, and then standardized by the mean and standard deviation. Since the STARS algorithm assumes normality and does not explicitly account for autocorrelations, the time series were transformed to normal distribution using Box Cox transformation and passed through a white-noise filter using the ordinary least-squares method

outlined in Rodionov (2006) prior to the application of the STARS algorithm.

Generalised Nonlinear Least Squares

To determine the shape and abruptness of the significant changes in the mean state of the relevant time series records that were first detected with the STARS algorithm, a set of models representing changes in mean state and variance were fitted to the records using Generalised Nonlinear Least Squares (GNLS) (Carstensen and Weydmann 2012; Seddon *et al.* 2014). Similar to the GLS models, GNLS allow for errors to be correlated and/ or have unequal variance. I applied several GNLS models (i.e. null, linear, step mean and segmented) and used temporal correlation and variance structures on the error components to allow unequal variance of the errors. Errors were specified to follow an autoregressive and moving average (ARMA) process and variance structure was fixed to the variance of the time series. The best fitting model was selected based on the lowest AIC coefficients with a simpler model selected whenever the difference in AIC coefficients between two models was smaller than 2.

Principal Component Analysis

Principal Component Analysis (PCA) was performed to assess the temporal relationship between multiple variables, identify any distinct groups and graphically illustrate the nature of such associations. PCA belongs to a set of multivariate ordination methods which are often used in ecological analysis to investigate co-variation in datasets with a large number of variables (Smilauer 2014). These methods quantify similarities between individual samples in a dataset using a distance gradient (e.g. Euclidean distance) and then rank the samples according to their similarities. The given scores allow them to be plotted and subsequently grouped on a multi-dimensional ordination plot. Indirect gradient analyses such as PCA are exploratory analyses used to describe associations between samples and response variables of interest, whereas direct gradient analysis, e.g. Redundancy Analysis (RDA), are used to determine which explanatory variables are responsible for trends in the response variables and among the samples.

Table 1 | Overview of the methodology used in the four research chapters (manuscripts).

Chapter	Materials	Lab techniques	Records generated	Records used	Statistical techniques
Chapter 3 (Manuscript 1)	Bulusan sediments	• Age-depth modelling • Lipid biomarker analysis • Optical and radiographic sediment profiling	• Deuterium/ hydrogen ratios of leaf wax alkanes • Optical and radiographic profiles of the sediments	• Deuterium/ hydrogen ratios of leaf wax alkanes • Optical and radiographic profiles of the sediments • Other hydrological and SST records from tropical Pacific • Instrumental records	• STARS • GNLS
Chapter 4 (Manuscript 2)	• Bulusan sediments • Herbarium samples	• Fresh pollen analysis • Fossil pollen analysis • Charcoal analysis	• Pollen reference collection • Dipterocarp PARs • Charcoal influx rates	• Pollen reference collection • Dipterocarp PARs • Charcoal influx rates • Deuterium/ hydrogen ratios of leaf wax alkanes	• GLS • STARS
Chapter 5 (Manuscript 3)	Bulusan sediments	• XRF spectroscopy analysis • Magnetic susceptibility analysis	• Chemical element abundances • Magnetic susceptibility measurements	• Dipterocarp PARs • Chemical element abundances • Magnetic susceptibility measurements	• GLS • PCA
Chapter 6 (Manuscript 4)	Bulusan sediments	/	/	• Pioneer taxa PARs • Charcoal influx rates • Deuterium/ hydrogen ratios of leaf wax alkanes	• GLS • STARS

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CHAPTER 3: ENHANCED EL NIÑO/ SOUTHERN OSCILLATION DYNAMICS IN THE TROPICAL PACIFIC DURING THE LITTLE ICE AGE

Abstract

The El Niño/ Southern Oscillation (ENSO) has a profound impact on oceanic and atmospheric circulation, shaping temperature and precipitation patterns worldwide. Problems with simulating realistic ENSO dynamics are introducing large uncertainties into future climate projections. Robust estimates of the magnitude and rate of past changes in ENSO state can help constrain these simulations, but there is a scarcity of high-resolution hydrological records in which ENSO driven changes can be distinguished from those caused by other precipitation drivers. This is particularly true for the Common Era, which is marked by major shifts in the Intertropical Convergence Zone (ITCZ) position during the Little Ice Age (LIA), i.e. ~AD 1300-1850. To address this problem, we generate a new high-resolution hydrological record from northern Philippines using the hydrogen isotope composition of terrestrial lipid biomarkers (δD_{wax}) from a 1,400-year old laminated lake sedimentary sequence. Results show a dramatic and abrupt increase in δD_{wax} values between ~AD 1650-1900, indicating significantly drier conditions in the region during this time. Given that precipitation at the site is predominately shaped by ENSO, we argue that the observed change signifies the weakening of the Pacific Walker circulation (PWC) and the persistence of an El Niño-like state. Our record is the first hydrological record to clearly support El Niño-like conditions during the LIA, and demonstrate that change from one ENSO state to another can occur within a 20-year span, i.e. well within the lifetime of a human generation. These findings have important implications for predicting the potential direction and rate of future changes in ENSO dynamics.

Introduction

There is a long-standing debate about the dynamics of the El Niño/ Southern Oscillation (ENSO) system during the Little Ice Age (LIA) and its influence on tropical hydrology, fuelled by conflicting evidence from sea surface temperature (SST) reconstructions and hydrological records. SST reconstructions show relative warming in the eastern (Conroy *et al.* 2008; Conroy *et al.* 2010) and central tropical Pacific (Cobb *et al.* 2003) and cooling in the western equatorial Pacific (Newton *et al.* 2006; Oppo *et al.* 2009), suggesting a more El Niño-like state in comparison to the conditions before and after this time interval. In contrast, the majority of hydrological records demonstrate wetter conditions in the Indo-Pacific (Tierney *et al.* 2010; Rodysill *et al.* 2011; Zeng *et al.* 2012, Yan *et al.* 2015), and drier conditions in the central (Sachs *et al.* 2009) and the eastern equatorial Pacific (Moy *et al.* 2002; Conroy *et al.* 2008; Nelson and Sachs 2016) during the LIA, indicative of enhanced Pacific Walker Circulation (PWC) and a La Niña-like phase during the LIA. The cause of this conflict may be at least partly related to the existence of two prominent sources of precipitation in the tropical Pacific. In addition to the PWC, hydrological conditions in many parts of the region are strongly influenced by the position of the Intertropical Convergence Zone (ITCZ). Due to marked shifts in the ITCZ position during the Holocene, it is difficult to differentiate the role of the two drivers in shaping the observed palaeohydrological patterns (Atwood and Sachs 2014). Further uncertainties stem from the unresolved question of the exact position and shape of the ITCZ and monsoonal zones during the LIA. One interpretation, based primarily on hydrological records from the central and eastern Pacific, suggests that the ITCZ shifted southwards during the LIA (Sachs *et al.* 2009). An alternative theory suggests that a contraction of ITCZ and subsequent reduction in both the East Asian Summer Monsoon (EASM) and Australian Summer Monsoon (ASM) has taken place in the western Pacific during the LIA (Yan *et al.* 2015), resulting in relatively dry conditions at the northern limit of the EASM and southern limit of ASM, and more precipitation in the central part of the region.

To address this issue, records from the western Pacific are needed that can tease apart the ENSO signal from the ITCZ signal, either by offering independent proxies for each of the two phenomena, or by selecting sites that are largely influenced by one or the other. We have generated a new hydrological record of bi-decadal resolution from a sedimentary sequence obtained from Bulusan Lake (12°45' N, 124°6' E), Sorsogon province, Philippines (Figures 1-

2), using δD values of higher plant leaf wax alkanes. Instrumental data show that ENSO dynamics are the main driver of local inter-annual precipitation variability at the Bulusan site while northern migration of ITCZ during the boreal summer (June to September) brings comparatively small amounts of precipitation (Figure S1 in Supplementary Information). Consequently, the Bulusan record is excellently poised to provide new insights into ENSO dynamics and its role in shaping hydrological processes in tropical Pacific during the LIA.

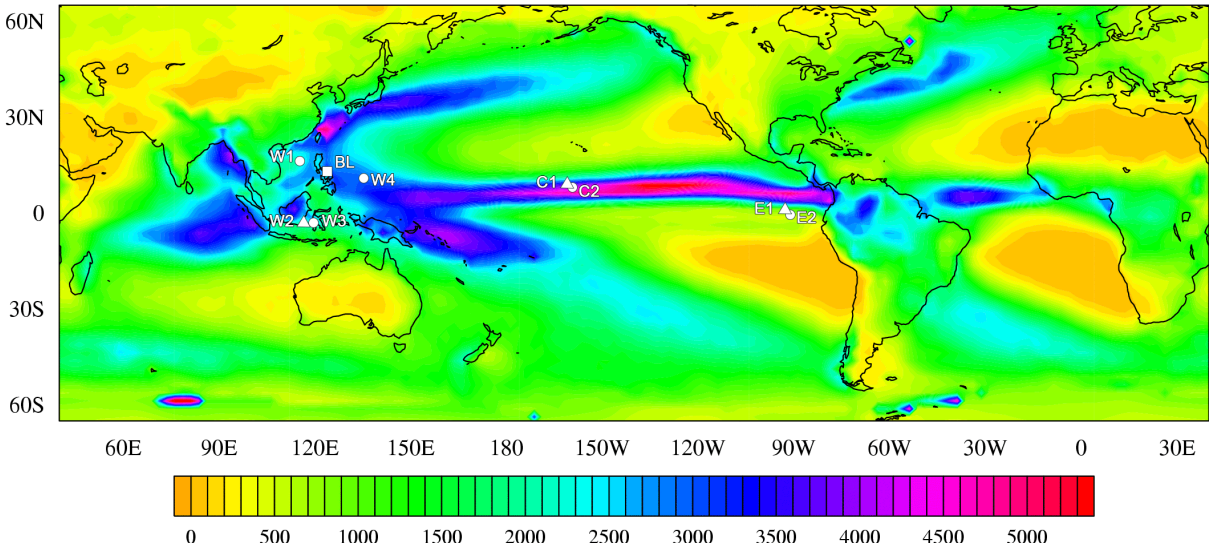


Figure 1 | Map of mean annual precipitation in the tropical Pacific showing the location of our study site, Bulusan Lake (BL, square) and the locations of other relevant hydrological (circles) and sea surface temperature records (triangles). In the western Pacific, Dongdao Island, W1 (Yan *et al.* 2011), Makassar Strait, W2 (Newton *et al.* 2006; Oppo *et al.* 2009) and W3 (Tierney *et al.* 2010)) and Palau Island, W4 (Sachs *et al.* 2009). In the central Pacific, Palmyra Island, C1 (Cobb *et al.* 2003) and Washington Island, C2 (Sachs *et al.* 2009). In the eastern Pacific, El Junco Lake, E1 (Conroy *et al.* 2008) and Poza de la Diablas, E2 (Nelson and Sachs 2016) in the Galapagos Islands. The band of heavy precipitation indicates the ITCZ. Data from Wallace *et al.* (1995).

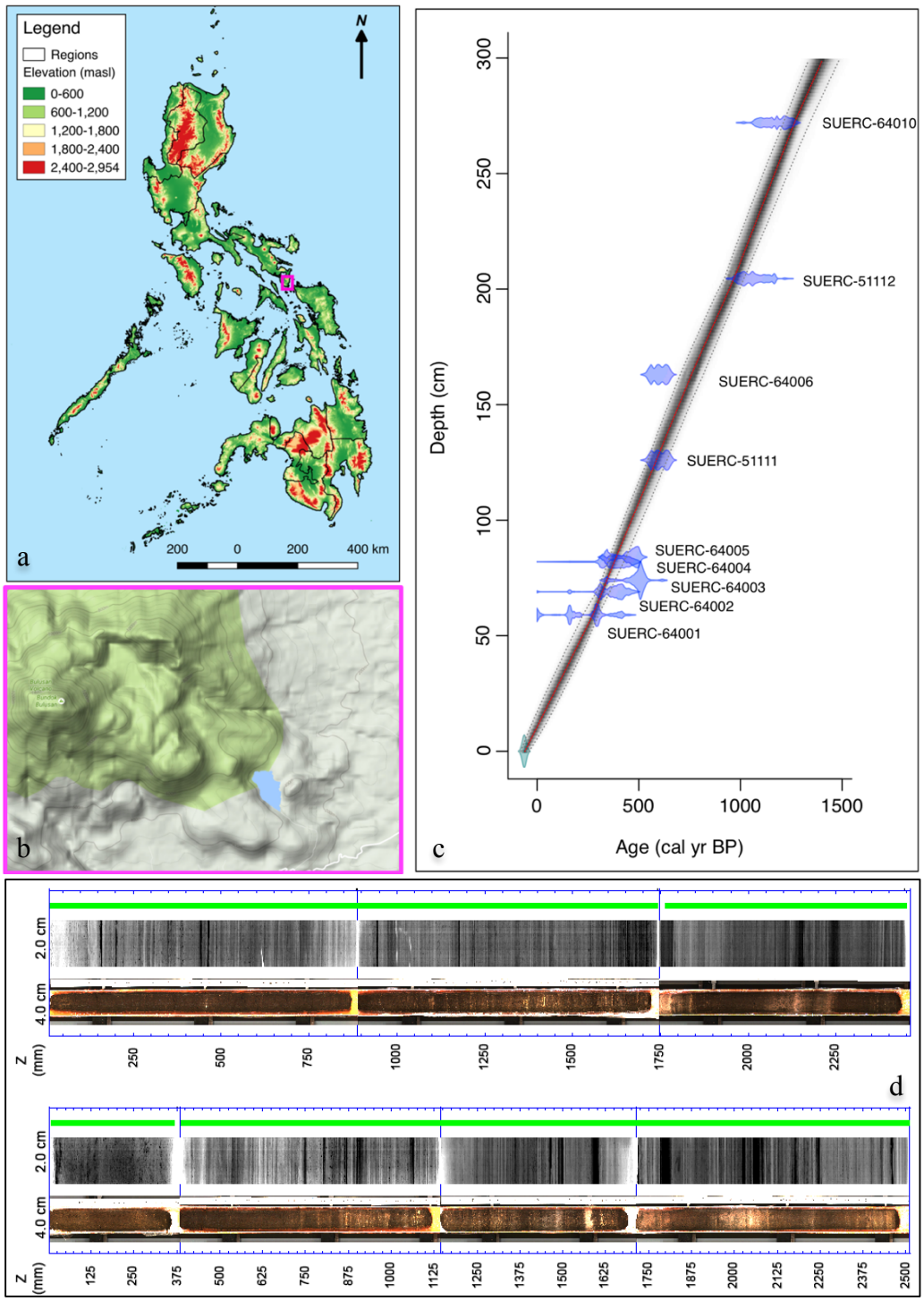


Figure 2 | Geographical and sedimentological features of the Bulusan site. a, Topographic map of the Philippines showing the location of our study site. Data from PhilGIS (PHILGIS 2016), map generated in QGIS version 2.14.3 (Quantum GIS Development Team 2016). **b,** Map showing Bulusan Lake (in blue) within its larger landscape, with Mt Bulusan volcano in the west (in green) (Google 2016). **c,** Age-depth model for the Bulusan sediment sequence, constructed in *Bacon 2.2* (Blaauw and Christen 2015). Probability distributions for the nine radiocarbon calibrations are shown in blue. SUERC-64011 is not shown here as it lies below the analysed section. The shaded areas represent the 1σ probability age ranges by interpolating between ^{14}C age control points. The red dashed line represent the age-depth calibration used in further analysis. **d,** Optical and radiograph profiles of the Bulusan sediments used in this study. The radiograph images depict the level of organic content, with higher values shown as lighter bands. The green line represents the validation of the measurement quality along the cores. Images generated in ItraxPlot program (Croudace and Rothwell 2015).

Results

Lake sediment records and their hydrological implications

The top 300 cm from two overlapping sediment cores (BUL1 and BUL2) collected from Bulusan Lake provides a continuous, undisturbed sedimentary sequence spanning the last 1,400 years (Figure 1d) (relevant section in Methods and Supplementary Information). An independent and precise age-depth model (Figure 1c) has been established using 10 AMS^{14}C dates (Table S1 in Supplementary Information). Bulusan sediments contain abundant terrestrial lipid biomarkers, specifically the n-alkanes with 27, 29 and 31 carbon atoms ($nC_{27\text{-}31}$) over this time period. We report H/D isotope ratio measurements of these alkanes (expressed as δD values), as well as an independent record of grass pollen abundance from the same sedimentary sequence to ensure adequate identification of biomarker sources (Figure 3, relevant sections in Methods and Supplementary Information).

The $nC_{27\text{-}31}$ alkanes are a major component of the leaf waxes of higher terrestrial plants (Eglinton and Hamilton 1967). At Bulusan these alkanes probably originated from leaves of the angiosperm trees, which dominate Dipterocarp forests, possibly with minor input from grasses. δD values of these alkanes (δD_{wax}) in the surface sediments of smaller lakes fed by precipitation and ground water, such as Bulusan Lake, are significantly correlated with rainfall δD values, offset by a biosynthetic fractionation (Aichner *et al.* 2010; Sachse *et al.* 2012). Modern precipitation δD values (δD_{precip}) show a strong negative correlation with precipitation amount in the areas within the equatorial Pacific where the correlation coefficient between the Southern Oscillation Index (SOI) and precipitation is above 0.6 (Trenberth and Caron 2000), including the area of our study site. δD_{wax} values can be additionally affected by evaporative deuterium enrichment of leaf water due to increased evapotranspiration under low atmospheric humidity (Sachse *et al.* 2012; Kahmen *et al.* 2013). At Bulusan, where relative humidity is high year round, leaf water isotope enrichment is expected to be minimal (Kahmen *et al.* 2013), and therefore δD_{wax} at the site should faithfully record changes in δD_{precip}.

The δD values of the three abundant terrestrial lipid biomarkers, $nC_{27\text{-}31}$, are highly correlated in the Bulusan core, with an r^2 ranging between 0.69 and 0.81 (Figure S2 in Supplementary Information), confirming a common origin of these alkanes. Fossil pollen from the same

sedimentary sequence reveals that the plant assemblages surrounding the lake during the last 1,400 years contain only a small fraction of grasses (Figure 3) and were dominated by trees and shrubs (e.g. *Syzygium*, *Elaeocarpus*, *Ficus*, *Macaranga*), the likely source of the $nC_{27\text{-}31}$ alkanes. The percentage of grass pollen remained between 0-5% throughout the record, indicating that there was no major change in the proportion of C_4 to C_3 plants, and rules out the possibility that vegetation changes have significantly affected δD_{wax} values (Sachse *et al.* 2012). However, the nC_{27} alkane showed higher variability in comparison to nC_{29} and nC_{31}, indicating more variable sources (Figure 3). Previous studies have suggested that nC_{31} dominate grasses and herbs (Schwark *et al.* 2002), so we focus our interpretation on the nC_{29} alkane to decrease further the potential distortion of the precipitation signal due to D-enrichment differences between C_3 and C_4 plants.

Large fluctuations in δD values of nC_{29} of up to 45‰ indicate significant hydrological changes at Bulusan Lake over the last 1,400 years (Figure 3). Relatively low and stable δD_{wax} values occur during AD 600-1600, followed by a distinct and abrupt increase in δD values at ~AD 1650 (i.e. 20‰ over the time period of ~20 years, see Tables S2-S3 and Figures S3-S4 in Supplementary Information). Based on the observed modern relationship between δD_{precip} and precipitation amount, a 20‰ increase in δD_{precip} would correspond to the reduction of annual rainfall by ~500-850 mm (Table S4 and Figure S5 in Supplementary Information). These high δD_{wax} values persist until ~AD 1900 only to drop just as abruptly to their lowest values in the record over the last 100 years. Based on these δD_{wax} values, we infer significantly lower precipitation at Bulusan Lake during the latter half of the LIA (~AD 1650–1900), compared to the rest of the examined record.

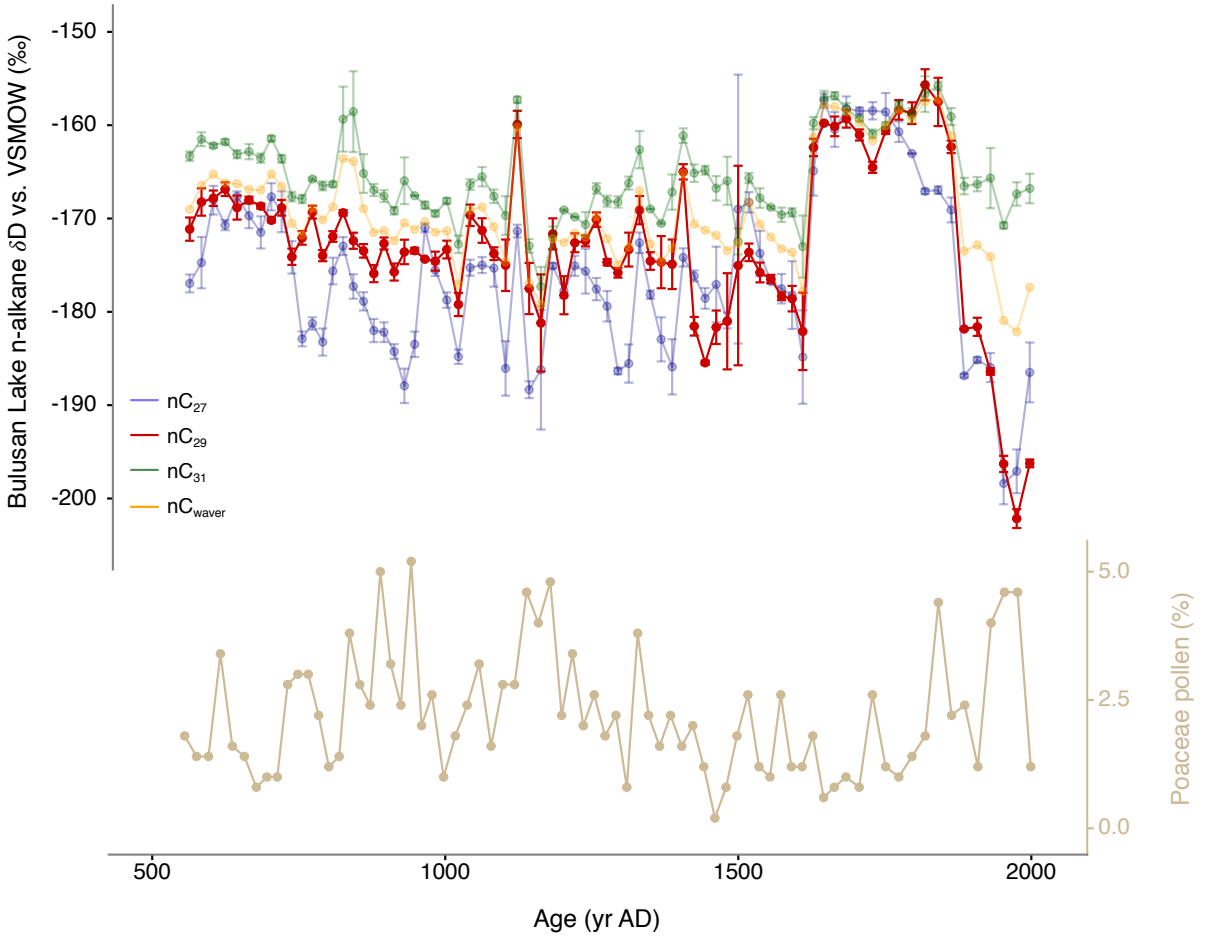


Figure 3 | Palaeorecords from the Bulusan site. A record of H/D isotope ratio measurements of leaf wax alkanes, expressed as δD values with error bars of 1 standard deviation (nC_{waver} is weighted average of the $nC_{27\text{-}31}$ alkanes based on their concentrations in the sediment samples), and a record of grass pollen abundance, expressed as the percentage of total terrestrial pollen. Data plotted with *ggplot2* package (Wickham 2009) in R version 3.2.4 (R Core Team 2013).

Discussion

In previous research three explanations have been put forward to account for rainfall changes in the western Pacific during the LIA: i) a southward shift of ITCZ (Sachs *et al.* 2009), ii) a contraction of the ITCZ/monsoon belt (Yan *et al.* 2015) and iii) a change in the strength of ENSO and the associated PWC (Yan *et al.* 2011). Given the location and precipitation sources of the Bulusan site, as well as the direction, timing and magnitude of the precipitation change in the Bulusan record, we can reject the first two hypotheses as follows. Presently, ITCZ in the continental portion of the western Pacific migrates between 25° N (July) and 15° S (January) (Newton *et al.* 2006). Given the latitudinal position of Bulusan Lake (12.7° N), a 5° movement of ITCZ to the south in the central Tropical Pacific Ocean (Sachs *et al.* 2009), where the ITCZ

is much more constrained, would still leave our site well within the range of the seasonal ITCZ movements over the continental areas during the boreal summer, making it an unlikely driver of the significant precipitation reduction observed in the record. Indeed, two sites in the South China Sea, Dongdao Island (Yan *et al.* 2011) and Huguangyan Lake (Zeng *et al.* 2012), with more northern locations than Bulusan Lake (16.7° N and 21° N, respectively) and with intra-annual rainfall patterns that are strongly correlated with ITCZ migration, have not experienced dry conditions during the LIA. On the other hand, the postulated contraction of the ITCZ/ monsoon belt during the LIA (Yan *et al.* 2015) would cause an increase in the precipitation at the site given its central position in the western Pacific, which is opposite to our observations. The timing of the rainfall shift in the Bulusan record is also indicative of its weak response to the ITCZ changes. ITCZ shifts observed in previous studies have been linked to the period of low solar irradiance between AD 1400-1750, which would provide the forcing to cool either the northern hemisphere, i.e. in the case of the hypothesised southward ITCZ shift, or both hemispheres, i.e. as suggested in the 'ITCZ contraction' theory. This period of low solar irradiance has little overlap with the observed rainfall change at the Bulusan Lake (~AD 1650-1900), even if we consider the uncertainties of the Bulusan sequence's age-depth model (Figure S6 in Supplementary Information). As such, we rule out that the abrupt precipitation reduction at Bulusan Lake at ~AD 1650 was driven by changes in the ITCZ position or its latitudinal extent.

We propose that a weakening of the PWC and the establishment of an El Niño-like state was responsible for these hydrological changes at the western rim of the Tropical Pacific Ocean. This is corroborated by tropical Pacific SST records which suggest the rise of cooler conditions in the western Pacific (Newton *et al.* 2006; Oppo *et al.* 2009) and warmer conditions in the central and eastern Pacific (Cobb *et al.* 2003; Conroy *et al.* 2008; Conroy *et al.* 2010) during this time period (Figure 5). In contrast, other hydrological records from the region indicate the opposite situation, i.e. wetter conditions in the western Pacific and drier conditions in the central and the eastern Pacific during the LIA (between ~AD 1300-1700) (Figure 4). However, it must be noted that most of these records come from sites where total precipitation is significantly influenced by ITCZ, and therefore, the ITCZ-driven changes may be 'masking' the ENSO-driven changes. Consequently, these records do not conflict with our findings; rather our data reconcile the observed changes in SST with hydrological changes. Furthermore, some of these

records show a slight decrease in precipitation in the western Pacific (i.e. Dongdao Island (Yan *et al.* 2011) and Makassar Strait (Tierney *et al.* 2010)) and increased precipitation in the central and eastern Pacific (i.e. Washington Lake (Sachs *et al.* 2009) and Poza de la Diablas (Nelson and Sachs 2016)) between AD 1600 and 1900 (Figure 4) which provides further support to our conclusion. For a more detailed comparison of the Bulusan record with other regional records, see the relevant section in Supplementary Information.

Our data also suggest that changes from one ENSO state to the other can occur on decadal timescales and well within the lifetime of a human generation. The shift from weak to strong ENSO regime recorded at the Bulusan site at ~AD 1650 happened over the period of only ~20 years, as did the subsequent return to the weak regime ~250 years later. This finding is in accordance with other SST reconstructions from the region. For instance, Conroy *et al.* (2010) used a lake sediment record from the Galápagos archipelago located in the eastern equatorial Pacific cold tongue (Conroy *et al.* 2008) and a high-resolution marine sediment record from the Makassar Strait in the Indo-Pacific warm pool (Oppo *et al.* 2009) to reconstruct the changes in the zonal gradient of tropical Pacific SST (Figure 5). They found that the change to a state of weak SST zonal gradient, interpreted as El Niño-like conditions, happened over the course of a couple of decades, similarly to the precipitation shifts recorded in the Bulusan record. The Palmyra record from the central tropical Pacific (Cobb *et al.* 2003) also suggests a rapid, though more linear, rise and termination of the marked period of low SST values recorded during the LIA (Figure 5). Together, these findings help to constrain the upper rates of change in ENSO dynamics.

In conclusion, our results demonstrate that the Bulusan site has experienced a rapid and pronounced reduction in precipitation during the LIA. We postulate that this is due to weakening of the PWC and rise of an El Niño-like state. This finding is important because unlike most other hydrological records in the region, it corroborates the numerous SST records that indicate El Niño-like state in Southeast Asia during the LIA. Our results do not conflict with the evidence of ITCZ changes during LIA provided by other hydrological records in the region because our site is unlikely to be significantly influenced by such changes due to its latitudinal position and precipitation sources. Instead, our findings suggest that, in addition to changes in the ITCZ position, the hydrology of the region during the last millennium has also been profoundly influenced by notable changes in the ENSO dynamics. Finally, our data also

provide further evidence that a change from one ENSO state to the other can occur on decadal scales, highlighting the need for factoring such rapid rates of change into future climate projections.

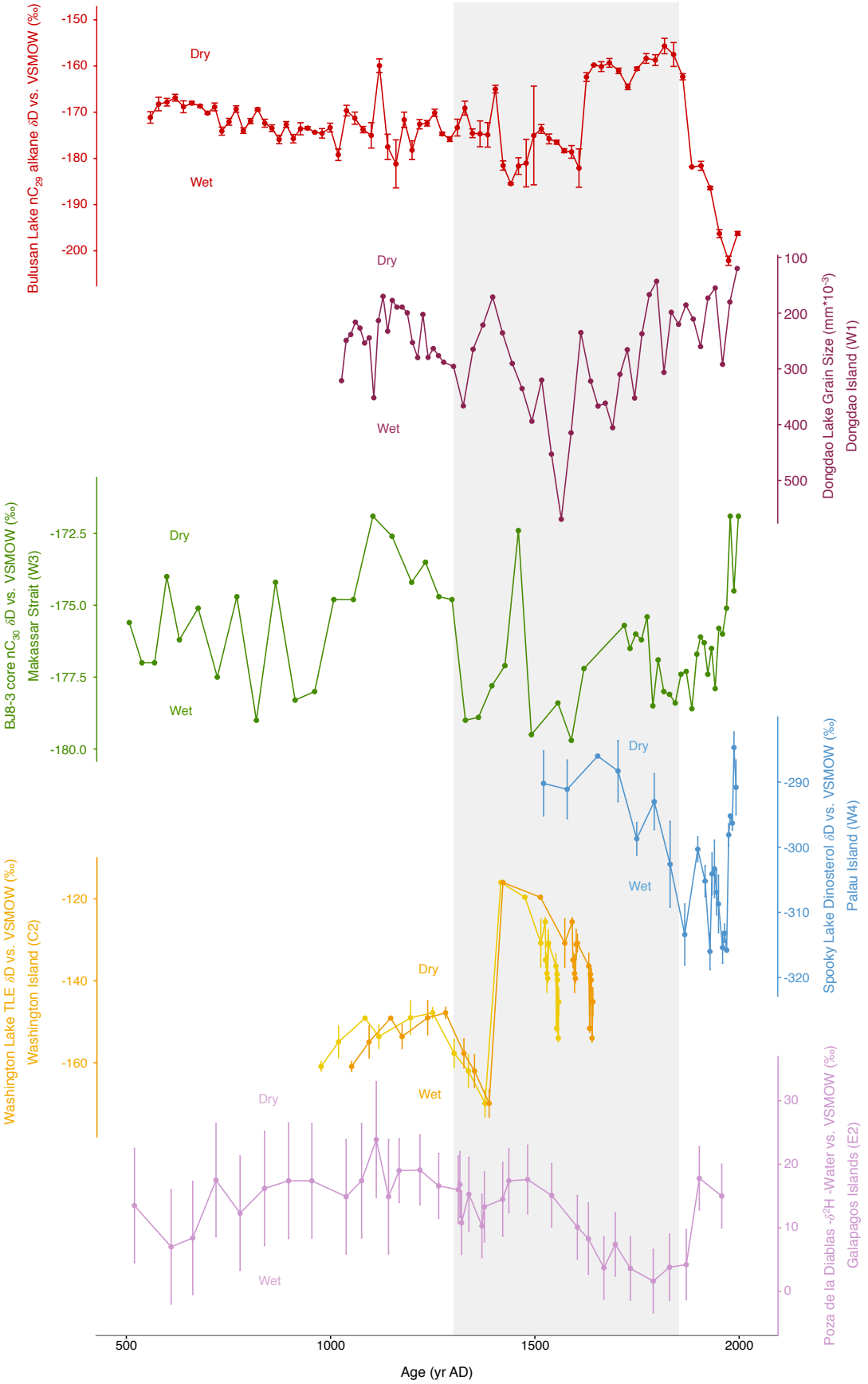


Figure 4 | Comparison of Bulusan record (nC_{29} alkane δD values) with other regional palaeohydrological records. In the western Pacific, Dongdao Lake, W1 (Yan *et al.* 2011), Makassar Strait, W3 (Tierney *et al.* 2010) and Spooky Lake, W4 (Sachs *et al.* 2009). In the central Pacific, Washington Island, C2 (Sachs *et al.* 2009), and in the eastern Pacific, Poza de las Diablas, E2 (Nelson and Sachs 2016). Data plotted with *ggplot2* package (Wickham 2009) in R version 3.2.4 (R Core Team 2013). Grey strip denotes the Little Ice Age (AD 1300-1850).

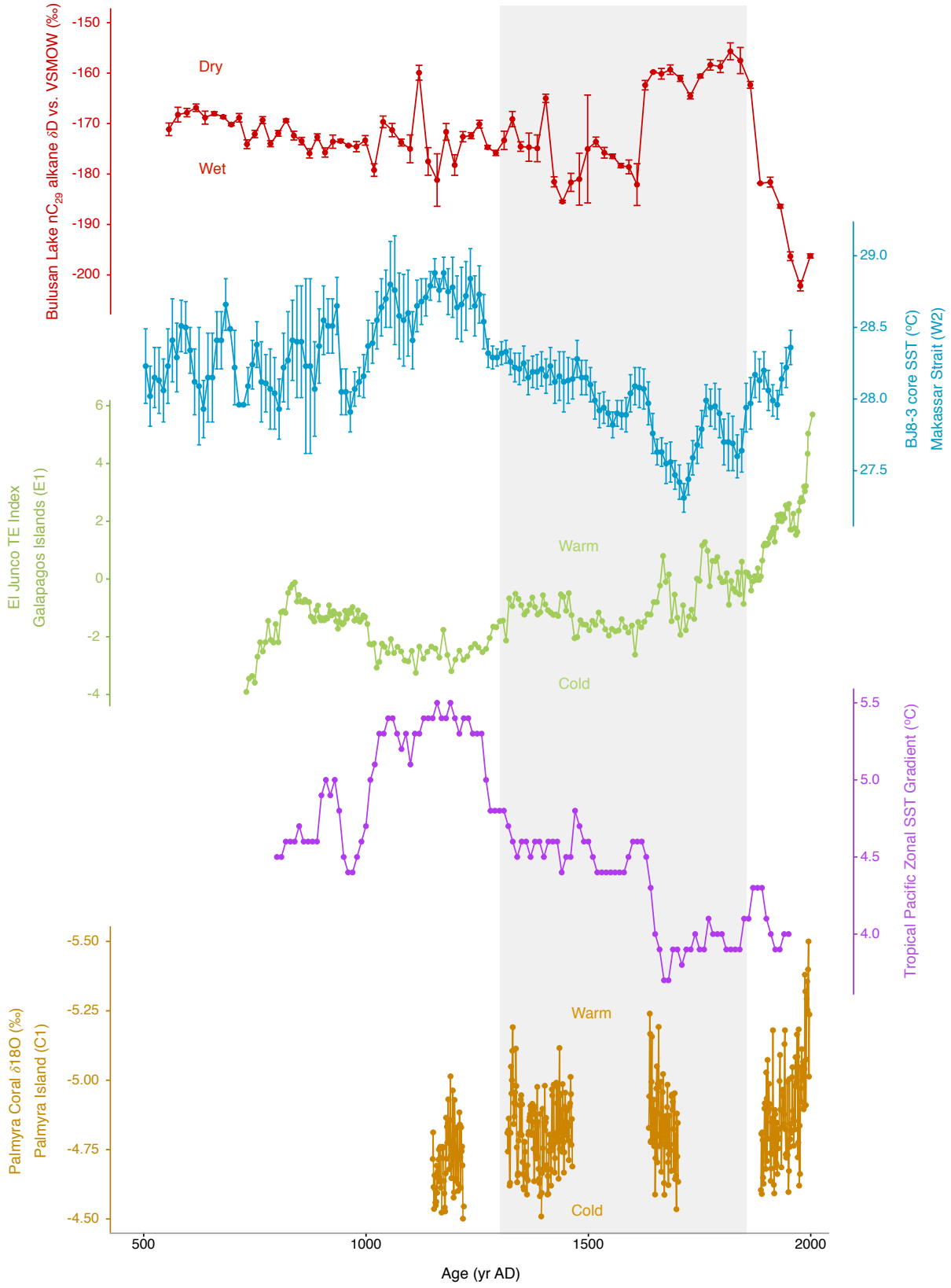


Figure 5 | Comparison of Bulusan record (nC_{29} alkane δD values) with the regional SST records. In the western Pacific, Makassar Strait, W2 (Newton *et al.* 2006; Oppo *et al.* 2009), in the central Pacific, Palmyra Coral, C1 (Cobb *et al.* 2003), and in the eastern Pacific, El Junco Lake in the Galapagos Islands, E1 (Conroy *et al.* 2008). Data plotted with *ggplot2* package (Wickham 2009) in R version 3.2.4 (R Core Team 2013). Grey strip denotes the Little Ice Age (AD 1300-1850).

Methods

Sediment samples were extracted at the University of Oxford as a continuous series of 4 cm long slices (i.e. 2-6 g dry weight per sample) from a 300 cm long sequence, with each slice corresponding to a ~20-year interval. The samples were freeze-dried and lipid biomarkers extracted at the University of Potsdam with a dichloromethane (DCM): methanol mixture (9:1) at 100 °C and 103 bar using a Dionex accelerated solvent extraction system (ASE) 350. The extracts were separated into aliphatic and aromatic/alcohol/fatty acid fractions by solid phase extraction in 8 ml glass columns filled with 2 g silica gel using hexane and DCM: methanol mixture (9:1) as solvents, respectively. Compound-specific hydrogen isotope ratios of the aliphatic fraction were measured in triplicates[1] using a ThermoFisher Delta-V-Plus Isotope Ratio Mass Spectrometer coupled to a ThermoFisher TraceGC 1310 gas chromatograph at the University of Potsdam. A standard containing nC_{16} to nC_{30} alkanes with known δD values (mix A4 was obtained from Arndt Schimmelmann, University of Indiana) was measured in duplicate at the beginning and the end of each sequence or after six sample injections, and then used for conversion of δD values to the Vienna Standard Mean Ocean Water (VSMOW) scale. The record of grass pollen abundance, expressed as the percentage of total terrestrial pollen, was generated using fossil pollen counts from the Bulusan core at the same extent and resolution as the δD_{wax} records. Further technical information, including the additional data analyses, is provided in Supplementary Information.

[1] A small set of samples has been measured in duplicates due to low compound concentrations.

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Supplementary Information

Supplementary Methods

Modern climate at Bulusan Lake

Bulusan Lake experiences aseasonal tropical climate characterised by the lack of a dry season (i.e. mean monthly rainfall >100 mm). Annual temperature and precipitation in the area has ranged between 25-28 °C and 2000-4800 mm, respectively, over the last 60 years (Menne *et al.* 2012a; Menne *et al.* 2012b). Intra-annually, Bulusan receives most of its rainfall from the north-eastern monsoon (Figure S1a), and inter-annually, its precipitation is strongly linked to El Niño/ Southern Oscillation (ENSO) variability (Figure S1b). Both of these climatic phenomena take place during the boreal winter (November-February) (Philippine Atmospheric, Geophysical and Astronomical Services Administration 2016). Instrumental records over the last 60 years from Legaspi weather station (13°8' N, 123°44' E) (Menne *et al.* 2012a; Menne *et al.* 2012b), ca. 55 km north from Bulusan Lake, show that rainfall amount in this area is statistically correlated with the Southern Oscillation Index (SOI) with less precipitation during El Niño years (r = 0.55, p-value <0.0001, Figure S1b). While northern migration of the Intertropical Convergence Zone (ITCZ) during the boreal summer (June to September) brings additional rainfall to Bulusan, its contribution is relatively small compared to that of the north-eastern monsoon (October to January). Specifically, in comparison to the driest period in the year (February-May) - which is not influenced by neither the northern migration of the ITCZ nor by the north-eastern monsoon - the boreal summer and the north-eastern monsoon bring ~30% and ~120% increase, respectively, to the mean monthly rainfall.

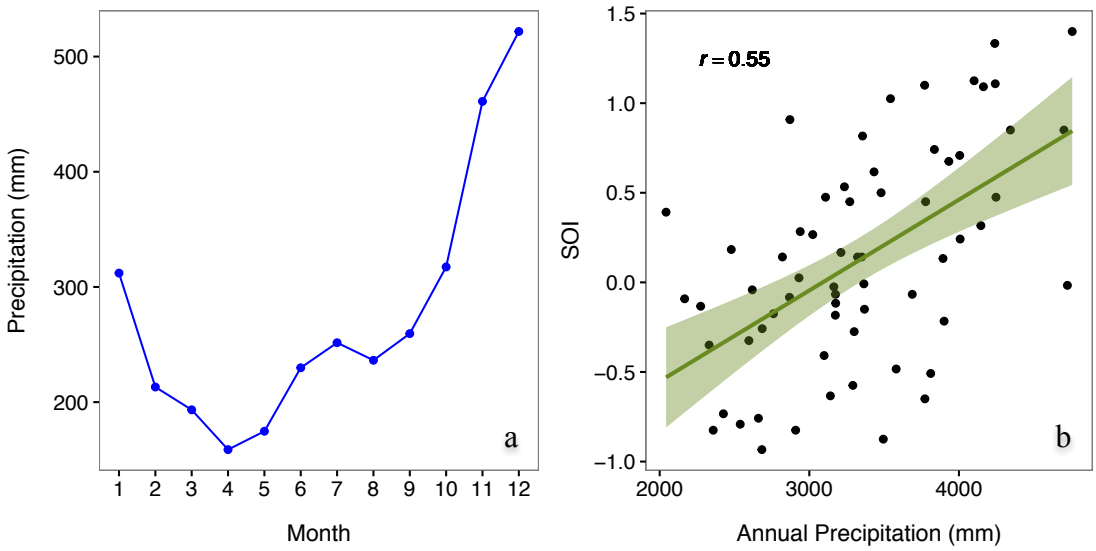


Figure S1 | Precipitation conditions at the Bulusan site. a, Monthly mean precipitation at the Legaspi weather station, Philippines, from 1951 to 2015. **b,** Correlation between annual rainfall amount at the Legaspi weather station and ISO index, from 1951-2015. Data from Menne *et al.* (2012a), plotted with ggplot2 package (Wickham 2009) in R version 3.2.4 (R Core Team 2013).

Study site and material collection

Bulusan Lake is a 0.28 km^2 oval shaped maar located at 360 m.a.s.l., at the foot-slopes of Mt Bulusan volcano at the southeast end of the Bicol Volcanic Arc (Delfin *et al.* 1993). It consists of two basins: a small round basin, and a larger narrow basin, which are 12 and 24 m deep respectively. The two basins comprise a closed system fed primarily by precipitation and ground water. The vegetation surrounding Bulusan Lake, and up the slope of Mt Bulusan, is classified as a Dipterocarp rainforest, i.e. aseasonal lowland tropical rainforest dominated by the Dipterocarpaceae tree family (Abada Gatumbato *et al.* 2011).

Two overlapping sedimentary sequences, 5.3 m BUL1 and 5.0 m BUL2, were collected as 1 m segments from the smaller basin with a Livingstone Piston corer using an anchored platform in March 2013. The sediments were sealed in protective plastic containers and shipped to the University of Oxford where they have been stored at 5 °C. Bulusan sediments are finely laminated though these formations do not represent varves and remain of unknown origin. Laminations were mapped using a combination of optical and radiograph images taken with the Itrax Core Scanner (Croudace *et al.* 2006) at 0.2 mm resolution at the University of Aarhus in September 2013 and used to link the 1 m segments of the two sedimentary sequences into a single composite core with undisturbed sediments.

The origin of laminations in the Bulusan sediments remains an open question due to non-conclusive evidence. A radiographic profile taken with the Itrax Core Scanner shows high diversity in colour, thickness and order of individual laminations. Such complex and non-repetitive patterning is uncharacteristic of seasonal/ annual laminations (i.e. varves) (A Brauer, pers. comm.), and instead indicates the presence of multiple laminating mechanisms operating on different time scales. Additionally, the difference between radiocarbon dating-based estimation of the Bulusan sequence age (i.e. 1,400 years) and the number of its laminations (i.e. <500) provides further evidence against the laminations being annual or seasonal in nature. Many of the laminations detected by the radiographic scan are not visible in the optical profile; the laminations visible in both profiles are yellow bands several mm thick which occur throughout the sequence at irregular intervals. A preliminary microscopic analysis of four thin sections, each spanning 6 cm and taken at even intervals from the sequence, revealed that these yellow laminations are composed solely of diatoms, while the darker sections in between are a complex mixture of diatoms, pollen, mineral particles and decomposing organic matter. The yellow bands may be capturing past diatom blooms, caused for instance by the reduction in lake levels during severe drought episodes (e.g. Brasil *et al.* 2016) or by water column mixing and nutrient uplift during typhoon events (e.g. Tsuchiya *et al.* 2013), and thus may be suitable for reconstructing past environmental change. However, further microscopic and geochemical analysis is needed to elucidate the origin(s) of the Bulusan laminations before they can be used for environmental reconstruction.

Age-Depth Modelling

A precise age-model for the Bulusan sediments has been established with AMS^{14}C dates (Table S1) and the surface sediment set to year 2013. The radiocarbon analysis was done on identified terrestrial plant macrofossils (e.g. leaves, twigs) to avoid reservoir effects and minimize age uncertainty. AMS^{14}C samples were measured at the NERC Radiocarbon Facility, East Kilbride. The age-depth modelling of the Bulusan core was performed with the Bacon 2.2 package in R (Blaauw and Christen 2011; Blaauw and Christen 2015) at 1 cm resolution and the IntCal13 radiocarbon calibration curve for the Northern Hemisphere (Reimer 2013), and model output shows the age span per cm being between 4.5-6 years. The high bi-decadal variability of δD_{wax} values (up to ±10 ‰) suggests rapid transfer of leaf waxes into the sediment as opposed to the scenario of substantial residence time (e.g. in soils) which would result in signal dampening.

Table S1 | AMS^{14}C dates of the Bulusan sedimentary sequence measured at the NERC Radiocarbon Facility, East Kilbride.

Lab ID	Sample Material	Core Depth (cm)	Age (yr BP)	Error (yr)
SUERC-64001	Terrestrial plant	59	240	±35
SUERC-64002	Terrestrial plant	69	293	±37
SUERC-64003	Terrestrial plant	74	450	±37
SUERC-64005	Terrestrial plant	82	323	±37
SUERC-64004	Terrestrial plant	84	401	±37
SUERC-51111	Terrestrial plant	126	617	±38
SUERC-64006	Terrestrial plant	163	609	±37
SUERC-51112	Terrestrial plant	204.5	1146	±35
SUERC-64010	Terrestrial plant	272	1235	±37
SUERC-64011	Terrestrial plant	342.5	1629	±37

Biomarker extraction, identification and quantification

The *n*-alkanes (nC_{23-31} homologues) from aliphatic fraction were identified and quantified using a gas chromatograph (GC 7890-A) equipped with a mass selective detector-mass and a flame ionisation detector (FID) (MS 5975-C) coupled via an electronic split interface. The MSD trace was employed for compound identification and the peak area from the FID chromatogram for compound quantification using the peak area of the internal standard 5α-androstane. Sulphur and unsaturated hydrocarbons were removed from the aliphatic fraction by elution through a pipette column of activated copper powder and a pipette column of activated mix of silver nitrate and silica gel, respectively, by applying a combination of hexane and DCM. The resulting aliphatic fraction produced clean chromatograms and no unresolved complex mixture (UCM) was detected (except in Samples 1-6). Concentrations of n-alkanes ranged widely between different alkanes, with nC_{27}-nC_{31} being the most dominant among them. While the nC_{29} and nC_{31} alkanes exhibit similar pattern in abundance variability along the sequence, the nC_{27} alkane showed a dissimilar pattern, indicating a differing origin of nC_{27} in relation to nC_{29} and nC_{31}.

Compound-specific hydrogen isotope measurement of n-alkanes

Compound-specific hydrogen isotope ratios of the aliphatic fraction were measured using a ThermoFisher Delta-V-Plus Isotope Ratio Mass Spectrometer coupled to a ThermoFisher TraceGC 1310 gas chromatograph at the University of Potsdam. The samples were measured on a 50 m HP ultra 1 column with an inner diameter of 0.2 mm and a film thickness of 0.33 μm. The samples were measured with the following GC-temperature program: i) temperature was held for 2 mins at 40 °C, i) temperature was increased to 256 °C at a rate of 4 °C per min, iii) oven temperature was increased to 300 °C at 2 °C per min, and iv) the final temperature was held for 45 mins. The alkane standard mix was measured with a shorter program where the final temperature of 300 °C was held for 3 mins only, as all standard peaks had eluted. The samples were measured in triplicates, with a small set of samples measured in duplicates due to low compound concentrations. Correction of δD values to the VSMOW scale was done using a linear regression function derived from the relationship of Mix A4 measurements and Mix A4 known δD values. The mean standard deviation of all measured samples for the nC$_{27}$, nC$_{29}$ and nC$_{31}$ alkanes (n=75) was about 1.6‰, 1.3‰ and 0.9‰, respectively.

Isotope evaluation

Compounds with intensities below 800 mV (on mass 2) (i.e. C$_{23}$ and C$_{25}$) were not used for evaluation, since this was outside of the linear range of the GC-IRMS system. In addition, an exclusively higher terrestrial plant origin of nC$_{25}$ is difficult to assume because the alkane can be produced by aquatic plants such as *Potamogeton*. Therefore, for our interpretations we only used δD values of the nC$_{27\text{-}31}$ alkanes, which showed clean, baseline separated peaks in all samples (except sample no.2). The nC$_{27\text{-}31}$ alkanes are the most widely used leaf wax biomarkers and their hydrogen isotopic composition has been shown as a robust recorder of plant source water δD along extraordinarily steep climatic gradients (Eglinton and Hamilton 1967).

Extraction and processing of fossil pollen

Sediment samples were extracted as a continuous series of 4 cm long 1 cm^3 slices from the top 3.0 m of the composite Bulusan core, with each slice corresponding to a ~20-year interval. Standardised protocols were employed for the extraction and processing of fossil pollen from

the sediment samples (Bennett and Willis 2001; Birks and Birks 2004). 500 terrestrial pollen grains were identified and counted in each sample and the relative abundance of grass taxa at each level was calculated as the proportion of grass pollen in the total terrestrial pollen counts, expressed in percentages.

Data analysis

Correlation between n-alkane records

To measure dependence between pairs of $nC_{29\text{-}31}$ alkanes, we calculated the Pearson product-moment correlation coefficient (Oxford University Press 2016). The significance of this dependence was evaluated with Welch's t-test, which does not require equal variance (Ruxton 2006). Prior to the calculation, we accounted for temporal autocorrelation in the alkane records using the effective sample size (i.e. the effective number of independence values) and following procedure used in previous studies (Bretherton *et al.* 1999; Trenberth and Caron 2000; Box *et al.* 2008), with autocorrelation set at lag l for both records. A *p*-value less than 0.05 was considered statistically significant. The calculated correlation coefficients and the associated *p*-values are given in Figure S2.

Relationship between precipitation amount and precipitation δD values

We examined the relationship between modern precipitation amount and modern precipitation δD (δD_{precip}) values from three different sites in Southeast Asia, Bonga station in the Sorsogon province, Philippines (13°1' N, 123°55' E), Jakarta station, Indonesia (6°10' S, 106°49' E) and Kuala Lumpur station, Malaysia (3°8' N, 101°41' E) (IAEA/WMO 2016). All three sites are within the central Pacific area where the correlation coefficient between the Southern Oscillation Index (SOI) and precipitation is above 0.6 (Trenberth and Caron 2000). The nature and significance of the precipitation amount - δD_{precip} relationship was assessed using the Generalised Linear Least Squares (GLS), with precipitation amount as the response variable and δD_{precip} values as the explanatory variable. GLS is an extended linear fixed-effects model in which errors are permitted to be correlated and/ or have unequal variance (Pinheiro and Bates 2009). Several GLS models were applied in R version 3.2.4 (R Core Team 2013) using the nlme 3.1-128 package (Pinheiro et al. 2016) different combinations of temporal correlation and variance structures imposed on the error components to allow unequal variance of the errors

(Galecki and Burzykowski 2013). Errors were specified to follow an autoregressive-moving-average (ARMA) process and variance structure was defined with the explanatory variable as a variance covariate. The validity of individual models was then evaluated using standard diagnostic tests (Galecki and Burzykowski 2013). The best fitting model with satisfying diagnostics was selected based on the lowest Akaike information criterion (AIC) coefficients with a simpler model selected whenever the difference in AIC coefficients between two models was smaller than 2. Models were considered significant at the 95% level of confidence. Positive and negative slopes are indicated as (+) or (−), respectively.

Detection of regime shifts

The Sequential T-test Analysis of Regime-Shifts algorithm (STARS) (Rodionov 2004; Rodionov 2006), was used to detect significant changes (p-value set to <0.05) in the mean of δD values of the nC_{29} alkane. To address uneven spacing of the samples, the time series was sorted into the smallest bin size that still generated a continuous record (i.e. 22 years), and then standardized by the mean and standard deviation. Since the STARS algorithm assumes normality and does not explicitly account for autocorrelations, the time series was transformed to normal distribution using Box Cox transformation and passed through a white-noise filter using the ordinary least-squares method outlined in Rodionov (2006) prior to the application of the STARS algorithm. Following this, we determined the abruptness and shape of the significant changes in the mean detected by the STARS algorithm using Generalised Nonlinear Least Squares (GNLS) (Carstensen and Weydmann 2012; Seddon *et al.* 2014). We applied several GNLS models, i.e. null, linear, step mean and segmented, and included temporal correlation and variance structures on the error components to allow unequal variance of the errors. The models were run using *STARS* package (Seddon *et al.* 2014) in R version 3.2.4 (R Core Team 2013). Errors were specified to follow an ARMA process and variance structure was fixed to the variance of the nC_{29} alkane time series. The best fitting model was selected based on the lowest AIC coefficients with a simpler model selected whenever the difference in AIC coefficients between two models was smaller than 2.

Supplementary Discussion

Correlation between different alkanes

Results show that the δD values of the three abundant terrestrial lipid biomarkers in the Bulusan core, nC_{27-31}, are highly correlated (Figure S2). The relationship between nC_{27} and nC_{29} has received the highest correlation coefficient (~ 0.81), followed by the coefficients for the nC_{27} and nC_{31} and the nC_{29} and nC_{31} (~ 0.69). P-values were highly significant for all three relationships (i.e. $<10^{-6}$). The results confirm a common origin of these three n-alkanes.

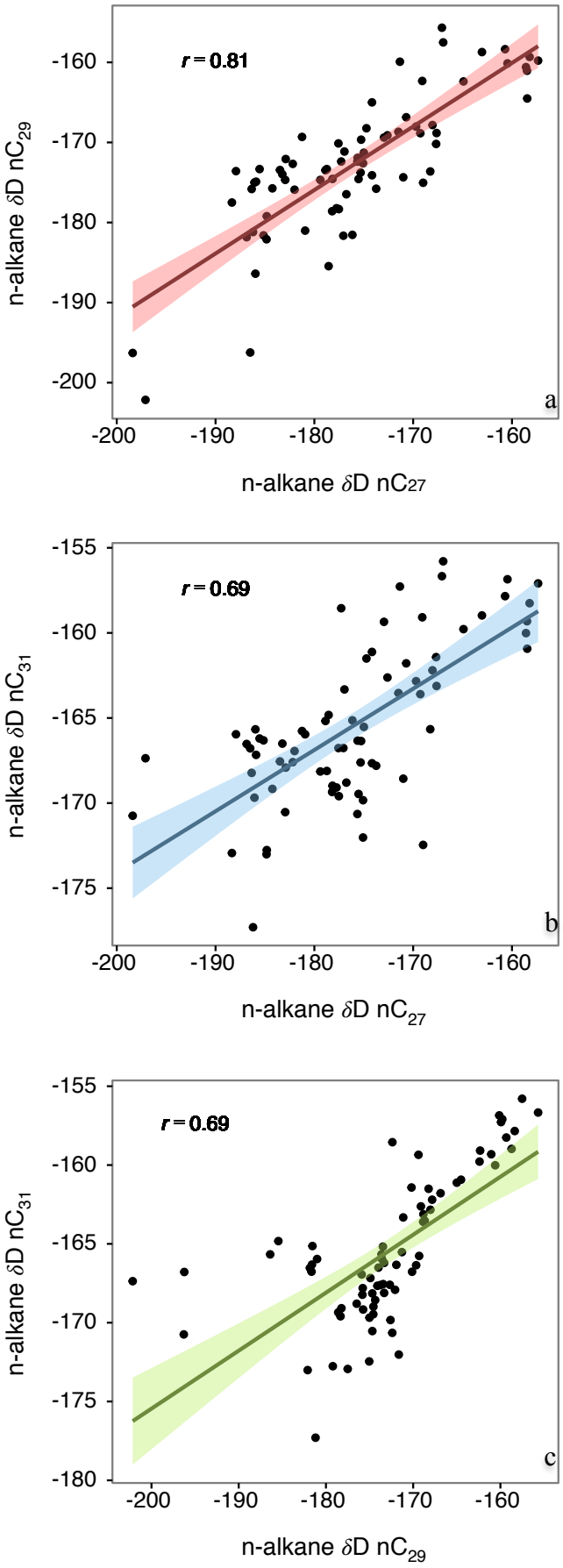


Figure S2 | Correlation between the δD values of n-alkanes from the Bulusan sedimentary core. a, nC_{27} and nC_{29} alkanes (p-value = $4.9x10^{-12}$), **b,** nC_{27} and nC_{31} alkanes (p-value = $1.8x10^{-7}$), and **c,** nC_{29} and nC_{31} alkanes (p-value = $2.1x10^{-7}$). Data plotted with *ggplot2* package (Wickham 2009) in R version 3.2.4 (R Core Team 2013).

Regime shifts in the nC_{29} alkane record

The STARS algorithm has detected two significant changes in the mean of δD values of the nC_{29} alkane record (Table S2, Figure S3). The first shift was towards lower δD values at ~AD 1650 and was followed by a shift to higher δD values at ~AD 1900. These results confirm significantly lower precipitation at Bulusan Lake during the latter half of the LIA (~AD 1600–1900), compared to the rest of the examined record. GNLS results revealed that for the ~AD 1650 shift (RS1) and the ~AD 1900 shift (RS2) the best fitted model was a step change in the mean and a segmented linear change, respectively (Carstensen and Weydmann 2012), suggesting a regime shift took place in both instances (Table S3, Figure S4).

Table S2 | The timing and p-values of the significant changes in the mean of δD values of the nC_{29} alkane (‰) in the Bulusan sequence identified by the STARS algorithm with incremental time window sizes. Increases and decreases in the sample mean are shown in green and red, respectively.

Time window (no. data points)	Change Point 1 (AD 1405 yr)	Change Point 2 (AD 1625 yr)	Change Point 3 (AD 1867 yr)	Change Point 4 (AD 1945 yr)
5	2.64E-05	3.77E-12	9.20E-04	4.94E-02
6	/	7.96E-12	3.04E-05	/
7	/	7.96E-12	3.04E-05	/
8	/	7.96E-12	3.04E-05	/
9	2.64E-05	3.77E-12	3.04E-05	/
10	2.64E-05	3.77E-12	3.04E-05	/
11	2.64E-05	3.77E-12	3.04E-05	/
12	/	7.96E-12	3.04E-05	/
13	/	7.96E-12	3.04E-05	/
14	/	7.96E-12	3.04E-05	/
15	/	7.96E-12	3.04E-05	/

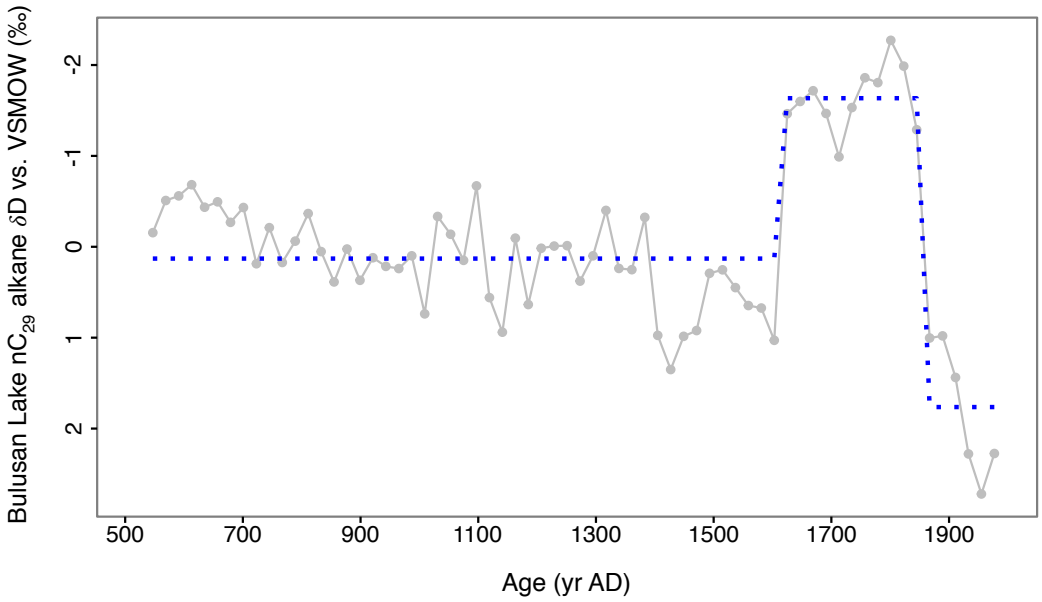


Figure S3 | Significant changes in the mean of δD values of nC_{29} alkane record from the Bulusan sequence (p-value <0.01 for both shifts), detected with the STARS algorithm. The two shifts separate the Bulusan record into three discrete periods, with the period of low δD values extending from ~AD 1650-1900. The time series was transformed to normal distribution using Box Cox transformation and passed through a white-noise filter using the ordinary least-squares method prior to the application of the STARS algorithm. Time window size is set to 8 data points (~160 yrs). Data plotted with *ggplot2* package (Wickham 2009) in R version 3.2.4 (R Core Team 2013).

Table S3 | Summary of the best fitted GNLS models for the two regime shifts (RS) in the nC_{29} alkane δD record from the Bulusan sequence detected by the STARS algorithm, i.e. the step change in mean model for RS1 and the segmented linear change model for RS2. k=change point, b0= intercept, b1= initial slope, b2= change in slope at the change point k.

Regime shift	RS1(AD 1625)	RS2 (AD 1867)
Model Structure	y ~ ifelse (x - k <= 0, b0, b0 + b1)	y ~ b0 + ifelse (x - k <= 0, b1 * x, b1 * x + b2 * (x - k))
Fixed effects		
Analysis of variance (F-test/p-value)		
k	380/na/na	5708.86/<0.01
b0	53423.84/<0.01	14094.05/<0.01
b1	55.48/<0.01	29.60/<0.01
b2	/	54.99/<0.01
Coefficients table (coefficient/ SE/p-value)		
k	380/na/na	171.14/14.68/0
b0	-159.75/1.70/0	-204.91/2.84/0
b1	-13.87/ 1.86/0	0.27/0.03/0
b2	/	-0.29/0.040/
Variance Function (95% CI)	/	/
Correlation Structure (95% CI)	ARMA (p=1, q=0) 0.34 (0.11, 0.54)	/
Scale (σ)	4.27 (3.54, 5.15)	4.36 (3.16, 7.02)

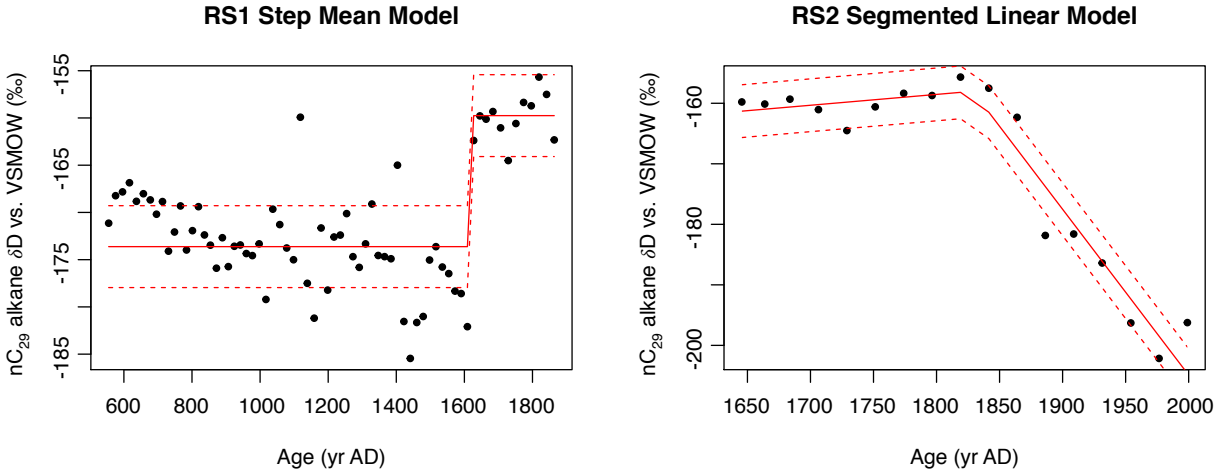


Figure S4 | Best fitted GNLS models for the two regime shifts (RS) in the nC_{29} alkane δD record from the Bulusan sequence detected by the STARS algorithm, i.e. AD 1625 (RS1) and AD 1867 (RS2). Data plotted with *ggplot2* (Wickham 2009) and *STARS* (Seddon et al. 2014) packages in R version 3.2.4 (R Core Team 2013).

Relationship between modern precipitation amount and δD_{precip} values

GLS modelling output shows a significant negative relationship between modern monthly precipitation amounts and the corresponding δD_{precip} values (p-value <0.05) for all three considered GNIP sites (Table S4, Figure S5). According to the estimated value of GLS models' coefficient for δD_{precip} for each of these sites, it follows that a difference of 20‰, such as the one observed in the Bulusan record between ~AD 1650-1900, would correspond to a change in the monthly rainfall in the range of 40-70 mm, which would amount to an annual difference of ~500-850 mm. Given that the modern annual precipitation varies between 2000-4800 mm, this difference would translate to approximately 40% decrease in the annual precipitation. However, given that rainfall variability at the Bulusan site is primarily associated with ENSO dynamics, it is probable that the recorded reduction was not distributed equally across the year, but was instead caused by droughts during the north-eastern monsoon/ El Niño season (October-January).

Table S4 | Summary of best fitted GLS models for the relationship between modern monthly precipitation amount and precipitation δD values from three GNIP stations (IAEA/WMO 2016)**.** Prec = monthly precipitation amount (mm), δD_{precip} = δD values of modern precipitation (‰).

Site	Bonga	Jakarta	Kuala Lumpur
Model Structure	prec = δD_{precip}	prec = δD_{precip}	prec = δD_{precip}
Fixed effects			
Analysis of variance(F-test/p-value)			
Intercept	25.48/<0.01	193.98/<0.01	251.68/<0.01
δD_{precip}	5.19/0.03	15.11/<0.01	20.19/<0.01
Coefficients table (coefficient/ SE/p-value)			
Intercept	231.55/78.2/<0.01	101.97/14.85/<0.01	82.10/27.18/<0.01
δD_{precip}	-3.60/1.55/0.02	-2.11/0.54/<0.01	-2.78/0.61/<0.01
Variance Function (95% CI)	/	expon(δD) -0.018 (-0.025, -0.011)	expon(δD) -0.009 (-0.018, 0.000)
Correlation Structure (95% CI)	ARMA (p=1, q=0) 0.63 (0.27, 0.83)	ARMA (p=1, q=0) 0.31 (0.16, 0.44)	ARMA (p=1, q=0) 0.25 (0.06, 0.42)
Scale (σ)	247.05 (173.05, 352.69)	69.51 (54.72, 88.30)	68.61 (44.48, 105.81)

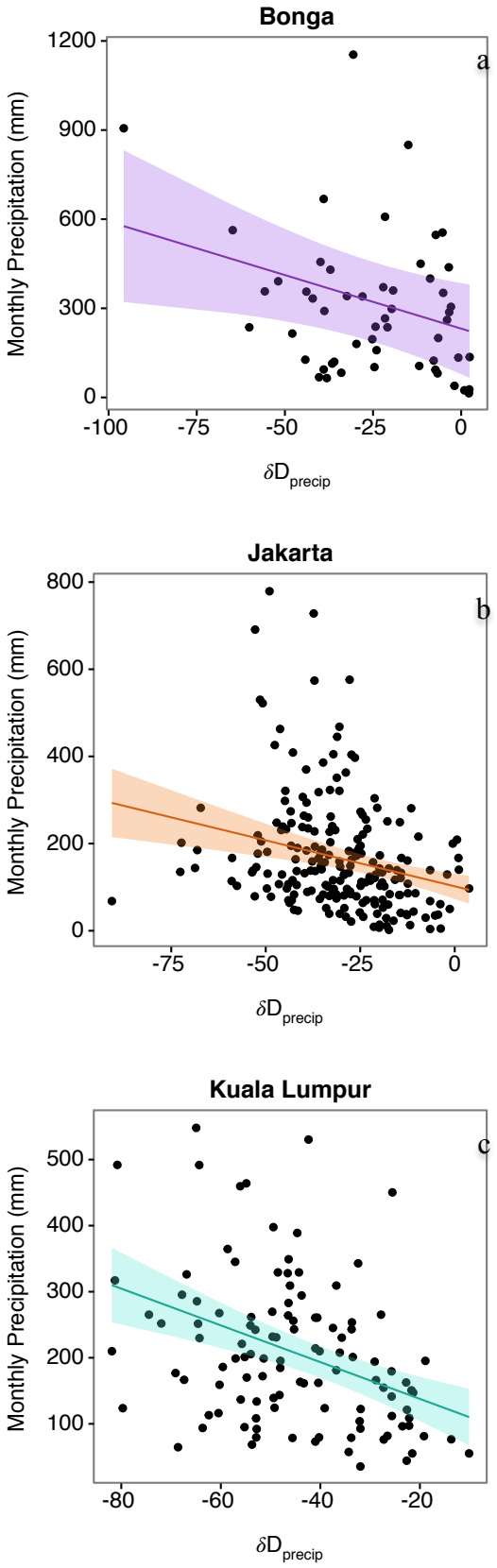


Figure S5 | Best fitted GLS models for the influence of monthly mean precipitation amount on the modern δD_{precip} values from instrumental readings near the Bulusan site. a, Bonga station, data from 1990-1994 and 1997-1998, fitted model: prec = 231.55-3.60*δD_{precip} (p-value = 0.02). **b,** Jakarta station, data from 1962-1997, fitted model: prec = 101.97-2.11*δD_{precip} (p-value <0.001). **c,** Kuala Lumpur station, data from 1993-1995 and 2000-2012, fitted model: prec = 82.10 - 2.78 * δD_{precip} (p-value <0.0001). Prec = monthly precipitation amount, δD_{precip} = δD values of modern precipitation. Data from GNIP (IAEA/WMO 2016). Data plotted with *ggplot2* package (Wickham 2009) in R version 3.2.4 (R Core Team 2013).

The influence of solar irradiance on hydrological conditions at Bulusan site

We have compared a solar irradiance record (Bard et al. 2000; Bard 2003; Bard et al. 2007) with the nC_{29} alkane record from the Bulusan Lake to examine the influence of irradiance variability on the precipitation conditions at the site over the last 1,400 years. The period of low solar irradiance between ~AD 1400-1750 has been linked to ITCZ migration and thus, notable changes in the precipitation dynamics of tropical Pacific records in response to this time interval are likely to be caused by changes in the ITCZ position or its latitudinal extent. However, the period of dry conditions at the Bulusan lake (i.e. ~AD 1650-1900) has a poor overlap with this period of low solar irradiance. This holds true even after the uncertainty of the Bulusan age-depth model is taken into account *(i.e. mean 95% confidence range is 101.2 years, min. 41 years at 0 cm, max. 154 years at 299 cm)* (Figure S6). Thus, it is unlikely that this abrupt precipitation reduction at Bulusan Lake was driven by the ITCZ changes.

Comparison of the Bulusan record with other regional records

Results from the Bulusan record indicating a stronger ENSO regime during the LIA (~AD 1300-1850) are in accordance with the regional Pacific sea surface temperature (SST) records, which suggest the rise of cooler conditions in the western Pacific (Newton *et al.* 2006; Oppo *et al.* 2009) and warmer conditions in the central (Cobb *et al.* 2003) and eastern Pacific (E1) (Conroy *et al.* 2008) during this time (Figure 5). Specifically, the foraminifera-based SST record from the Makassar Strait in the western Pacific (W2) (Newton *et al.* 2006; Oppo *et al.* 2009) shows temperature decrease between ~AD 1650-1900 while the El Junco diatom record (Conroy *et al.* 2008) indicates temperature rise during the same time period (Figure 5). Similarly, the coral record from Palmyra Island (C1) (Cobb *et al.* 2003); suggests a decrease in temperature between ~AD 1650-1900, providing further support for an enhanced ENSO dynamics during this time period.

In contrast, other hydrological records from the region provide less support towards a stronger ENSO regime during the LIA, as they suggest predominately wetter conditions in the western Pacific and drier conditions in the central and the eastern Pacific, which would be suggestive of weaker ENSO dynamics (Figure 4). For instance, the dinosterol δD record from Spooky Lake in Palau Island (W4) (Sachs *et al.* 2009) shows a significant decrease in δD values between

~AD 1650-1900, which advocates for weakening of ENSO during this time. However, many other hydrological records in the region do show a slight decrease in precipitation in the western Pacific and increased precipitation in the central and eastern Pacific in the second half of the LIA which indicates stronger ENSO dynamics and thus offer additional corroboration of our results. Specifically, hydrological record from Dongdao Island in the western Pacific (W1) (Yan *et al.* 2011) suggests a slow but steady decrease in grain size from ~AD 1650 onwards, indicating lower erosion rates and thus drier conditions at the site. Similarly, nC_{30} δD record from the Makassar Strat in the western Pacific (W3) (Tierney *et al.* 2010) shows higher values between ~AD 1650-1800, also indicative of a lower precipitation amount. Furthermore, Washington Lake total lipid extract (TLE) δD record from central Pacific (C2) (Sachs *et al.* 2009) shows a decrease in the δD values at ~ AD 1600, suggesting a transition to wetter conditions; though, since the record ends at ~AD 1650, it is not possible to determine duration of this transition from the record. Likewise, the Poza de la Diablas record from Galapagos Islands (E2) (Nelson and Sachs 2016) shows lower δD values between ~AD 1550-1850, indicating higher precipitation in the eastern Pacific during this time. The authors assigned this precipitation increase to the southward shift of ITCZ because an accompanying increase in salinity, which is indicative of sea level rise during strong El Niño activity, was lacking. It is not clear however if the additional increase in rainfall due to the southward ITCZ shift could not override any El Niño caused salinity increase in a shallow lagoon such as Poza de la Diablas (max. depth of 1 m, mean depth of 0.3 m), and therefore, this record could be actually capturing the combined effects of southward ITCZ shift and an El Niño-like state during the LIA.

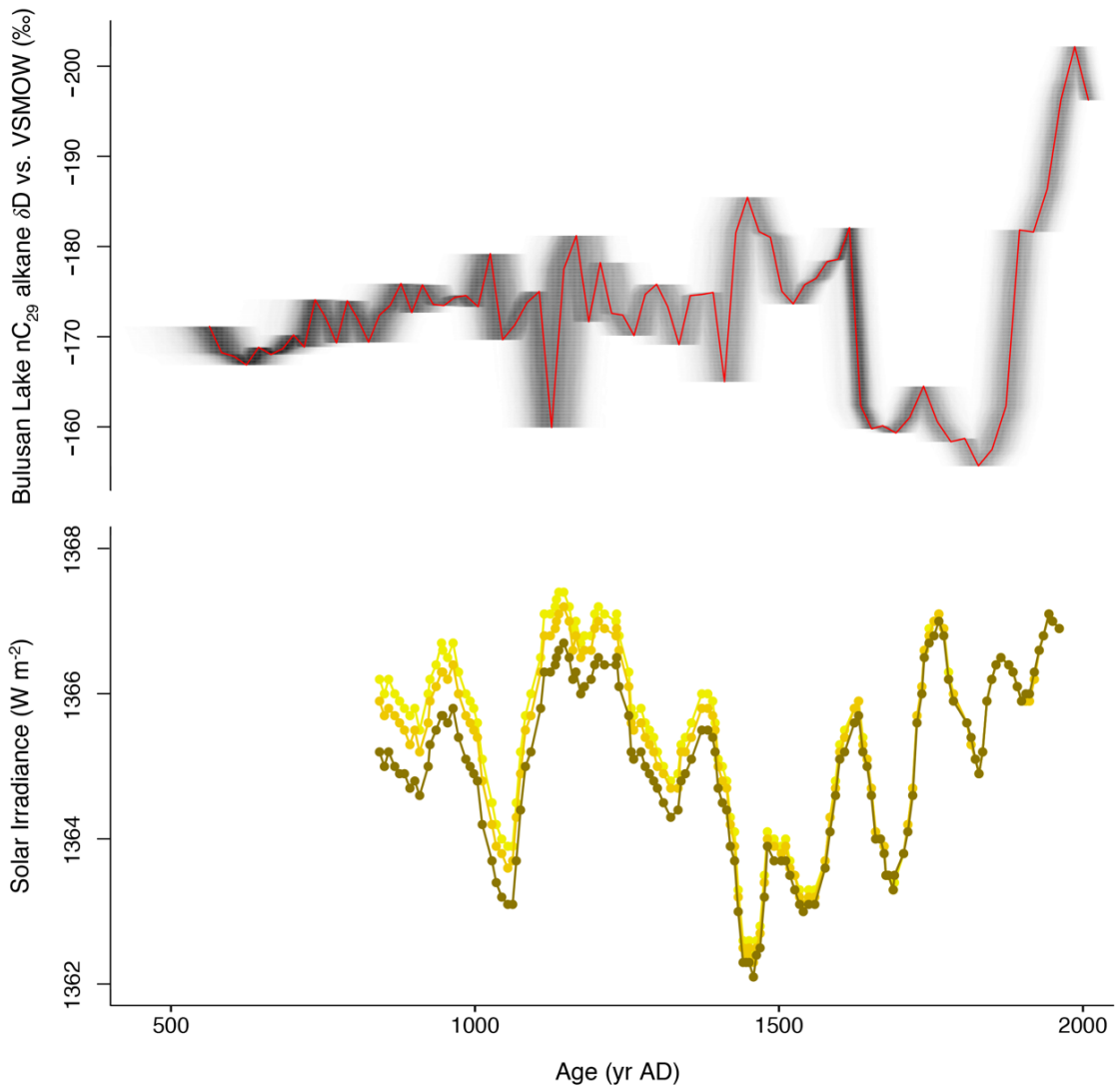


Figure S6 | Comparison of the nC_{29} alkane δD record from the Bulusan sedimentary sequence, which includes the uncertainty of the age-depth model (grey shading), and three different calibrations of the solar irradiance variability record, TSI (W m^{-2}) (Bard et al. 2000; Bard 2003; Bard et al. 2007). Data plotted with *ggplot2* package (Wickham 2009) in R version 3.2.4 (R Core Team 2013).

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CHAPTER 4: EFFECTS OF ENSO CHANGES ON TREE BIOMASS DYNAMICS IN DIPTEROCARP RAINFORESTS

Abstract

The aseasonal lowland rainforests of Southeast Asia, referred to as Dipterocarp rainforests, represent one of most biodiverse and threatened ecosystems globally. Climate projections for the 21st century indicate prominent changes in the El Niño/ Southern Pacific Oscillation (ENSO), yet the potential effects of these changes on the structure and functioning of Dipterocarp rainforests is poorly understood. Of particular interest are the responses of the Dipterocarpaceae family, given their dominant role in shaping the architecture, biomass production and reproductive behaviour of these forests. We examine for the first time the effects of past large-scale ENSO variability on the biomass dynamics of Dipterocarp trees using a range of proxies from a 1,400-year-old lacustrine sedimentary sequence from south-eastern Luzon, Philippines. Our results show no significant changes in Dipterocarp pollen accumulation rates in response to the changing ENSO dynamics. These findings suggest a high resilience of Dipterocarp woody biomass to enhanced ENSO activity and/ or a positive effect of enhanced ENSO activity on Dipterocarp reproductive biomass. Our results highlight that the effects of climate change on the structure and functioning of Dipterocarp rainforests may not be as large as previously believed, and that deforestation and forest degradation will likely remain the most prominent threats to these ecosystems in the future.

Introduction

The tropical lowland rainforests of Southeast Asia, known widely as Dipterocarp rainforests, are one of most diverse and endangered ecosystems on Earth (Ashton 1969; Ashton *et al.* 1988; Curran *et al.* 1999; Cannon *et al.* 2007). These aseasonal forests once covered much of peninsular Malaysia, Sumatra, Java, Borneo, and the Philippines (Appanah 1985), but today they occupy less than 50% of their original range due to record high rates of deforestation and forest degradation (Sodhi *et al.* 2004). While logging and agricultural expansion have been the

two principle drivers of the forest loss to date, the additional effects of anthropogenic climate change on Dipterocarp rainforests remain poorly understood (Corlett and Lafrankie Jr 1998). Climate projections for the 21st century suggest pronounced changes in the El Niño/ Southern Pacific Oscillation (ENSO), namely an increased frequency of extreme El Niño events (Latif and Keenlyside 2009; Collins *et al.* 2010). Previous work has documented the large influence that this climate phenomenon exerts on key ecological processes in Dipterocarp rainforests (Van Nieuwstadt and Sheil 2005). Thus, major changes in ENSO dynamics may lead to considerable changes in the structure and functioning of these forests.

ENSO is the main driver of drought events in Southeast Asia. Severe droughts increase mortality rates for the majority of tree species in Dipterocarp rainforests, with large trees being particularly susceptible. For instance, a single drought event can cause the mortality of up to 45% of large trees (Van Nieuwstadt and Sheil 2005). Severe droughts are also more likely to lead to fires, and the latter can cause near complete mortality of smaller trees. Thus, a combination of drought and fire can be particularly destructive to Dipterocarp rainforests as it affects both larger and smaller trees. Consequently, it has been argued that a regime of more frequent and intense droughts will result in a species-poorer forest with uneven structure, lower stature, reduced above ground biomass and an increased proportion of drought tolerant taxa (Newbery *et al.* 1999). While similar predictions have been made for other tropical rainforests around the world, Dipterocarp rainforests may be particularly vulnerable to a stronger drought regime due to the overwhelming dominance of the Dipterocarpaceae family which is a unique feature of these forests. The members of Dipterocarpaceae family normally constitute up to 10% of total tree diversity, over 50% of the basal area and nearly 80% of all emergent individuals (Appanah 1985), and comprise the largest size class of trees in Dipterocarp rainforests (i.e. genera *Shorea* and *Dipterocarpus*, with d.b.h. ca.100-200 cm). Previous studies have found that Dipterocarp species inhabiting Dipterocarp rainforests have on average higher sensitivity to drought than species of most other tree families; during drought events, their mortality can increase up to 30 times, as opposed to 2-11 times for other tree families (Nakagawa *et al.* 2000). It follows that enhanced ENSO activity could significantly increase the mortality rate of many Dipterocarp species.

On the other hand, ENSO also plays a key role in the regeneration of Dipterocarp rainforests. El Niño-induced drought events have been demonstrated to act as a trigger to general flowering,

which are community-wide masting events unique to Dipterocarp rainforests (Sakai *et al.* 2006). A large number of Dipterocarp species can only reproduce successfully during these general flowering events and they do so gregariously. For instance, more than 60% of ca. 200 Dipterocarp species in North Borneo were observed to flower and fruit during a single strong El Niño event (Woods 1955), and almost 50% of the mature Dipterocarp individuals have been shown to flower during mass flowering years (Burgess 1972; Cockburn 1975). Mass flowering of Dipterocarps is accompanied by heavy flowering of many other plant species, including members of Anacardiaceae, Euphorbiaceae, Annonaceae, Fabaceae, Burseraceae, Moraceae and Myristicaceae, though for the majority of these it seems to be an opportunistic rather than obligatory behaviour (Appanah 1985). Stronger El Niño episodes generally result in stronger general flowering, and thus, an enhanced ENSO activity could potentially boost the reproduction of Dipterocarp rainforests. Furthermore, an ENSO-induced increase in mortality rates of large trees could also create favourable conditions for the recruitment of their pre-existing seedlings into the forest canopy. This is particularly true for many Dipterocarp species, where a combination of substantial fruit production rate (>100,000 seeds per individual) (Ashton 1988), poor seed dispersal and lack of seed dormancy results in the formation of thick layers of Dipterocarp seedlings around the mother trees (Ashton 1969; Curran and Webb 2000; Itoh *et al.* 2003). These seedlings can survive in shade for more than 10 years waiting for growth conditions to become more favourable, and are thus well positioned to capitalise on the new gap conditions when the mother tree dies.

Given that El Niño-caused drought events can have either negative (e.g. increase in tree mortality) or positive effects (e.g. facilitation of tree generation through increased mass flowering, boosted seedling establishment) in Dipterocarp rainforests, predicting the direction and magnitude of ecological responses to ENSO changes without empirical evidence is challenging. Since marked changes in ENSO dynamics, such as those suggested in climate change projections, have not been exhibited over the last few decades (Cobb *et al.* 2003), observational studies have limited capacity to address this problem. However, several distinct changes in the ENSO regime have been recorded over the past millennia (Cobb *et al.* 2003; Conroy *et al.* 2008; Conroy *et al.* 2010; Cobb *et al.* 2013) and long-term records that capture plant responses to these ENSO changes are vital for evaluating the potential effects of climate change on the structure and functioning of Dipterocarp rainforest.

Here, we investigate, for the first time, the impact of past large-scale ENSO variability on the biomass dynamics of Dipterocarp trees, using proxies from a 1,400 year-old laminated sedimentary sequence from Bulusan Lake in south-eastern Luzon, Philippines (Figure 1a, b). Specifically, we use the newly generated data on Dipterocarp pollen accumulation rates (PARs, grains $cm^{-2}yr^{-1}$) (Davis and Deevey 1964; Giesecke and Fontana 2008) and macrocharcoal influx rates (particles $cm^{-2}yr^{-1}$) (Clark 1988; Mooney and Tinner 2010), and a previously developed record of hydrogen isotope composition of terrestrial lipid biomarkers (δD_{wax}, ‰) (Aichner *et al.* 2010; Sachse *et al.* 2012) from the same sedimentary sequence (Prohaska *et al.*, Chapter 3) as independent proxy records of Dipterocarp biomass dynamics, local fire activity and ENSO variability, respectively. The δD_{wax} record indicates an abrupt and dramatic shift to significantly drier conditions between ~BP 300-50 (BP defined as 'years Before Present', i.e. AD 1950) (Prohaska *et al.*, Chapter 3). Given that precipitation at the Bulusan site is predominately shaped by ENSO, the observed changes reflect the weakening of the Pacific Walker circulation (PWC) and the persistence of an enhanced ENSO activity (i.e. El Niño-like state) in the tropical Pacific during this time period. This setting provides a framework for examining biotic responses to pronounced changes in ENSO dynamics, and our study pioneers its use for gaining fundamental insights into the sensitivity of Dipterocarp rainforests. Our focus is on Dipterocarp trees because given their overwhelming dominance in Dipterocarp rainforests today and their key role in shaping reproductive behaviour of the entire community, any major changes in their biomass dynamics alone could substantially alter the structure and functioning of these forests.

We ask two main questions: i) what is the effect of ENSO-driven precipitation changes on the biomass dynamics of Dipterocarp trees, and ii) to what extent does fire activity modify this effect? We use Generalised Linear Least Squares (GLS) regression to evaluate the effects of δD_{wax} values and macrocharcoal influx rates on Dipterocarp PARs over the last 1,400 years. We also apply a change-point detection method (i.e. Sequential T-test Analysis of Regime-Shifts algorithm, STARS) to identify any major changes in the mean of Dipterocarp PARs values in response to the prolonged period of increased δD_{wax} values from ~BP 300-50.

Dipterocarp trees are long lived and slow growing species whose size at first flowering is considerably smaller from their maximum size and, hence, sizes of flowering Dipterocarp individuals can vary considerably across the population. Given that larger Dipterocarp trees

usually produce more flowers, Dipterocarp pollen abundances are shaped by both the number and the size of Dipterocarp trees, and as such reflect more closely Dipterocarp biomass than their abundance. Previous studies have related modern pollen counts (i.e. pollen loading in traps, absolute unit of measure) to tree biomass (i.e. tree volume, $m^3\ h^{-1}$), and demonstrated that PARs can be used to estimate the biomass of adult trees (Seppä *et al.* 2009; Mazier *et al.* 2012). Additionally, since Dipterocarps have irregular flowering patterns in response to El-Niño droughts taking place every 2-7 years, the influence of potential changes in Dipterocarp pollen productivity on their PARs needs to be considered even on longer time scales. Consequently, Dipterocarp PARs are most likely to capture both woody and reproductive biomass dynamics (see Supplementary Information for further discussion), and this understanding has been applied to the interpretation of our findings.

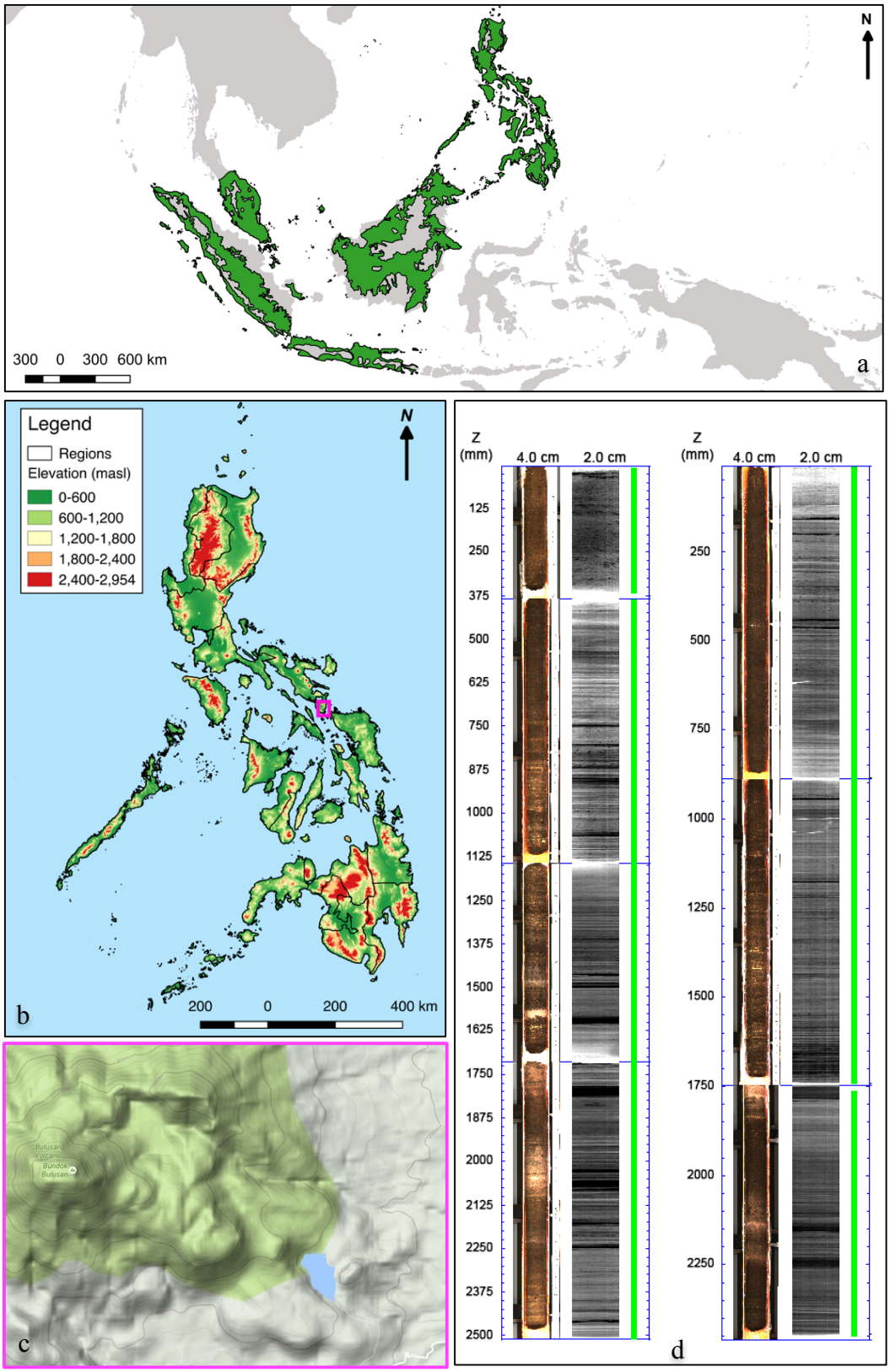


Figure 1 | Geographical and sedimentological features of the Bulusan site. a, Map showing the distribution of Dipterocarp rainforests (in green). Data from Olson et al. (2001), map generated in QGIS version 2.14.3 (Quantum GIS Development Team 2016). **b,** Topographic map of the Philippines showing the location of the study site. Data from PhilGIS (PHILGIS 2016), map generated in QGIS version 2.14.3.**c,** Map showing Bulusan Lake (in blue) within its larger landscape, with Mt Bulusan volcano in the west (in green) (Google 2016). **d,** Optical and radiographic profiles of the Bulusan sediments. The radiograph images depict the level of organic content, with higher values shown as lighter bands. The green line represents the validation of the measurement quality along the cores. Images generated in ItraxPlot program (Croudace and Rothwell 2015).

Results & Discussion

The results show that the variability in δD_{wax} values over the last 1,400 years, including the prolonged period of higher δD_{wax} values between ~BP 300-50, had no apparent influence on the Dipterocarp PARs at the Bulusan site. Though Dipterocarpaceae PARs exhibited relatively large fluctuations throughout the record (Figure 2), the best-fitted GLS model yielded a non-significant effect (p-value >0.05) of the nC_{29} alkane δD values (i.e. proxy for precipitation amount) on Dipterocarp PARs (i.e. proxy for Dipterocarp biomass) (Table 1, Figure 3). For more detailed description of the GLS results, please see Supplementary Information). Furthermore, while the STARS algorithm detected several significant changes in the mean of Dipterocarp PARs values, none of these were in response to the prolonged period of increased δD values of the nC_{29} alkane (~BP 300-50) (Figure 4, Tables S3-S4 in Supplementary Information). These findings suggest that over longer time scales the negative effects of enhanced ENSO strength, such as drought-induced mortality of Dipterocarp trees, can be offset by other mechanisms. While it is not possible on the basis of Dipterocarp pollen abundances alone to identify these mechanisms, we propose two probable candidates - positive effect of enhanced ENSO activity on Dipterocarp flower production and resilience of Dipterocarp woody biomass to enhanced ENSO activity.

Previous research supports the possibility that enhanced ENSO conditions increased Dipterocarp flower production at the Bulusan site. Stronger El Niño drought events usually result in stronger general flowering events, and while there is some evidence to suggest that a relatively short wet period before the drought decreases sensitivity of plants to the trigger, the period between two mass flowering events can be as short as 2 years (Sakai *et al.* 2006). It can therefore be expected that a stronger ENSO regime, bringing higher incidence and strength of El Niño droughts, will also increase the frequency and magnitude of general flowering events. An increasing production of Dipterocarp flowers would also increase Dipterocarp PARs and mask any decreases in Dipterocarp tree biomass. Given the high longevity of Dipterocarp trees (i.e. lifespan of 100s of years), the effect of ENSO-facilitated mass flowering may be carried on long into the future by the surviving individuals. Further support for this interpretation comes from the study by van der Kaars *et al.* (2010) which showed that the higher frequency of El Niño events over the last 250 years was accompanied by higher abundance of Dipterocarpaceae pollen in the marine core from Kau Bay, Indonesia.

Also plausible is the possibility that Dipterocarp woody biomass remained unchanged under enhanced ENSO activity. Firstly, stronger and more frequent general flowering events could have potentially led to stronger and more frequent mast seeding. Such increased supply of Dipterocarp seeds would also increase the germination success in the face of generalist seed predators and non-general flowering plant competitors (Toy 1991; Kelly 1994), as well as expand the total genetic diversity of the offspring pool, thereby facilitating adaptation of the species to the newly established drought regime. Secondly, increased mortality of Dipterocarp trees due to enhanced ENSO conditions is likely to facilitate the recruitment of pre-existing Dipterocarp seedlings around the mother trees into the canopy through the creation of favourable gap conditions (Ghazoul 2016). Thus, the initial high mortality of Dipterocarp trees could have been subsequently offset by the cumulative effect of an increased recruitment of seedlings and positive selection for individuals with a higher tolerance to drought conditions (e.g. lower vulnerability to hydraulic deterioration (Rowland *et al.* 2015)), precluding significant changes in Dipterocarp tree biomass.

Furthermore, we found no evidence that Dipterocarpaceae PARs were affected by the changes in macrocharcoal influx rates. Specifically, the best-fitted GLS model showed that both macrocharcoal and its interaction with δD_{wax} (Table 1, Figure 3) had non-significant effect (p-value >0.05) on Dipterocarpaceae PARs. Similarly, none of the significant changes in Dipterocarpaceae PARs detected by the STARS algorithm overlapped with the period of increased macrocharcoal influx rates (~BP 550-50) (Figure 4, Tables S3 and S5 in Supplementary Information). This finding indicates that the mechanisms which helped offset any negative effects of enhanced ENSO regime had not been inhibited by an increasing fire activity. For example, previous studies have shown how fire-related mortality decreases substantially across tree size classes; whereas fire can cause almost complete mortality among small stem trees (i.e. <10 cm d.b.h), it leaves large trees (i.e. >80 cm d.b.h) mainly unaffected (Van Nieuwstadt and Sheil 2005). Given that only Dipterocarp seedlings up to 5-10 years of age belong to the small stem class, our results suggest that fire frequency was lower than that during this time interval, allowing Dipterocarp seedlings to grow enough to escape fire-related mortality. With the exception of the peak at ~ BP 500, the macrocharcoal influx rates were relatively low throughout the Bulusan record (Figure 2). Similarly, microcharcoal influx rates were consistently low along the Bulusan core (see Figure S2 in Supplementary Information).

Given such low charcoal influx rates, it is difficult to determine if their origin is primarily climatic, volcanic or anthropogenic (for further discussion, see the relevant section in Supplementary Information). Nevertheless, the low charcoal counts indicate generally low frequency of fires at both local and regional scales, and support our interpretation that fire frequency at the Bulusan site was low enough to allow the survival and growth of Dipterocarp seedlings.

Given low taxonomic resolution of Dipterocarp pollen morphology (i.e. mostly family-specific), it was not possible to determine from our pollen data if changes in Dipterocarp species composition contributed to the apparent resilience of Dipterocarp biomass at the Bulusan site. For instance, species more tolerant of drier conditions (e.g. *Shorea contorta*, *Parashorea malaanonan*, *Dipterocarpus grandifloras* (Pelser *et al.* 2016)) could have increased their abundance and thereby compensated for any decrease in the abundance of less tolerant taxa (e.g. *Hopea plagata*, *Dipterocarpus kunstleri*, *Shorea malibato* (Pelser *et al.* 2016)). The fact that the two most abundant species of Dipterocarps at the Bulusan Volcano National Park are *Shorea contorta* and *Parashorea malaanonan* (Abada Gatumbato *et al.* 2011) gives validity to this hypothesis. However, it remains to be determined if even those Dipterocarp species that are more tolerant to drier conditions have the physiological capacity to withstand prolonged periods of enhanced ENSO-induced droughts. In the future, ancient DNA approaches may provide some evidence to this end, given their ability to identify plants to species level (Pedersen *et al.* 2014).

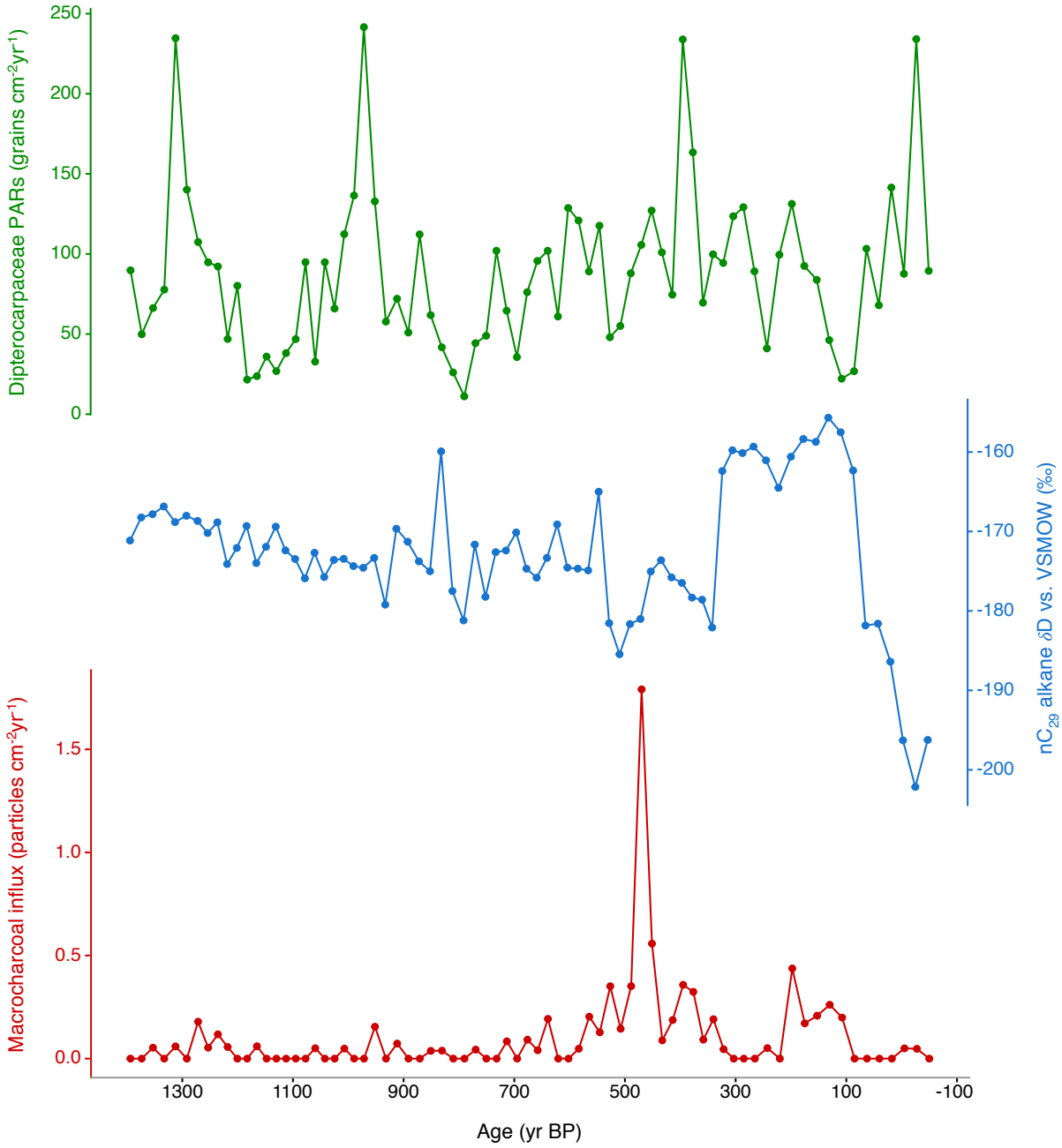


Figure 2 | Records of PARs dynamics of Dipterocarpaceae taxa, δD values of nC_{29} alkane and macrocharcoal influx rates at the Bulusan site spanning the last 1,400 years. Data plotted with *ggplot2* package (Wickham 2009) in R version 3.2.4 (R Core Team 2013).

Table 1 | Summary of GLS results for the best fitted models of Dipterocarpaceae PARs dynamics with different combinations of explanatory variables. PARs = pollen accumulation rates, $cm^{-1}yr^{-1}$ (i.e. proxy for taxon biomass dynamics), char = macrocharcoal influx rates, $cm^{-1}yr^{-1}$ (i.e. proxy for fire activity), δDC_{29} = nC_{29} alkane δD values (i.e. proxy for precipitation), SE = standard error, : = interaction.

Model Structure	log(PARs) = δDC_{29} + char + δDC29 : char	log(PARs) = δDC_{29} + char	log(PARs) = δDC_{29}	log(PARs) = char
Fixed effects				
Analysis of variance (F-test/p-value)				
Intercept	1369.42/<0.01	1404.51/<0.01	1379.03/<0.01	1376.23/<0.01
δDC_{29}	0.85/0.36	0.87/0.35	0.87/0.35	/
Char	0.62/0.43	0.64/0.43	/	0.74/0.39
δDC_{29} : char	1.00/0.32	/	/	/
Coefficients table (coefficient/ SE/p-value)				
Intercept	1.97/1.87/0.29	2.78/1.70/0.10	2.71/1.70/0.11	4.29/0.12/0.00
δDC_{29}	-0.01/0.01/0.22	-0.01/0.01/0.37	-0.01/0.01/0.35	/
Char	9.44/8.93/0.29	0.24/0.29/0.42	/	0.25/0.29/0.39
δDC_{29} : char	0.05/0.05/0.30	/	/	/
Variance Function (95% CI)	/	/	/	/
Correlation Structure (95% CI)	ARMA (1,0) 0.47 (0.25, 0.64)	ARMA (1,0) 0.47 (0.24, 0.64)	ARMA (1,0) 0.48 (0.26, 0.65)	ARMA (1,0) 0.48 (0.26, 0.65)
Scale (standardised residuals, σ)	0.58 (0.48, 0.71)	0.58 (0.48, 0.71)	0.59 (0.48, 0.72)	0.59 (0.48, 0.72)

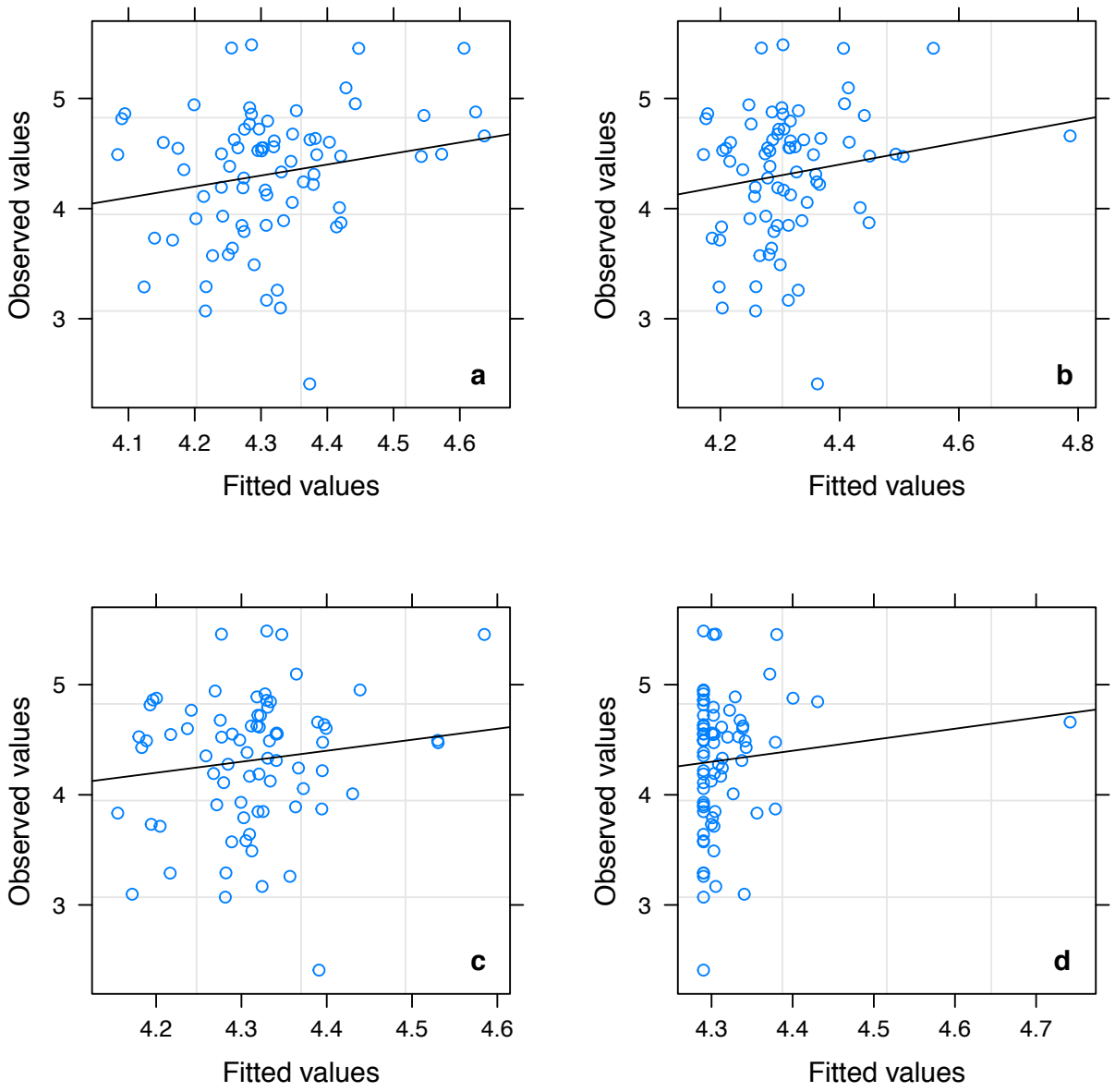


Figure 3 | The relationship between observed values and predicated values for the four fitted Dipterocarpaceae PARs models. a, log(PARs) = 1.97 - 0.01*δDC_{29} + 9.44*char + 0.05*δDC_{29} : char. **b,** log(PARs) = 2.78 - 0.01*δDC_{29} + 0.24*char. **c,** log(PARs) = 2.71 - 0.01*δDC_{29}. **d,** log(PARs) = 4.29 + 0.25*char. Char = macrocharcoal influx rates, δDC_{29} = δD values of the nC_{29} alkane. Data plotted in R version 3.2.4 (R Core Team 2013).

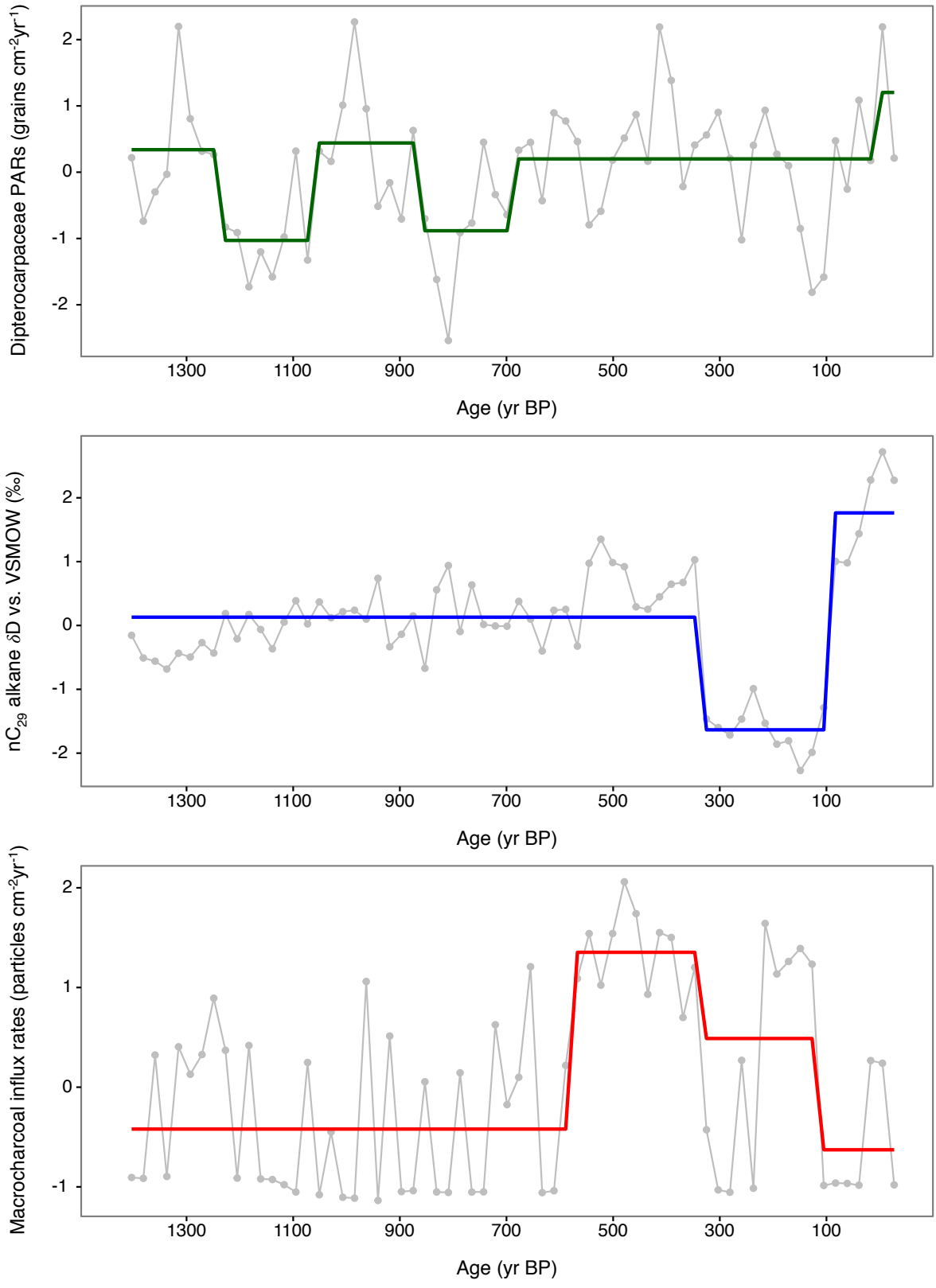


Figure 4 | Significant changes in the values of proxy records from the Bulusan sequence detected by the STARS algorithm. The grey lines depict proxy values after Box Cox transformation and pre-whitening. Green, blue and red lines depict significant changes in the sample mean of Dipterocarpaceae PARs, nC_{29} δD values and macrocharcoal influx rates, respectively. Significance of the change in the mean is set to p-value <0.05. Time window size is set to 8 data points (~160 yrs). Data plotted with *ggplot2* package (Wickham 2009) in R version 3.2.4 (R Core Team 2013).

Our findings have implications for the conservation of Dipterocarp rainforests. Given that conservation funds are extremely limited, comprehensive evaluation of different threats is essential for developing effective strategies (Wilson *et al.* 2006; Wintle *et al.* 2011). It is well established that deforestation and forest degradation is the largest threat facing Dipterocarp rainforests today, however, recent studies have suggested that anthropogenic climate change, and the associated changes in the ENSO dynamics, could also have negative consequences for these forests (Corlett and Lafrankie Jr 1998; Corlett 2012). Our results suggest that Dipterocarps rainforests are to remain dominated by the Dipterocarp species in the face of enhanced ENSO dynamics, retaining the key structural and functional features that this family provides. However, if general flowering is indeed a key coping mechanism for overcoming the negative effects of climate change, then reducing the density of Dipterocarp trees through selective logging and fragmentation of the forest cover with agricultural land, is likely to reduce its effectiveness (Curran *et al.* 1999), and exacerbate the negative effects of climate change. It could therefore be argued that deforestation and forest degradation will continue to be the biggest peril to Dipterocarp rainforests into the future and should thus remain the main focus of conservation efforts. There is also a possibility that while the overall dominance of Dipterocarp trees persists, their species composition changes substantially, favouring drought tolerant species, and putting in question the long-term survival of the drought intolerant species. More long-term studies are needed to rigorously examine these different scenarios, particularly in areas where an increase in the intensity and strength of general flowering may be limited (e.g. fragmented forest tracts). Likewise, we call for more studies on the factors shaping pollen productivity in Dipterocarp species, and on the relationship between Dipterocarp pollen productivity and biomass production, in order to constrain the interpretation of Dipterocarp biomass dynamics from fossil pollen records. This information will be vital for comprehensively evaluating the sensitivity of Dipterocarp forests to climatic changes and, thereby, facilitating the development of effective conservation strategies for this globally important ecosystem in a warming world.

In conclusion, our results show that Dipterocarp PARs at the Bulusan site have been unaffected by the magnitude and frequency of ENSO changes occurring over the last 1,400 years. These findings indicate that the positive effects of enhanced ENSO activity such as higher seed production due to stronger mass flowering and increased recruitment success of Dipterocarp

seedlings into the canopy due to higher availability of forest gaps could have out-weighed the impacts of increased tree mortality on Dipterocarp woody biomass. The other plausible explanation is that enhanced ENSO activity had increased Dipterocarp flower production rates, increasing PARs values and hiding any reductions in Dipterocarp woody biomass. Both of these mechanisms would facilitate the resilience of Dipterocarp trees to enhanced ENSO activity and the continuation of their ecological dominance in Dipterocarp rainforests. Our study thus suggests that the effects of climate change on the structure and functioning of Dipterocarp rainforests may not be as prominent as formerly expected.

Methods

Study site

Bulusan Lake is a 0.28 km^2 oval shaped lake lying at 360 m.a.s.l. at the foot-slopes of Mt Bulusan, a stratovolcano at the southeast end of the Bicol Volcanic Arc (Delfin *et al.* 1993). The lake consists of two basins: a 12 m deep round basin, and a larger, 24 m deep basin of more narrow profile. The two basins have no inlets or outlets and thus comprise a closed system fed primarily by precipitation and ground water. The waters of Bulusan Lake are of clear, bright green colour and no floating or submerged vegetation has been recorded at the lake. Bulusan Lake is part of the Bulusan Volcano National Park, a nature reserve that was first established in 1935, and where logging, hunting and burning activities are strictly regulated (Abada Gatumbato *et al.* 2011).

The Bulusan area experiences aseasonal tropical climate which is characterised by lack of dry season (i.e. mean monthly rainfall >100 mm) (PAGASA 2016). Intra-annually, the Bulusan area receives most of its rainfall from the north-eastern monsoon, and inter-annually, its precipitation is strongly linked to ENSO variability (see Prohaska *et al.* Chapter 3) (Fisheries and Aquaculture Department 1983). Both of these climatic phenomena take place during the boreal winter (November-February). Instrumental records over the last 60 years from Legaspi weather station (13°8' N, 123°44' E), ca. 55 km north of Bulusan Lake, show that rainfall in this area is statistically correlated with the Southern Oscillation Index (SOI) with less precipitation during El Niño years (Prohaska *et al.* in press, Chapter 3). While northern migration of the Intertropical Convergence Zone during the boreal summer also brings rainfall to the Bulusan area, its total effect is small in comparison to the north-eastern monsoon.

The vegetation surrounding Bulusan Lake, and up the slope of Mt Bulusan, is classified as a Lauan Dipterocarp rainforest, dominated by *Shorea contorta* (Abada Gatumbato *et al.* 2011). In addition to Dipterocarp genera *Shorea* and *Dipterocarpus*, other common large tree taxa in Philippine Dipterocarp rainforests include *Nephelium*, *Dysoxylum*, *Drypetes*, *Chisocheton*, *Strombosia*, *Pinanga, Leptonychia* and *Ficus* (Co *et al.* 2006). *Litsea, Aglaia, Xanthophyllum* and *Syzygium* are dominant medium size trees while *Leea, Praravinia, Lepisanthes, Cyrtandra, Psychotria* and *Maesa* are small trees prominent in the subcanopy (Co *et al.* 2006).

Collection of lake sediments

In March 2013 two overlapping sedimentary sequences were collected as 1 m segments from the smaller basin of Bulusan Lake with a Livingstone Piston corer from an anchored platform. The sediments were sealed in aluminium foil and protective plastic containers, shipped to the University of Oxford and stored at 5 °C. The two sedimentary sequences were used to create a continuous, undisturbed composite core using laminations present throughout the sequence (Figure 1d). For a more detailed account of the possible origins of the Bulusan laminations, see Prohaska *et al.* In prep. (Chapter 3).

Extraction and processing of fossil proxies

Fossil pollen from sedimentary sequences was used to reconstruct the dynamics of key plant taxa in the landscape surrounding Bulusan Lake. Standardised protocols were employed for the extraction and counting of fossil pollen from 1 cm^3 samples (Bennett and Willis 2001), and a reference collection of different Dipterocarpaceae pollen types was generated using herbarium samples (Appendix A) and combined with printed and online sources (e.g. Australasian Pollen and Spore Atlas Online Database (APSA Members 2007), Pollen flora of the Philippines (Bulalacao 1997), Pollen Flora of Taiwan (Huang 1972)). In each sediment sample, we counted and identified 500 terrestrial grains. The pollen of Dipterocarpaceae family is highly distinct, allowing reliable identification and counting under light microscope. Dipterocarp PARs were calculated as the number of Dipterocarpaceae pollen grains deposited in 1 cm^2 of sediment per year according to the standard procedures (Stockmarr 1971) and used to infer the changes in the biomass of Dipterocarp taxa, respectively, over time. For calculating the influx of macrocharcoal as a proxy of local fire activity, we calculated the total number of macrocharcoal particles (>150 μm) identified and counted in each 1 cm^3 sediment sample under a Nikon stereoscope at 18x magnification (Clark 1988; Mooney and Tinner 2010). Finally, we used hydrological record from Prohaska *et al.* (Chapter 3) as a proxy of ENSO variability. All three records come from the same sedimentary sequence and have the same temporal resolution, and use a high-resolution age-depth model established by Prohaska *et al.* (Chapter 3) (see Supplementary Information for more details).

Data analysis

The relationship between Dipterocarp biomass dynamics, i.e. *Dipterocarpaceae* PARs, and precipitation, i.e. $nC2_9$ δD values, and fire, i.e. macrocharcoal influx rates, has been assessed using the GLS model. GLS is a linear fixed-effects model that permits errors to be correlated and/ or have unequal variance (Pinheiro and Bates 2009). Several GLS models were applied in R version 3.2.4 (R Core Team 2013) using the nlme 3.1-128 package (Pinheiro et al. 2016) with and without different correlation and variance structures imposed on the error components to allow unequal variance of the errors (Galecki and Burzykowski 2013). We started with the most complicated model in which the response variable was Dipterocarpaceae PARs and the explanatory variables included nC_{29} alkane δD values, macrocharcoal influx rates and their interaction, as well as the sediment age (cal. yr BP, to account for any potential pollen preservation bias along the core). Errors were specified to follow an autoregressive and moving average (ARMA) process, and variance structure was defined as either fixed, exponent or power of variance covariates, with covariates being individual or combined explanatory variables. These different models were then tested and their Akaike information criterion (AIC) coefficients compared. The validity of individual models was evaluated using standard diagnostic tests (Galecki and Burzykowski 2013). The best fitting model with satisfying diagnostics was selected based on the lowest AIC coefficients with a simpler model selected whenever the difference in AIC coefficients between two models was smaller than 2. Once the best fitted GLS model with respect to the correlation and variance structure has been identified, we have tested several mean model structures by sequentially removing variables. As before, the simplest model with satisfying diagnostics and lowest AIC coefficients was selected. Explanatory variables were considered significant at the 95% level of confidence. Positive and negative slopes are indicated as (+) or (−), respectively.

STARS algorithm with time windows of incremental sizes (i.e. 5-15 points, ~100-300 years) and a p-value <0.05 was applied to detect significant changes in the mean of Dipterocarp PARs (Rodionov 2004; Rodionov 2006). Given that the STARS algorithm assumes normality and does not explicitly account for autocorrelations, the application of the STARS algorithm to the time series was preceded by its transformation to a normal distribution using Box Cox transformation and passed through a white-noise filter using the ordinary least-squares method outlined in Rodionov (2006). To address uneven spacing of the samples, each time series was

sorted into the smallest bins that still generated a continuous record (i.e. 22 years), and then standardized by the mean and standard deviation.

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Supplementary Information

Age-depth modelling

A high-resolution age-depth model was established for the Bulusan sedimentary sequence using 10 AMS^{14}C dates measured at the NERC Radiocarbon Facility, East Kilbride (Table S1) and the surface sediment age set to 2013. The radiocarbon analysis was undertaken on terrestrial plant macrofossils (e.g. leaves, twigs) to avoid reservoir effects and minimize age uncertainty. The model was computed with the Bacon 2.2 package at 1 cm resolution (Blaauw and Christen 2011; Blaauw and Christen 2015) (Figure S1, Prohaska *et al.* In prep. Chapter 3) using R version 3.2.4 (R Core Team 2013) and the IntCal13 radiocarbon calibration curve for the Northern Hemisphere (Reimer 2013). According to the model, the resolution of sediment samples used in proxy analysis is ~20 years, which corresponds to the minimum tree regeneration time (i.e. the age at which first flowering commonly occurs (Ng 1966)).

Table S1 | AMS^{14}C dates of the Bulusan sedimentary sequence measured at the NERC Radiocarbon Facility, East Kilbride.

Lab ID	Sample Material	Core Depth (cm)	Age (yr BP)	Error (yr)
SUERC-64001	Terrestrial plant	59	240	±35
SUERC-64002	Terrestrial plant	69	293	±37
SUERC-64003	Terrestrial plant	74	450	±37
SUERC-64005	Terrestrial plant	82	323	±37
SUERC-64004	Terrestrial plant	84	401	±37
SUERC-51111	Terrestrial plant	126	617	±38
SUERC-64006	Terrestrial plant	163	609	±37
SUERC-51112	Terrestrial plant	204.5	1146	±35
SUERC-64010	Terrestrial plant	272	1235	±37
SUERC-64011	Terrestrial plant	342.5	1629	±37

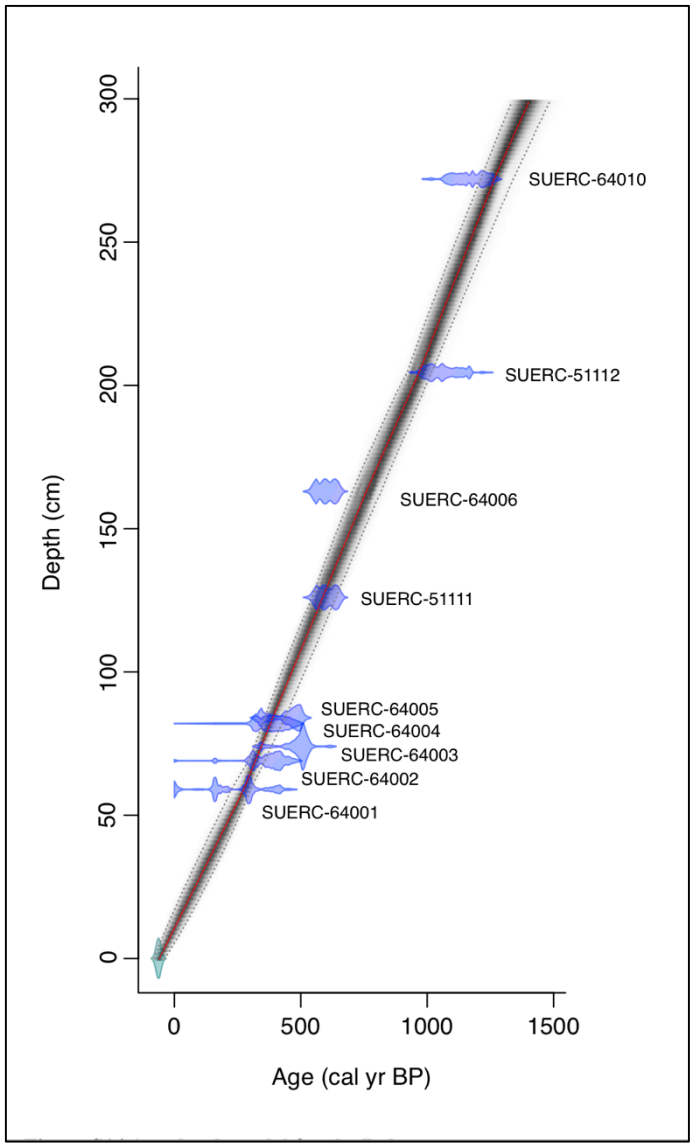


Figure S1 | Age-depth model for the Bulusan sediment sequence constructed in *Bacon 2.2* (Prohaska *et al.* In prep., Chapter 3). Probability distributions for the nine radiocarbon calibrations are shown in blue. SUERC-64011 is not shown here as it lies below the analysed section. The shaded areas represent the 1σ probability age ranges by interpolating between ^{14}C age control points. The red dashed line represent the age model used in further analysis.

Microcharcoal influx rates

Microcharcoal influx rates (particles $cm^{-2}yr^{-1}$, particle size <150 μm) were calculated by counting the total number of particles in each pollen sample, determining its concentration using known marker concentrations (Stockmarr 1971) and dividing these with the corresponding sediment accumulation rate (Clark 1988; Mooney and Tinner 2010).

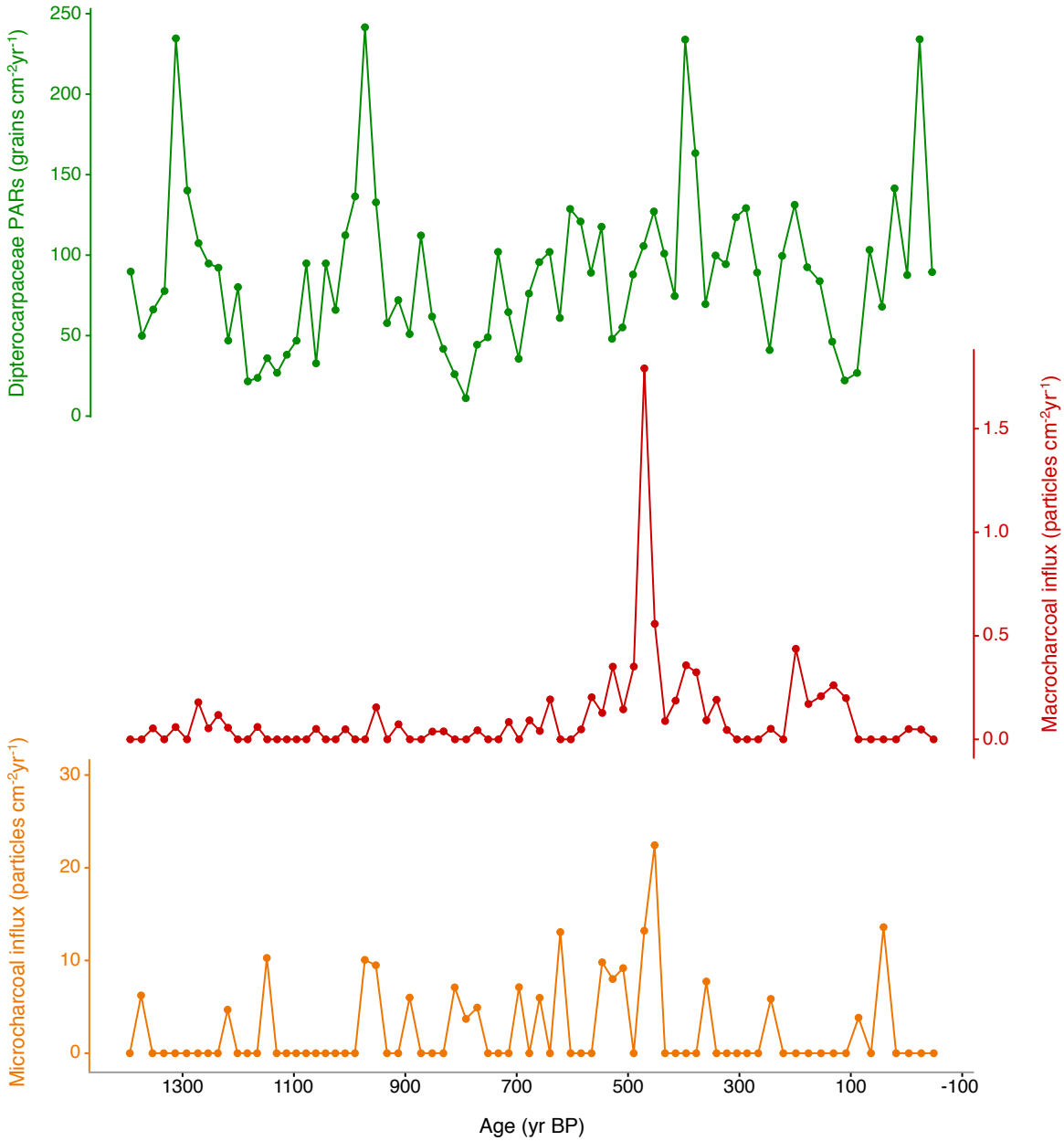


Figure S2 | Microcharcoal influx rates in relation to the macrocharcoal influx rates and Dipterocarpaceae PARs. Both micro- and macro-charcoal influx rates are relatively low throughout the Bulusan sequence. The peak in macrocharcoal influx rates at ~BP 500 is not accompanied by an increase in microcharcoal influx rates, suggesting that this was a local fire event. Data plotted with *ggplot2* package (Wickham 2009) in R version 3.2.4 (R Core Team 2013).

Timing of significant shifts in palaeorecords

The details on the timing of the significant shifts in the mean of Dipterocarp PARS, nC_{29} δD values and macrocharcoal influx rates are given in Tables S3-S5.

Table S3 | The timing and p-values of the significant changes in the mean of Dipterocarpaceae PARs values (grains cm^{-2}-$yr1^{-1}$) in the Bulusan sequence identified by the STARS algorithm with incremental time window sizes. Increases and decreases in the sample mean are shown in green and red, respectively.

Time window (no. data points)	Change Point 1 (1227 yr BP)	Change Point 2 (1051 yr BP)	Change Point 3 (853 yr BP)	Change Point 4 (677 yr BP)
5	/	/	/	/
6	3.00E-03	1.00E-03	/	/
7	3.00E-03	1.00E-03	/	/
8	3.00E-03	1.00E-03	8.00E-03	1.00E-02
9	3.00E-03	1.00E-03	/	/
10	/	/	/	/
11	/	/	/	/
12	/	/	/	/
13	/	/	/	/
14	/	/	/	/
15	/	/	/	/

Table S4 | The timing and p-values of the significant changes in the mean of δD values of the nC_{29} alkane (‰) in the Bulusan sequence identified by the STARS algorithm with incremental time window sizes. Increases and decreases in the sample mean are shown in green and red, respectively.

Time window (no. data points)	Change Point 1 (545 yr BP)	Change Point 2 (325 yr BP)	Change Point 3 (83 yr BP)	Change Point 4 (-5 yr BP)
5	2.64E-05	3.77E-12	9.20E-04	4.94E-02
6	/	7.96E-12	3.04E-05	/
7	/	7.96E-12	3.04E-05	/
8	/	7.96E-12	3.04E-05	/
9	2.64E-05	3.77E-12	3.04E-05	/
10	2.64E-05	3.77E-12	3.04E-05	/
11	2.64E-05	3.77E-12	3.04E-05	/
12	/	7.96E-12	3.04E-05	/
13	/	7.96E-12	3.04E-05	/
14	/	7.96E-12	3.04E-05	/
15	/	7.96E-12	3.04E-05	/

Table S5 | The timing and p-values of the significant changes in the mean of macrocharcoal influx rates (particles $cm^{-2}yr^{-1}$) in the Bulusan sequence identified by the STARS algorithm with incremental time window sizes. Increases and decreases in the sample mean are shown in green and red, respectively.

Time window (no. data points)	Change Point 1 (567 yr BP)	Change Point 2 (325 yr BP)	Change Point 3 (215 yr BP)	Change Point 4 (104 yr BP)
5	2.03E-11	4.76E-04	8.33E-04	5.29E-05
6	2.03E-11	4.76E-04	8.33E-04	5.29E-05
7	2.03E-11	4.76E-04	8.33E-04	5.29E-05
8	2.03E-11	2.05E-02	/	3.80E-02
9	2.03E-11	2.05E-02	/	3.76E-02
10	1.21E-05	/	/	1.53E-04
11	2.03E-11	2.05E-02	/	3.76E-02
12	1.21E-05	/	/	1.53E-04
13	1.21E-05	/	/	1.53E-04
14	1.21E-05	/	/	1.53E-04
15	1.21E-05	/	/	1.53E-04

Potential drivers of charcoal influx rates in the Bulusan record

Macrocharcoal influx rates in the Bulusan record ranged between 0-1.8 particles $cm^{-2}yr^{-1}$ (Figure 2). These are low values even when compared to other records from tropical rainforests, which document maximum macrocharcoal influx rates from 500 to up to 4000 particles $cm^{-2}yr^{-1}$ (e.g. Haberle 2005; Hermanowski *et al.* 2015) and maximum macrocharcoal concentrations from 100 to over 4000 particles cm^{-3} (e.g. Biagioni *et al.* 2015; Cole *et al.* 2015). Similarly, microcharcoal influx rates were consistently low along the Bulusan core (i.e. 0-22 particles $cm^{-2}yr^{-}1$, Figure S2) in comparison to other lacustrine cores from tropical forest regions which record a maximum of 40,000-80,000 particles $cm^{-2}yr^{-1}$ (e.g. Haberle 2005; Cordeiro *et al.* 2014).

Given the relatively low charcoal influx rates in the Bulusan record, it is difficult to pinpoint key drivers of fire activity at the site. Overall, the charcoal influx rates are low enough to suggest fire of climatic origin, such as ENSO-induced drought conditions. Previous work has demonstrated the positive relationship between ENSO-induced drought and fire (Fuller and Murphy 2006; Langner and Siegert 2009; Wooster *et al.* 2012), and while undisturbed tropical rainforests are usually highly resistant to fire due to low amounts of burning fuel, the association

of fire with severe ENSO-induced droughts have been recorded as early as 1914 in the Southeast Asian region (Goldammer *et al.* 1996). However, the poor overlap between ENSO-induced drought conditions and enhanced fire activity in the Bulusan record suggests that factors other than ENSO dynamics have influenced fire dynamics at the site. Previous studies from other regions have demonstrated that volcanic activity can cause widespread fires that last several years to several decades (Wilmshurst and McGlone 1996; Zhao *et al.* 2015). Still, the period of enhanced fire activity in the Bulusan record does not coincide well with tephra layers, suggesting a limited effect of volcanic activity on fire dynamics at the Bulusan lake. Humid tropical environments have low incidence of natural fire (Scott 2000) and therefore high charcoal influx rates in absence of drier conditions in tropical rainforest records are often linked to humans (e.g. Bush *et al.* 2008). However, the relatively low charcoal rates at the Bulusan site fail to provide a compelling evidence of human activities. Furthermore, while early written accounts of human settlement in the wider Bulusan area can be traced back to AD 1630, when it was declared a parish independent from Casiguran, and excavated artefacts from native burial grounds document a number of human settlements in this area prior to Spanish arrival (Abada *et al.* 2011), no archaeological evidence has been found in the vicinity of the lake to date. Though low microcharcoal counts during the peak in macrocharcoal influx rates at ~BP 500 suggest that this was a period of localised fire at the site, such as those caused by human-activities (Bennett *et al.* 1990), more charcoal records from neighbouring areas are needed to confirm the lack of spatial and temporal autocorrelation of fire activity on the wider landscape characteristic of human burning. Notably, the decrease in macrocharcoal influx rates from its peak values at ~BP 500 to present conflicts with the narrative of human-related fire activity at the site, as it is unlikely that human burning would have reduced towards present times given the accelerating expansion of agriculture and urbanisation. Finally, an increase in Poaceae pollen in humid tropics can also be indicative of human disturbance (Bush 2002), yet Poaceae pollen remained relatively low throughout the Bulusan record with no significant increases even during periods of increased fire activity (Prohaska *et al.* In prep., Chapter 3). Given these different lines of evidence, humans are unlikely to be the main driver of fire activity at the site, though they may have contributed to some extent to the observed fire patterns.

Pollen accumulation rates as a proxy for biomass dynamics

Pollen accumulation rates (PARs) of a particular plant taxon can provide independent estimates of its quantity on a landscape. Consequently, PARs have been widely used to reconstruct the dynamics of individual plant taxa over time (Bennett and Willis 2001), namely their population size (e.g. Magyari *et al.* 2011; Jeffers *et al.* 2012), abundance (e.g. Davis 1969; Bjune and Birks 2008), and biomass (e.g. Mazier *et al.* 2012; Jeffers *et al.* 2015). However, it is important to consider life history traits of the plants in question when interpreting their PARs. Dipterocarps are long lived and slow growing species whose size at first flowering is considerably smaller than their maximum size, meaning that there may be a large disparity in the sizes of flowering individuals across the landscape. Since larger tree individuals usually produce a larger quantity of flowers, Dipterocarp PARs will depend on both the number of flowering individuals on a landscape (i.e. absolute abundance) and their sizes, and it is therefore more appropriate to interpret their PARs in terms of relative biomass. Furthermore, previous work has showed that PARs of some plant taxa can be affected by changes in pollen productivity over time, for instance due to changes in environmental conditions (e.g. temperature, precipitation, CO_2 concentration) (Mazier *et al.* 2012). This is particularly applicable to Dipterocarp species because they flower irregularly and in response to an environmental cue (i.e. El Niño-induced droughts taking place every 2-7 years), and thus, changes in pollen productivity rates can affect Dipterocarp PARs even on longer time scales. Consequently, Dipterocarp PARs should reflect a combination of woody and reproductive biomass dynamics, and this understanding was used for interpreting Dipterocarp PARs in this study.

Changes in pollen taphonomy, i.e. depositional conditions of pollen grains, can also influence lacustrine PARs records. These include: i) changes in the lake's size and shape, usually due to changing level of the water column, ii) changes in sediment accumulation rates, e.g. due to differing soil erosion rates along the record, and iii) changes in the preservation conditions of pollen grains caused by large differences in age, sediment types and the level of water saturation along the core (Birks and Birks 2004; Giesecke and Fontana 2008, Bennett and Buck 2016). However, Bulusan lake is a permanent, medium-sized lake of considerable depth and steep slopes with sediments that are uniform, highly organic and relatively young. This makes major modifications in the lake's size and shape as well as differential preservation conditions along the sequence unlikely. Additionally, the robust, high-resolution age-depth model that was

developed for the Bulusan sequence (Figure S1) suggests stable sedimentation accumulation. We therefore conclude that taphonomic factors played only a minor role in shaping PARs values in the Bulusan sequence.

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CHAPTER 5: THE EFFECT OF PHOSPHORUS AVAILABILITY ON TREE BIOMASS DYNAMICS IN DIPTEROCARP RAINFORESTS

Abstract

Understanding nutrient limitations on the productivity of lowland tropical rainforests is essential for predicting their responses to the increasing levels of CO_2 projected for this century. While phosphorus is widely assumed to be the main limiting nutrient in these ecosystems, the evidence for this is not strong. This is particularly true for large trees because their slow growth rates and infrequent flowering make it challenging to measure their responses over short time scales. Here we use a 1,400-years long sediment record from Bulusan Lake, Philippines, to investigate how phosphorus availability affects the biomass dynamics of large trees in the lowland rainforests of Southeast Asia, known as the Dipterocarp rainforests. Pollen accumulation rates are used to infer changes in a combination of reproductive and woody plant biomass over the 1,400-year study period, while phosphorus availability is inferred from geochemical data. We focus on Dipterocarp trees given their leading role in shaping both the wood and reproductive biomass of these forests. Our results show that phosphorus has had a significant positive effect on Dipterocarp pollen accumulation rates, suggesting that phosphorus availability influences the biomass dynamics of Dipterocarp trees. No apparent lags in the pollen responses suggests that Dipterocarps responded to the changes in phosphorus availability at the Bulusan site within one generation (~20 years). Our study is the first to suggest that phosphorus plays an important role in determining the long-term biomass dynamics of Dipterocarp trees and highlights the importance of factoring in phosphorus constraints on Dipterocarp rainforest productivity in future climate-vegetation models.

Introduction

The extent to which nutrient availability affects the productivity of lowland tropical rainforests is poorly understood (Cleveland *et al.* 2011). This is a major knowledge gap because lowland tropical rainforests make up the most productive terrestrial biome and cover nearly 10% of Earth's land surface (Beer *et al.* 2010; Saatchi *et al.* 2011), and as such are a key component of the models predicting Earth's capacity to combat increasing levels of CO_2 (Bonan and Levis 2010; Huntingford *et al.* 2013).

Phosphorus is a primary plant macronutrient with particularly low concentrations in tropical soils, and is thus widely assumed to be the main limiting nutrient to the productivity of lowland tropical rainforests (Vitousek 1984). However, the evidence of such limitation is not strong (Cleveland *et al.* 2011). Previous work has indicated that the nature and magnitude of the response of tropical trees to increased phosphorus supply is highly heterogeneous, depending upon light conditions (Thompson *et al.* 1988), successional status (Lawrence 2003), mycorrhizal association (Moyersoen *et al.* 1998) and size class (Wright *et al.* 2011; Alvarez-Clare *et al.* 2013). This knowledge comes predominately from experimental studies, such as stand-level fertilisation experiments in the field (Vitousek *et al.* 1993; Mirmanto *et al.* 1999; Newbery *et al.* 2002; Campo and Vázquez-Yanes 2004; Davidson *et al.* 2004; Wright *et al.* 2011; Alvarez-Clare *et al.* 2013;), small-scale experiments at the level of individual trees in pots (Burslem *et al.* 1996; Gunatilleke *et al.* 1997; Lawrence 2003) and in the field (Yavitt and Wright 2008), and observational studies across environmental gradients that vary in soil nutrient availability (Vitousek *et al.* 1992; Santiago *et al.* 2004; Santiago and Mulkey 2005; Baltzer *et al.* 2008; Fyllas *et al.* 2009). While these approaches each have their own notable strengths, they share a common weakness - their relatively short duration (<50 years).

A large portion of the biomass production in a tropical rainforest stand is carried on by large trees (Rutishauser *et al.* 2010; Slik *et al.* 2010; Slik *et al.* 2013), and according to a hypothesis by Vitousek (1984), it is these individuals that are most limited by phosphorus availability. Their regeneration time ranges from 20 to 50 years, and their life span extends several hundred years. As a result, both experimental and observational studies have a limited ability to measure the influence that phosphorus variability exerts on two key components of rainforest

productivity, i.e. the reproduction and growth of large tree species, given that a clear pattern of this influence is likely to emerge over centennial to millennial time scales.

To address this problem, we use a set of high-resolution proxy records from a 1,400-year old sedimentary sequence from Bulusan Lake in eastern Philippines (Figure 1b, c) to investigate how the availability of phosphorus limits the biomass dynamics of large trees in lowland tropical rainforests. The Bulusan site is uniquely positioned to address this problem because its close proximity to the active Mt Bulusan volcano has caused considerable fluctuations in nutrient supply, including phosphorus, over the given time period, which has been captured in the Bulusan sediments (Figure 2, Figure S2 in Supplementary Information). In addition, the site is surrounded by the tropical forest type with the highest recorded above ground biomass production– the lowland rainforests of Southeast Asia, known as Dipterocarp rainforests (Slik *et al.* 2010; Banin *et al.* 2014) (Figure 1a). The above ground biomass of Dipterocarp rainforests can be up to 60% higher than the Amazonian average and this difference has been linked to considerably higher density of large trees (Paoli *et al.* 2008). Members of the Dipterocarpaceae tree family contribute immensely to the woody biomass of Dipterocarp rainforests; they can make up over 50% of the basal area, 80% of all emergent individuals (Appanah 1985), and 60% of total aboveground wood biomass (Paoli *et al.* 2008). Dipterocarp species also initiate general flowering events - gregarious, community-wide masting events (Woods 1955; Burgess 1972; Cockburn 1975), and therefore have the leading role in shaping the production of reproductive biomass in these forests. Hence, Dipterocarp biomass dynamics is highly indicative of the overall biomass dynamics of Dipterocarp rainforests and it is Dipterocarp trees that we focus on here.

High sediment accumulation rates of the Bulusan sequence (Figure 1d) and a robust age-depth model (Figure S1 in Supplementary Information) allowed the reconstruction of proxy records at a bi-decadal scale. Changes in phosphorus availability are inferred from XRF measurements taken by an Itrax Core Scanner (Croudace *et al.* 2006), whilst Dipterocarp pollen accumulation rates (PARs, i.e. grains $cm^{-2}yr^{-1}$) are used as a proxy of Dipterocarp biomass dynamics over the study period. Previous work has demonstrated a positive relationship between modern pollen counts (i.e. pollen loading in traps, absolute unit of measure) and plant biomass (i.e. tree volume, $m^3\ h^{-1}$), and showed that PARs can be used to approximate the biomass of adult trees (Seppä *et al.* 2009; Mazier *et al.* 2012). For Dipterocarps, we expect PARs to act as a proxy for

a combination of woody plant biomass (linked to the number of individuals and their volume) and reproductive biomass (linked to droughts-induced mass flowering events related to ENSO dynamics) (see Methods/ Supplementary Material). We examine the relationship between phosphorus abundance and Dipterocarp PARs in the Bulusan sediments using Generalised Least Squares (GLS) regression (Pinheiro and Bates 2009) in order to address the following question - what is the nature and rate of response in Dipterocarp biomass dynamics to long-term changes in phosphorus supply?

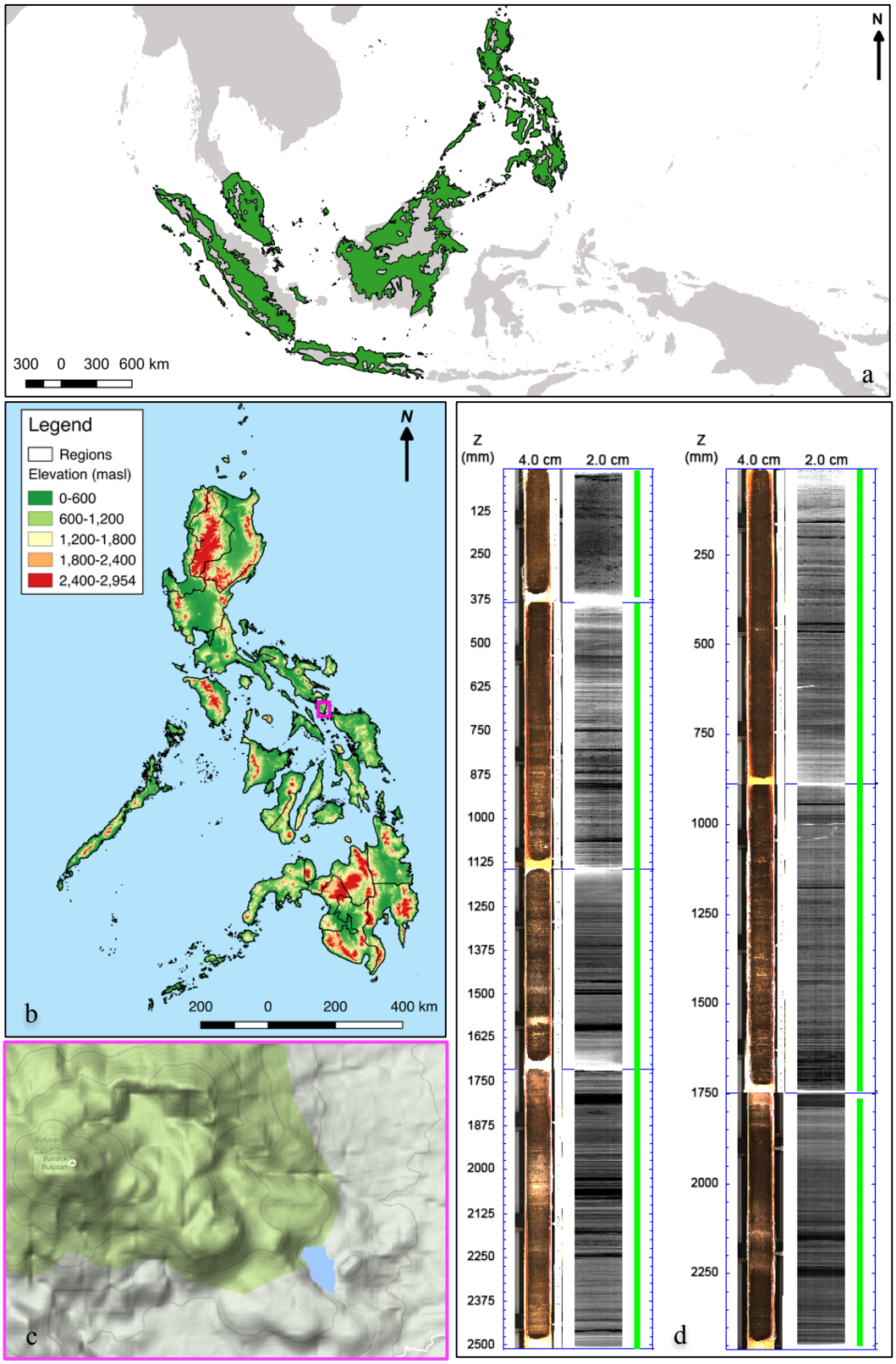


Figure 1 | Geographical and sedimentological features of the Bulusan site. a, Map showing the distribution of Dipterocarp rainforests (in green). Data from Olson et al. (2001), map generated in QGIS version 2.14.3 (Quantum GIS Development Team 2016). **b,** Topographic map of the Philippines showing the location of the study site. Data from PhilGIS (PHILGIS 2016), map generated in QGIS version 2.14.3.**c,** Map showing Bulusan Lake (in blue) within its larger landscape, with Mt Bulusan volcano in the west (in green) (Google 2016). **d,** Optical and radiographic profiles of the Bulusan sediments. The radiograph images depict the level of organic content, with higher values shown as lighter bands. The green line represents measurement validation along the cores. Images generated in ItraxPlot program (Croudace and Rothwell 2015). Figure from Prohaska *et al.* (In prep., Chapter 4).

Results & Discussion

Results from the XRF scanning analysis show distinct, but gradual changes in phosphorus abundance in the Bulusan sedimentary sequence over the last 1,400 years. Potential drivers of such changes in phosphorous abundance in lake sediments include rock weathering (Ruttenberg 2003), soil leaching and erosion (Ruttenberg 2003), sediment re-working (Robbins 1982), animal-mediated translocation of nutrients (Doughty *et al.* 2013) and pH changes in the soil surrounding the lake (Broberg and Persson 1984; Jansson *et al.* 1986; Kopáček *et al.* 2015). Geochemical and magnetic susceptibility data suggest a negative relationship between volcanic ash deposition (inferred from the abundance of leachable volcanic cations (state ions) and magnetic susceptibility values) and phosphorus abundance (Figure 2), while little evidence was found in support of the other potential drivers listed above (for a detailed description, see the relevant section in Supplementary Information). These findings point towards phosphorus solubility via volcanic ash acidification of the soil as the most likely driver of the phosphorus fluctuations recorded in the Bulusan sediments. The close proximity of the active Mt Bulusan volcano (i.e. ~4 km up slope from the lake), whose most frequent historic activities have been acidic ash-fall eruptions (Delfin *et al.* 1993; McDermott *et al.* 2005), further supports this interpretation. The deposition of volcanic ashes can reduce soil pH, and subsequently, reduce the solubility of phosphorus forms (Cronin *et al.* 1998; Cronin *et al.* 2003; Ranatunga *et al.* 2009; Wilson *et al.* 2011), including phosphates (i.e. $H_2PO_4^-$ and HPO_4^{2}) which are the main source of phosphorus to plants (Sutton and Larsen 1964). We therefore argue that during the intervals of volcanic ash deposition in the Bulusan area, the pH of the soils surrounding the Bulusan Lake decreased, and the solubility of phosphates reduced, leading to a decrease in their availability to plants and their rain-based transport to the lake.

Phosphorus abundance had a significant positive effect on Dipterocarp PARs in the Bulusan sedimentary sequence (p-value <0.05) (Table 1, Figure 3). In addition, we found no apparent lags in the changes of Dipterocarp PARs in response to the changes in sediment derived phosphorus (Table 1, Figure S5). These results suggest that Dipterocarps responded to the changes in phosphorus availability at the Bulusan site within one generation (~20 years), and shed some light on the probable mechanisms underlying these responses.

On the one hand, the positive relationship of PARs to phosphorus changes observed in the Bulusan record could be, at least partly, related to pollen productivity rates. Previous studies have shown that in any mass flowering event, only a portion of reproductively mature Dipterocarp individuals actually produce flowers (Ashton *et al.* 1988; Sakai *et al.* 1999), and this was attributed to the nutritional status of the trees. Early on, it was postulated that stored carbohydrates were the decisive factor in the magnitude or frequency of Dipterocarp masting (Janzen 1974; Ashton 1982), but later work provided evidence against it (Ichie *et al.* 2005) and showed the high phosphorus cost of mass flowering and subsequent mast fruiting for Dipterocarp species (Ichie *et al.* 2005; Ichie and Nakagawa 2011). Therefore, accumulation of phosphorus has been put forward as a potentially decisive factor in the magnitude and frequency of mast reproduction on the relatively nutrient poor soils prevailing in Southeast Asia (Ichie and Nakagawa 2011). Given this evidence, decreasing phosphorus availability at the Bulusan site could have potentially decreased the frequency and magnitude of mass flowering in Dipterocarps, resulting in lower production rates of their pollen.

On the other hand, the positive effect of sedimentary phosphorus on Dipterocarp PARs may be indicative of long-term phosphorus limitation to the woody biomass production in Dipterocarp forests. Banin *et al.* (2014) showed that Dipterocarp trees gain woody biomass faster than otherwise equivalent, neighbouring non-dipterocarp trees, highlighting that Dipterocarp growth is an important contributor to the woody biomass production in Dipterocarp rainforests. Though experimental work suggests that the effect of phosphorus availability on the rate of woody biomass increase in Dipterocarps is relatively small on an annual scale (Mirmanto *et al.* 1999), it is possible that this effect accumulates and becomes notable on a multi-decadal scale. For instance, observational studies looking at the biomass production in Dipterocarp rainforest plots across nutrient gradients showed that tree biomass increment is positively related to nutrient availability, particularly phosphorus, and that this increment is more strongly related for large trees than for small ones (Paoli *et al.* 2005; Paoli and Curran 2007, Paoli *et al.* 2008). Though observational studies are relatively short in duration, if soil characteristics in the forest plots have remained relatively stable over the last few decades (i.e. little to no change in the climatic conditions, land use or nearby volcanic activity), then the observed tree growth rates are likely to be at equilibrium with the nutrient concentrations and reflect long-term nutrient limitation to biomass production at these sites.

In conclusion, our study is the first to link changes in pollen numbers to large-scale variability in phosphorus abundance spanning hundreds to thousands of years, highlighting the values of such long-term records for studying the effects of nutrient limitation on the ecosystems dominated by long-lived and slow reproducing organisms, such as the lowland tropical rainforests. Furthermore, our study suggests that phosphorus has positive influence on the biomass dynamics of Dipterocarp trees over longer time scales and thus plays a key role in shaping the productivity of Dipterocarp rainforests. However, it is not clear from the fossil pollen record alone what aspect of Dipterocarp biomass production is chiefly influenced by phosphorus supply; plausible candidates include woody and reproductive biomass. More long-term studies are needed to validate and refine our findings on a larger spatial and temporal scale. This research topic would also benefit from modern studies on the relationship between pollen/ flower productivity and woody biomass in Dipterocarp tree species and under different environmental conditions. Nevertheless, our study highlights the importance of factoring in the constraints that phosphorus availability imposes on Dipterocarp rainforest productivity in future climate-vegetation models.

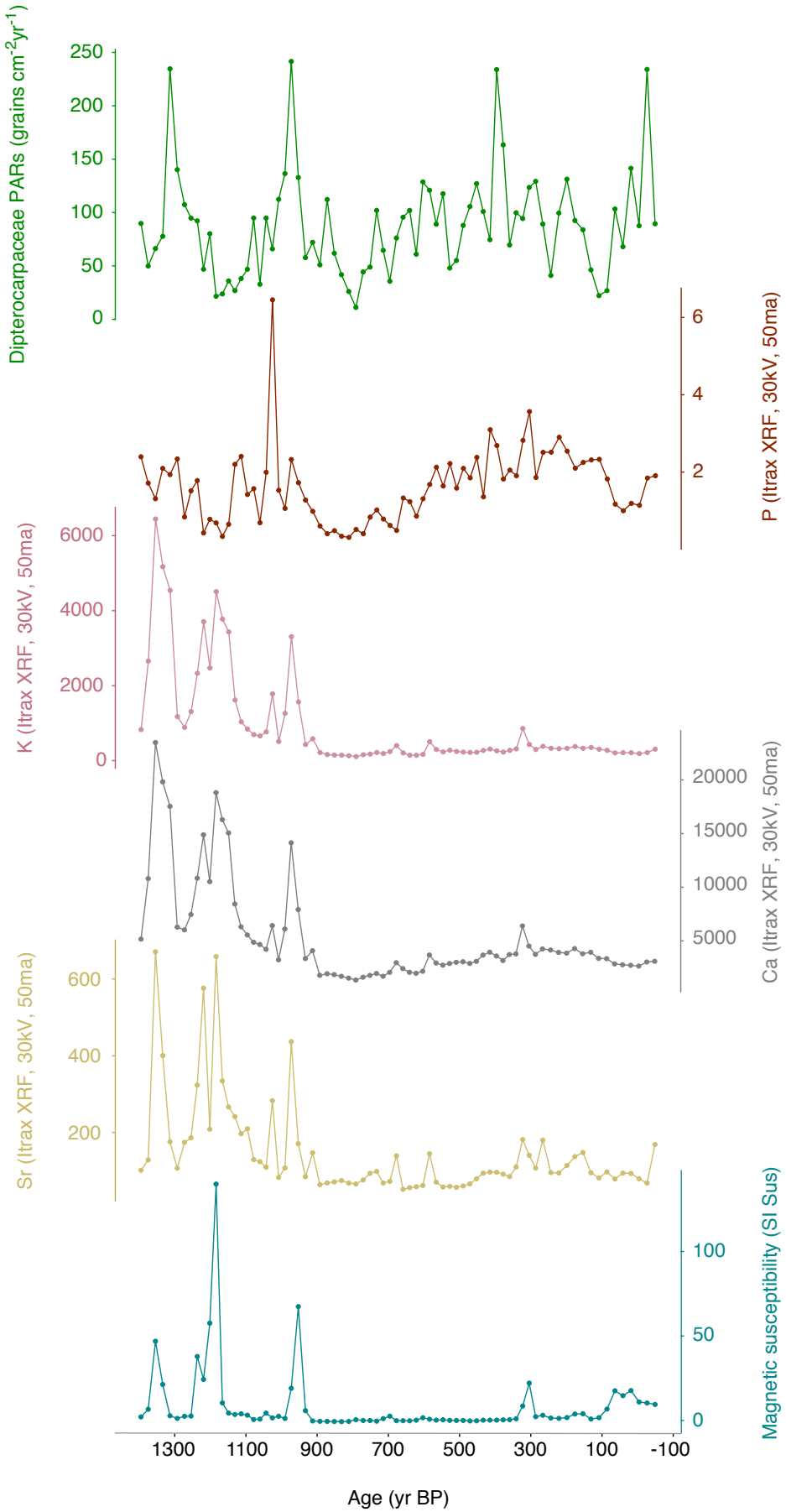


Figure 2 | Dynamics of Dipterocarp PARs, phosphorus abundance (P), potassium abundance (K), calcium abundance (Ca), strontium abundance (Sr) and magnetic susceptibility in the Bulusan sequence during the last 1,400 years. Data plotted with *ggplot2* package (Wickham 2009) in R version 3.2.4 (R Core Team 2013).

Table 1 | Summary of best fitted GLS models for the effect of phosphorus abundance on Dipterocarpaceae PARs, including immediate (no lags) and lagged responses (i.e. 1-4 data points, ~20-80 years). Dipterocarpaceae PARs (grains $cm^{-2}yr^{-1}$), phosphorus abundance (XRF counts), SE = standard error.

Model Structure	log(Dipterocarpaceae PARs) = log(phosphorus)				
No. lags	0	1	2	3	4
Fixed effects					
Analysis of variance (F-test/p-value)					
Intercept	2010.42/<0.01	1710.47/<0.01	1808.43/<0.01	1692.78/<0.01	1269.30/<0.01
Phosphorus	6.33/0.01	2.02/0.16	3.88/0.05	4.14/0.05	0.64/0.43
Coefficients table (coefficient/ SE/p-value)					
Intercept	4.22/0.10/<0.01	4.25/0.11/<0.01	4.24/0.11/<0.01	4.24/0.11/<0.01	4.30/0.13/<0.01
Phosphorus	0.30/0.12/0.01	0.17/0.12/0.15	0.24/0.12/0.05	0.25/0.12/0.04	0.10/0.13/0.42
Variance Function (95% CI)	/	/	/	/	/
Correlation Structure (95% CI)	ARMA (1,0) 0.38 (0.15, 0.58)	ARMA (1,0) 0.41 (0.14, 0.62)	ARMA (1,0) 0.39 (0.14, 0.60)	ARMA (1,0) 0.41 (0.17, 0.60)	ARMA (1,0) 0.48 (0.22, 0.67)
Scale (Standardised residuals, σ)	0.55 (0.45, 0.66)	0.57 (0.47, 0.70)	0.56 (0.46, 0.68)	0.57 (0.47, 0.69)	0.60 (0.48, 0.74)

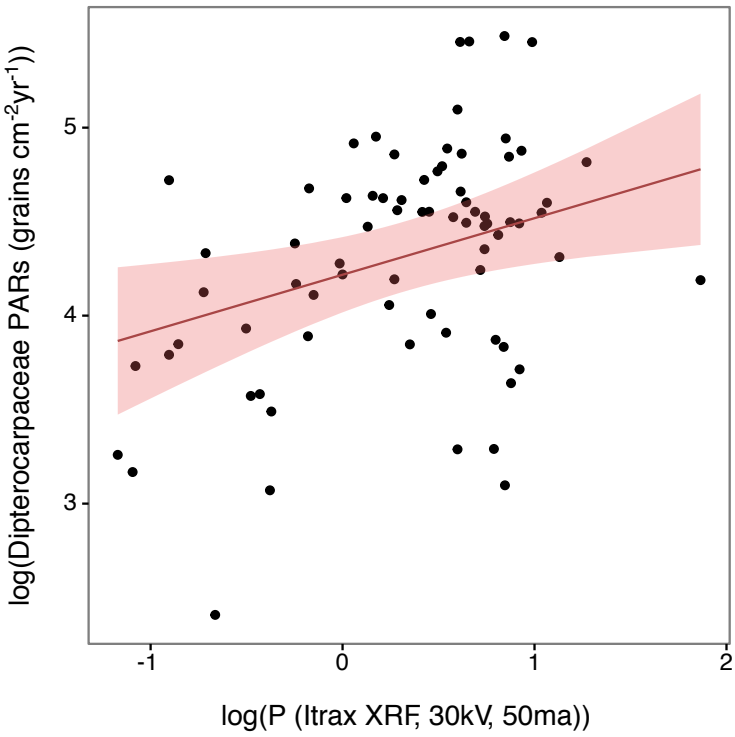


Figure 3 | The relationship between Dipterocarpaceae PARs and phosphorus abundance (P) in the Bulusan sequence over the last 1,400 years according to the best fitted model (0 lags): log(Dipterocarpaceae PARs) = 4.22 + 0.30*log(P). Data plotted with *ggplot2* package (Wickham 2009) in R version 3.2.4 (R Core Team 2013).

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Supplementary Information

Materials & Methods

Ecological dominance of Dipterocarp species

The Dipterocarpaceae family constitutes the largest tree size class in Dipterocarp rainforests, and can comprise over 50% of the basal area, 80% of all emergent individuals (Appanah 1985), and 60% of total aboveground wood biomass (>10 cm d.b.h.) (Paoli *et al.* 2008). Recent work suggests that the high density of large wind-dispersed Dipterocarp species, which need to be tall and emergent to disperse their seeds, is likely to be the main cause of the unusually high woody above ground biomass of Dipterocarp rainforests (Slik *et al*. 2010, Slik *et al.* 2013). A large number of Dipterocarpaceae species can only reproduce successfully during general flowering, which are gregarious, community-wide masting events taking place every 2-7 years and are most likely triggered by El Niño-induced droughts (Woods 1955; Burgess 1972; Cockburn 1975). Previous studies have shown that nearly 50% of the mature Dipterocarp individuals and more than 70% of emergent Dipterocarps individuals can flower during mass flowering years (Burgess 1972; Cockburn 1975; Sakai *et al.* 1999). This mass flowering of Dipterocarps is accompanied by heavy flowering of many other plant species, including members of Anacardiaceae, Euphorbiaceae, Annonaceae, Fabaceae, Burseraceae, Moraceae, and Myristicaceae (Appanah 1985). Consequently, Dipterocarps play the key role in shaping the reproductive biomass production in Dipterocarp rainforests.

Drivers of phosphorus variability in lake sediments over different time scales

There are several potential drivers of phosphorous (P) variability in lake sediments including rock weathering (Ruttenberg 2003), soil leaching and erosion (Ruttenberg 2003), sediment re-working (Robbins 1982), animal-mediated translocation of nutrients (Doughty *et al.* 2013) and changes in soil pH in the lake's watershed (Broberg and Persson 1984; Jansson *et al.* 1986; Kopáček *et al.* 2015).

Weathering of continental bedrock is the main source of P to the soils that support continental vegetation over geological time scales (i.e. 10^3s to 10^6s years). P is weathered from bedrock by dissolution of P-bearing minerals e.g. apatite by naturally occurring acids, namely from

microbial activity (e.g. Cosgrove 1977; Frossard *et al.* 1995). Changes in the rates of tectonic uplift and exposure of P-bearing rocks can therefore cause changes in the P availability in an ecosystem which would be eventually reflected in its lake sediments.

Soil development can also affect the deposition of P in lake sediments on longer time scales (i.e. 10^3s to 10^4s years). According to the classic model by Walker and Syers (1976), later validated by numerous studies (e.g. Smeck 1985; Crews *et al.* 1995; Filippelli and Souch 1999), soil development entails systematic changes in the total amount and chemical form of P; while initial stages have P present mainly as primary minerals (e.g. apatite), its fraction decreases in mid-stage soils which instead harbour increasing levels of less-soluble secondary minerals and organic P, until finally in late stages of soil development P is partitioned primarily between refractory minerals and organic P. Leaching is the process by which water-soluble plant nutrients such as P are lost from the soil, by means of rivers, rain or irrigation (agriculture). Changes in river discharge, precipitation amount, fire activity or agricultural practices can influence the leaching rates of soluble P from the soil and its deposition in lake sediments on shorter time scales (i.e. annual to millennial scales) (Schlesinger 1997; Ruttenberg 2003). Similarly, changes in the soil erosion rates, due to precipitation variability, landslides or changes in land-use can affect the influx of insoluble P, bound by various soil constituents, to the lake.

Sediment re-working is a mechanism by which P abundance can vary in lake sediments independently of its availability on the land. For instance, rates of sediment reworking by high concentration of zoobenthos (e.g. oligochaete worms) in North American Great Lakes are comparable to or exceed sedimentation rates (Robbins 1982). Thus, significant changes in the concentration of zoobenthos species over time can alter P sedimentation rates following its introduction to the lake. Furthermore, changes in the redox-driven coupled Fe–P cycling of bottom waters and benthic P efflux can also affect P abundance in the sediments (Mortimer 1941, 1942; Boström *et al.* 1988). Microbial reduction and re-oxidation/re-precipitation of ferric oxyhydroxides controls P release and retention rates by sediments through both direct and indirect responses of microbial community to changes in redox state of bottom waters (e.g. Mortimer 1941, 1942; Gächter and Meyer 1993).

Animals are an important vector of nutrients in terrestrial ecosystems, and large bodied animals play a central role in nutrient translocation because they travel larger distances and digest food at a slower rate in comparison to smaller animals (Demmet and Soest 1985; Kelt 2001). For instance, previous work has suggested that reduction in the biomass of large mammals due to Pleistocene megafaunal extinctions has significantly reduced the lateral flux of P on all continents outside of Africa (Doughty *et al.* 2013). Given that permanent water bodies are known hotspots of animal activity in forested landscapes, changes in the biomass of large mammals in such landscapes may lead to notable change in P deposition in lacustrine sediments.

Finally, changes in soil pH in a lake's watershed can also affect the influx rates of nutrients to the lake (Broberg and Persson 1984; Jansson *et al.* 1986; Kopáček *et al.* 2015). P is particularly affected by the soil pH and its solubility is usually highest in neutral soils (i.e. pH 6.5 -7.5). At alkaline pH values (pH >7.5) phosphate ions tend to react quickly with calcium (Ca) and magnesium (Mg) to form less soluble compounds, while at acidic pH values (pH <6.5), phosphate ions react with aluminium (Al) and iron (Fe) to again form less soluble compounds (Lajtha and Harrison 1995). Soil acidification by means of volcanic ash deposition has been well documented (Cronin *et al.* 1998; Cronin *et al.* 2003; Ranatunga *et al.* 2009; Wilson *et al.* 2011), demonstrating that changes in volcanic activity over time can exert significant changes in P solubility, and consequently, its availability to plants as well as its leaching out of the soil and into lakes.

Study site and material collection

Bulusan Lake is a maar lake situated at the foot-slopes of Mt Bulusan, a stratovolcano at the southeast end of the Bicol Volcanic Arc in the Philippines (Delfin *et al.* 1993). The wider area around the lake has been proclaimed Bulusan Volcano National Park in 1935, with logging, hunting and burning activities in the park strictly prohibited (Abada Gatumbato *et al.* 2011). The area experiences aseasonal tropical climate where no month has mean rainfall less than 100 mm. Intra-annually, the Bulusan area receives most of its rainfall from the north-eastern monsoon, while inter-annually its precipitation is strongly related to El Niño/ Southern Oscillation (ENSO) variability (see Prohaska *et al.* Chapter 2). Both of these climatic phenomena take place during the boreal winter (November-February). Instrumental records

over the last 60 years from Legaspi weather station (13°8' N, 123°44' E), ca. 55 km north from Bulusan Lake, show that rainfall in this area is statistically correlated with the Southern Oscillation Index (SOI) with less precipitation during El Niño years (Prohaska *et al.* In prep., Chapter 3). While northern migration of the Intertropical Convergence Zone (ITCZ) during the boreal summer also brings rainfall to the Bulusan area, its total effect is small in comparison to the north-eastern monsoon.

Soils in the greater Bulusan Lake area are loamy clay soils and have high fertility in comparison to other regional soil types (Abada Gatumbato *et al.* 2011). The proximity of Lake Bulusan to the active Mt Bulusan volcano, which generates large deposits of andesitic rocks, has acted as an additional source of plant nutrients for the surrounding vegetation. The dominant forest type in the Bulusan Volcano National Park, including the area around the lake and up the slope of Mt Bulusan until 600 m.a.s.l, is Lauan Dipterocarp rainforest dominated by *Shorea contorta*. The dominant large tree genera are Shorea, Parashorea, *Nephelium*, *Dysoxylum*, Drypetes, *Chisocheton*, *Strombosia*, *Pinanga, Leptonychia* and *Ficus* (Co *et al.* 2006). Species of *Litsea, Aglaia, Xanthophyllum* and *Syzygium* are among the most abundant medium sized trees while species of *Leea, Praravinia, Lepisanthes, Cyrtandra, Psychotria* and *Maesa* are the most common small trees (Co *et al.* 2006).

We collected two overlapping sedimentary sequences, 5.3 m BUL1 and 5.0 m BUL2 in 1 m segments from the smaller 12 m deep basin of the Bulusan Lake (Figure 1d) in March 2013 using a Livingstone Piston corer from an anchored platform. The sediments were sealed in protective plastic containers and shipped to the University of Oxford where they have been stored at 5 °C. We overlapped two sedimentary sequences to create a single undisturbed composite sequence using the fine laminations present throughout the sediments. A more detailed discussion on the possible origins of the Bulusan laminations is given in Prohaska *et al.* In prep. (Chapter 3).

Extraction and processing of fossil proxies

A high-resolution age-depth chronology was established using 10 AMS^{14}C dates on identified terrestrial plant material (Table S1) and computed with the *Bacon 2.2* package (Blaauw and Christen 2011; Blaauw and Christen 2015) using R version 3.2.4 (R Core Team 2013) and the

IntCal13 radiocarbon calibration curve for the Northern Hemisphere (Reimer 2013) (Figure S1).

Sediment samples were extracted from the Bulusan sequence at the University of Oxford as a continuous series of 4 cm long slices of 1 cm^3 volume from the top 3.0 m, with each slice corresponding to a ~20-year interval according to the age-depth model. Pollen was extracted from the sediment samples and counted following standardised protocols (Bennett and Willis 2001). For pollen identification, a reference collection of different Dipterocarpaceae pollen types was developed using herbarium samples from Kew Gardens, UK (Appendix A), and complemented with online sources (e.g. Australasian Pollen and Spore Atlas Online Database (APSA Members 2007), Pollen flora of the Philippines (Bulalacao 1997), Pollen Flora of Taiwan (Huang 1972)). We counted and identified 500 terrestrial pollen grains per sample under light microscope. Pollen accumulation rates (PARs) were calculated as the number of pollen grains accumulated in 1 cm^2 of sediment per year according to the standard procedures (Stockmarr 1971, Birks and Birks 1980) and used to infer the changes in the Dipterocarpaceae biomass dynamics (a combined signal of reproductive biomass and woody plant biomass) over time at the Bulusan site. The sample resolution of ~20 years corresponds to the minimum tree regeneration time, i.e. the age at which first flowering commonly occurs (Ng 1966).

We also used a recently developed hydrological record from the same sequence, based on δD values of leaf wax alkanes (δD_{wax}, Prohaska *et al.* in prep, Chapter 3), as a proxy of ENSO variability over the last 1,400 years. Similarly, we used a recently reconstructed record of fossil macrocharcoal influx rates (particles $cm^{-2}yr^{-1}$, particle size >150 μm) (Prohaska *et al.* In prep., Chapter 4) to reconstruct local fire activity over the same time period.

We conducted high-resolution analysis of major and trace chemical elements in the Bulusan sedimentary sequence using the ITRAX Core Scanner (Croudace *et al.* 2006) at the Arhus University, Denmark. The core sections were scanned at a step-size of 0.2 mm to obtain an ED-XRF spectrum at each step. A digital continuous-strip X-radiograph, 22 mm in width, was collected immediately prior to the XRF scan using a charge-coupled (CCD) line camera. The count time for each measurement was 30 seconds to ensure that minor elements are well detected. The X-ray beam used to irradiate the core is generated using a 3kW Mo X-ray tube run at 55kV and 50 ma for x-radiography and 30kV and 50ma for the XRF scan. The recorded

spectra were deconvolved in live time to construct profiles of peak area integrals for individual elements. The element peak area reflects element abundances within the sediment.

Magnetic susceptibility was measured on intact Bulusan cores using the Barrington MS2 Magnetic Susceptibility System made of a magnetic susceptibility meter coupled with a core logging sensor at 2 cm spatial resolution and 11s SI (9s CGS) measurement period.

We calculated arithmetic mean of XRF counts for each chemical element, as well as of magnetic susceptibility values, over 4 cm long slices to align these data with the sample resolution of other fossil proxies (i.e. pollen, lipid biomarkers, charcoal).

Table S1 | AMS^{14}C dates of the Bulusan sedimentary sequence measured at the NERC Radiocarbon Facility, East Kilbride.

Lab ID	Sample Material	Core Depth (cm)	Age (yr BP)	Error (yr)
SUERC-64001	Terrestrial plant	59	240	±35
SUERC-64002	Terrestrial plant	69	293	±37
SUERC-64003	Terrestrial plant	74	450	±37
SUERC-64005	Terrestrial plant	82	323	±37
SUERC-64004	Terrestrial plant	84	401	±37
SUERC-51111	Terrestrial plant	126	617	±38
SUERC-64006	Terrestrial plant	163	609	±37
SUERC-51112	Terrestrial plant	204.5	1146	±35
SUERC-64010	Terrestrial plant	272	1235	±37
SUERC-64011	Terrestrial plant	342.5	1629	±37

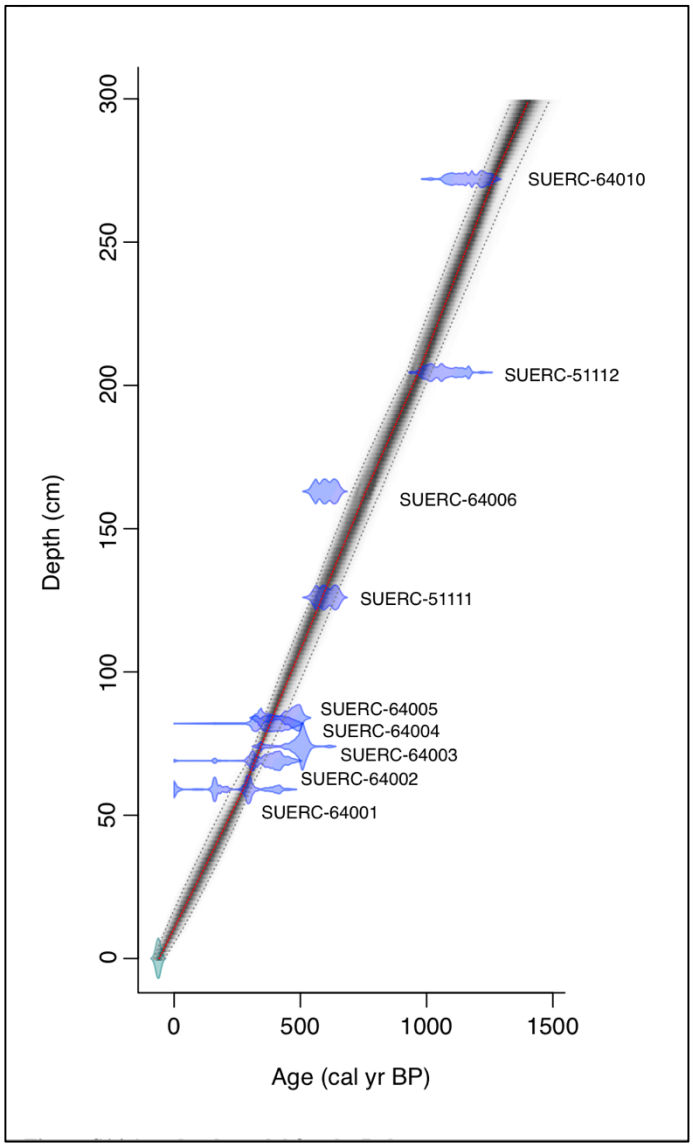


Figure S1 | Age-depth model for the Bulusan sediment sequence constructed in *Bacon 2.2* (Prohaska *et al.* In prep., Chapter 3). Probability distributions for the nine radiocarbon calibrations are shown in blue. SUERC-64011 not shown here as it lies below the analysed section. The shaded areas represent the 1σ probability age ranges by interpolating between ^{14}C age control points. The red dashed line represent the age model used in further analysis.

Data analysis

We used the Generalised Linear Least Squares (GLS) to evaluate the relationship between Dipterocarpaceae PARs and P abundance in the Bulusan record. GLS is a linear fixed-effects model that allows the errors to be correlated and/ or have unequal variance (Pinheiro and Bates 2009). Using the nlme 3.1-128 package (Pinheiro et al. 2016) in R version 3.2.4 (R Core Team 2013), we developed several GLS models that had different correlation and variance structures

imposed on the error components to allow unequal variance of the errors. Errors were specified to follow an autoregressive and moving average (ARMA) process. Several mean model structures were examined where Dipterocarpaceae PARs were the response variable and P the explanatory variable. We then tested and compared these models with and without inclusion of different autocorrelation and variance structures (Galecki and Burzykowski 2013). We selected the best fitting model based on the lowest Akaike Information criterion (AIC) coefficients, and selected a simpler model whenever the difference in AIC coefficients between simpler and more complex models was smaller than 2. Models were considered significant at the 95 % level of confidence with positive and negative slopes indicated as (+) or (−), respectively. Following the same procedure, we selected the best-fitted models for the PARs-P relationship with incremental temporal lags (i.e. 1-4 points, ~20-80 years) to determine the most likely rate of response in Dipterocarpaceae PARs to the changes in P abundance.

One important first step was to determine the main driver(s) behind the variability of P abundance in the Bulusan sediments. Firstly, we performed a Principal Component Analysis (PCA) on the chemical elements detected by the Itrax XRF Core Scanner to test the relationship between P and the main leachable elements of volcanic ash material, i.e. potassium (K), calcium (Ca) and strontium (Sr). Prior to the PCA application, Itrax data were Hellinger transformed to reduce the influence of abundant elements. To investigate the effect of soil erosion on the P abundance, we reconstructed the record of organic to inorganic matter ratio using the ratio of barium to titanium (Ba/Ti) values (Croudace *et al.* 2006) and compared it to the P record. Finally, to examine the influence of weathering and burning on P abundance, we compared the rainfall and fire variability records (Chapters 3 and 4, respectively) with the P record.

Supplementary Discussion

Itrax XRF and magnetic susceptibility records

The XRF results show relatively high counts and low noise-to-signal ratio for K and Ca in the Bulusan sediments, which allows them to be analysed at the sub-mm resolution (Figure S2). In contrast, Sr and P have relatively low counts and high noise-to-signal ratio, precluding analysis at such high resolution. Nevertheless, at lower resolution, clear trends also emerge in the Sr and P records. By averaging the XRF counts of the chemical elements over 4 cm long slices (Figure 2) in order to align them with the pollen, lipid biomarker, and macrocharcoal records, we have also reduced the noise-to-signal ratio in the Sr and P records.

Magnetic susceptibility values are relatively low throughout the Bulusan sequence, with the exception of the peaks that overlap with the tephra layers. These results demonstrate a low proportion of ferromagnetic material in the Bulusan sediments between the volcanic eruptions. The generated magnetic susceptibility record has a relatively low noise-to-signal ratio.

Drivers of phosphorus abundance in the Bulusan sediments

Analysis of the Bulusan sediments suggests opposite dynamics between P and the volcanic ash deposition proxies, i.e. K, Ca, Sr and the magnetic susceptibility values (MS). K^+ and Ca^+ cations are among the most abundant ionic species in volcanic ash leaches (Jones and Gislason 2008; Wilson *et al.* 2011), and these leaches also represent an important source of Sr in nature (Koshikawa *et al.* 2016), making the three chemical elements suitable proxies for volcanic ash deposition. Similarly, magnetic susceptibility has been shown to be particularly useful for detecting the presence of tephra layers in lacustrine sequences because tephra is usually rich in ferromagnetic material, which shows up as peaks in magnetic susceptibility values (Oldfield *et al.* 1983a; Oldfield *et al.* 1983b; Oldfield 1988; Lozano-García *et al.* 1993). The PCA analysis on the individual abundances of chemical elements and magnetic susceptibility magnitude in the Bulusan record shows clear clustering of K, Ca, Sr and MS, demonstrating similar dynamics among these four variables and suggesting a common source (Figure S3). We argue that these four variables capture the signal of volcanic ash deposition at the Bulusan site over the last 1,400 years. In contrast, K, Ca, Sr and MS are separated from other elements, including P, by the first PCA axis, suggesting that the latter have not been introduced into the sediments by ash

deposition. Figure S2 shows that the peaks in K, Ca, Sr and MS closely match the drops in the P abundance and vice versa during the ~BP 1400-900 period (BP defined as 'years Before Present', i.e. AD 1950), and a gradual but continuous growth in P values takes place during the prolonged period of low ash deposition ~BP 900-100. These results suggest that volcanic ash deposition has influenced P abundance in the Bulusan sediments.

Further analysis has yielded little evidence in support of the other potential drivers of P variability in the Bulusan record. Firstly, weathering of continental bedrocks and soil development influence P abundance in soils on geological time scales and they are thus an unlikely cause of the decadal to centennial variability in P abundance recorded in the Bulusan sediments. Secondly, comparison between the P record and the record of δD values of the nC_{29} alkane, i.e. proxy for precipitation amount, reveal a stark difference between the two variables (Figure S4). Of particular importance is a lack of response in P abundance to the large decrease in precipitation between ~BP 300-50. Moreover, other palaeorecords from the region suggest relatively stable air temperature conditions over this time period, with somewhat colder conditions ~BP 350-100 (Mann and Jones 2003; Jones and Mann 2004). Furthermore, a poor overlap between the changes in macrocharcoal influx rates and those of P abundance (Figure S4), as well as generally low charcoal counts indicative of weak fire activity, make it improbable that fire activity exerted notable influence on the leaching of P at the site. It is hence overall unlikely that differential soil leaching has caused the observed changes in P abundance recorded in the Bulusan sediments over the last 1,400 years. Similarly, while the Ba/Ti record indicates a large increase in organic matter content in the Bulusan sequence between ~BP 1000-700, this change has a poor overlap with the changes in P abundance (Figure S4), suggesting that the erosion rates at Lake Bulusan over the last 1,400 years are not behind the recorded changes in P abundance. Furthermore, the basin we cored the sediments from is more than 12 m deep, which minimises the chances of sediment re-working by external forces such as wind and terrestrial animals. Moreover, fine laminations of diatomaceous origin detected throughout the sedimentary sequence provide evidence against sediment re-working by benthic organisms (Figure 1d), while the different dynamics of P and Fe demonstrated by the PCA analysis (Figure S3) offer little support towards changes in redox state of bottom waters being a major driver of P abundance in the Bulusan sediments. While algal blooms and die-off can create peaks in nutrient deposition in lake sediments, these processes are dependent on nutrient input from

external sources, and planktonic dynamics in the lake would be the consequence, not the cause, of changes in nutrient abundance in lake sediments (Smith 1983; Anderson 2002; Conley *et al.* 2009). Consequently, planktonic activity is an unlikely driver of the observed P changes in the Bulusan sequence. Finally, no *Sporormiella* spores were detected in the Bulusan record during pollen identification and counting, suggesting the biomass of large mammals at the Bulusan site has been consistently low over this time period, making animal-based translocation of P an improbable driver of the recorded fluctuations in P abundance. Taking into account the different lines of evidence discussed above, we conclude that volcanic ash deposition was the dominant driver of P changes in the Bulusan record over the last 1,400 years.

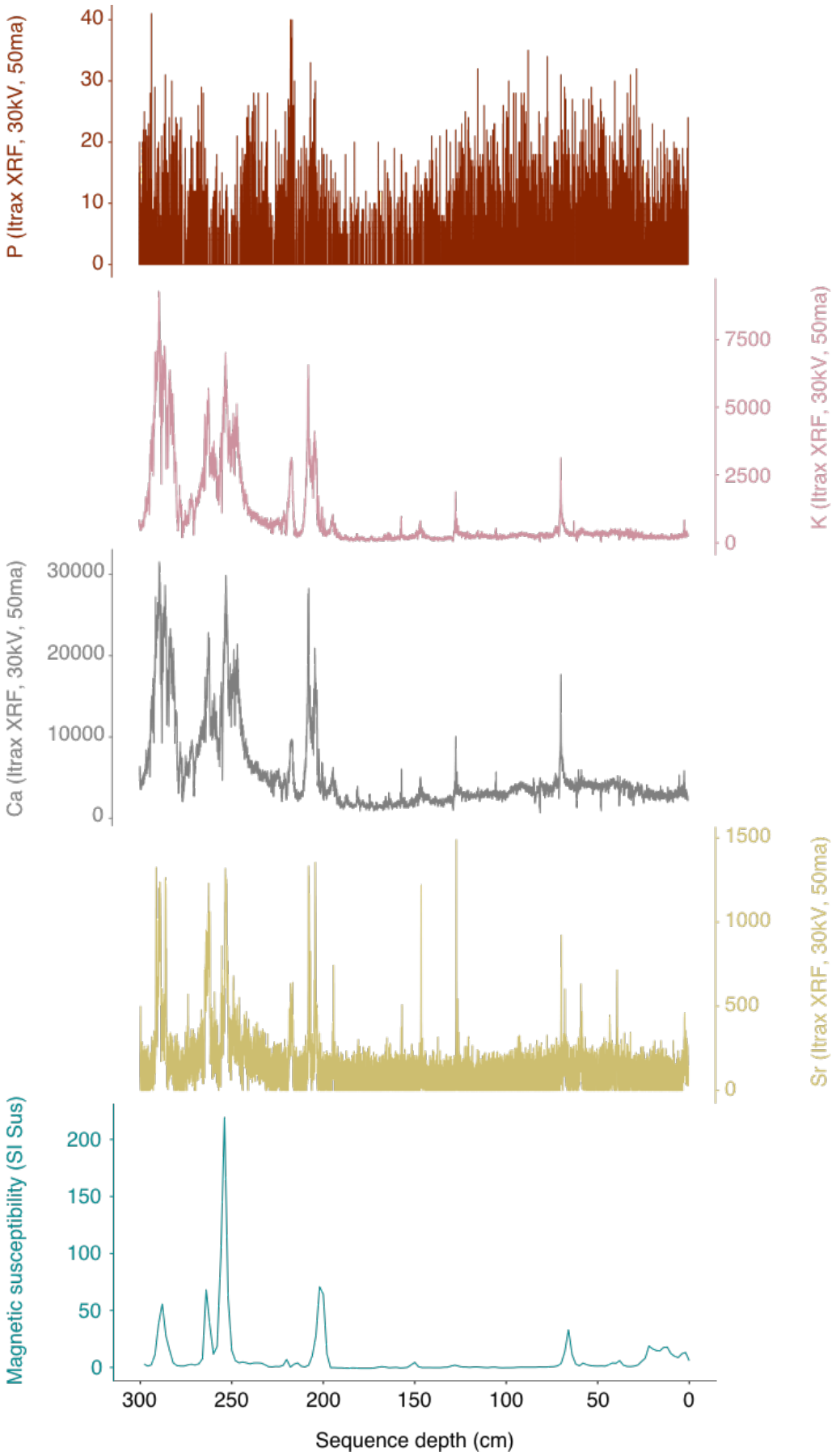


Figure S2 | Raw Itrax XRF and magnetic susceptibility data showing their original sampling resolutions of 0.02 mm and 2 cm, respectively. Phosphorus (P), potassium (K), calcium (Ca) and strontium (Sr). Data plotted with *ggplot2* package (Wickham 2009) in R version 3.2.4 (R Core Team 2013).

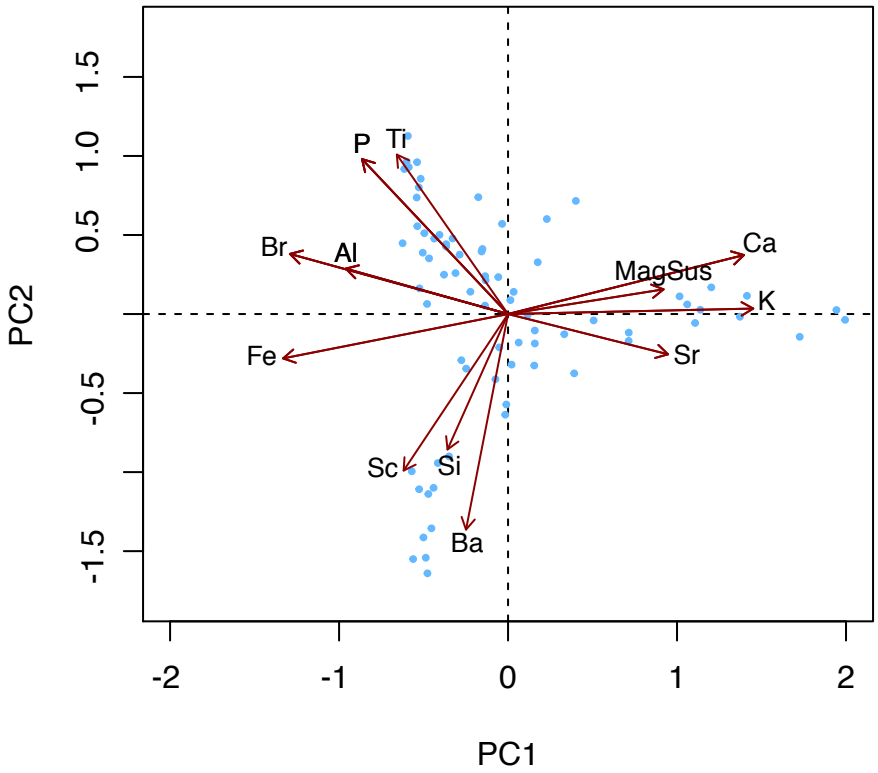


Figure S3 | PCA results on the abundance dynamics of main chemical elements, as measured by Itrax Core scanner, and the magnitude of magnetic susceptibility (MagSus), as measure by Barrington MS2 System. Phosphorus (P), potassium (K), calcium (Ca), strontium (Sr), iron (Fe), aluminium (Al), silica (Si), titanium (Ti), bromine (Br), barium (Ba), and scandium (Sc). The 1st and 2nd axes of the ordination explains 39.9% and 19.8%, respectively, of the variance in the distribution of the elements over time. Elements Ca, K, Sr and magnetic susceptibility are clustered together and separated from the other elements by the 1st axis, which suggest their similar dynamics and a common source. Data plotted with *vegan* package (Oksanen et al. 2016) in R version 3.2.4 (R Core Team 2013).

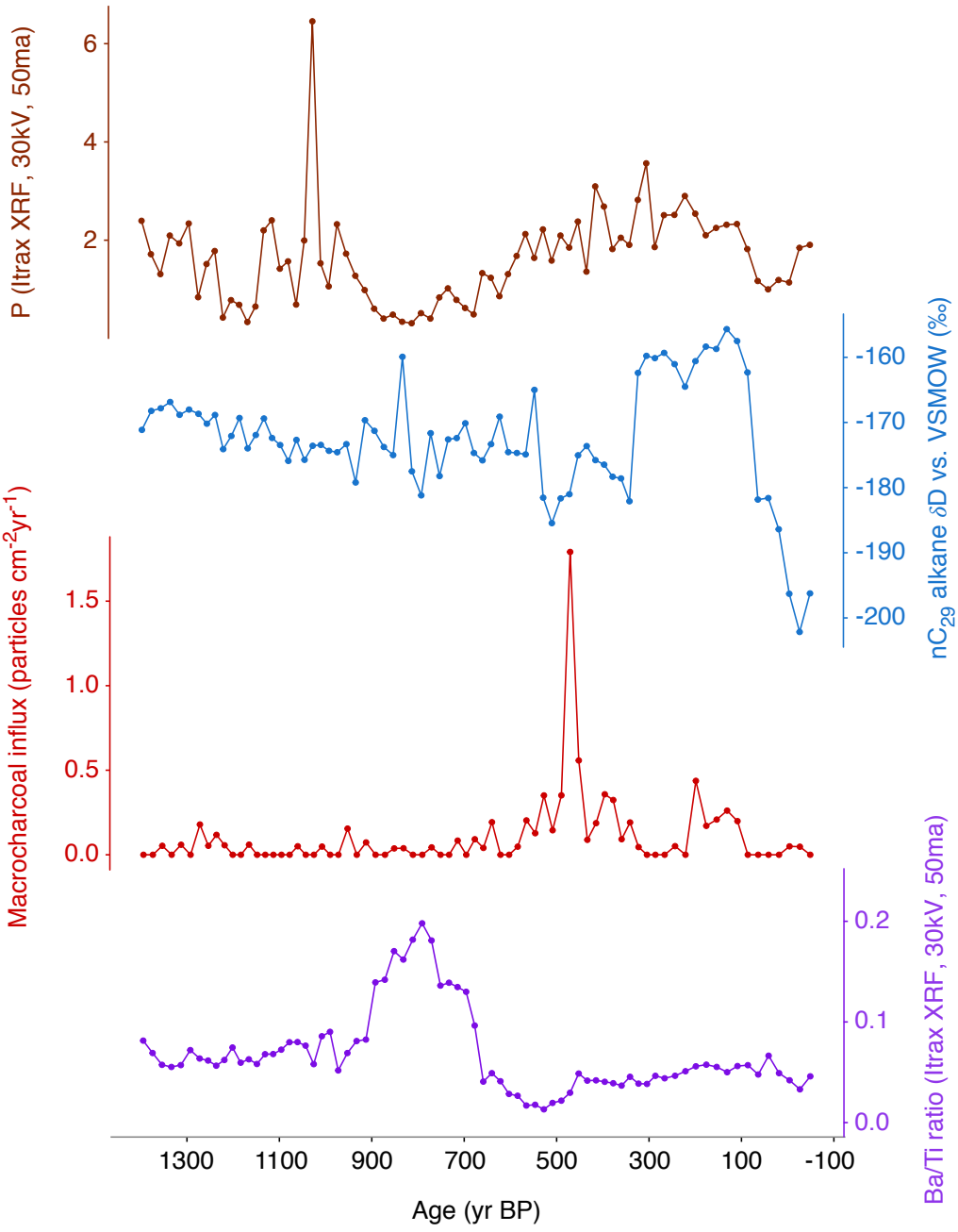


Figure S4 | Comparison of the phosphorus (P) record from the Bulusan sedimentary sequence spanning the last 1,400 years, with the matching record of nC_{29} alkane δD values (i.e. proxy for precipitation amount), macrocharcoal influx rates (i.e. proxy for local fire activity), and Ba/Ti ratio (i.e. proxy for organic to inorganic matter ratio). Data plotted with *ggplot2* package (Wickham 2009) in R version 3.2.4 (R Core Team 2013).

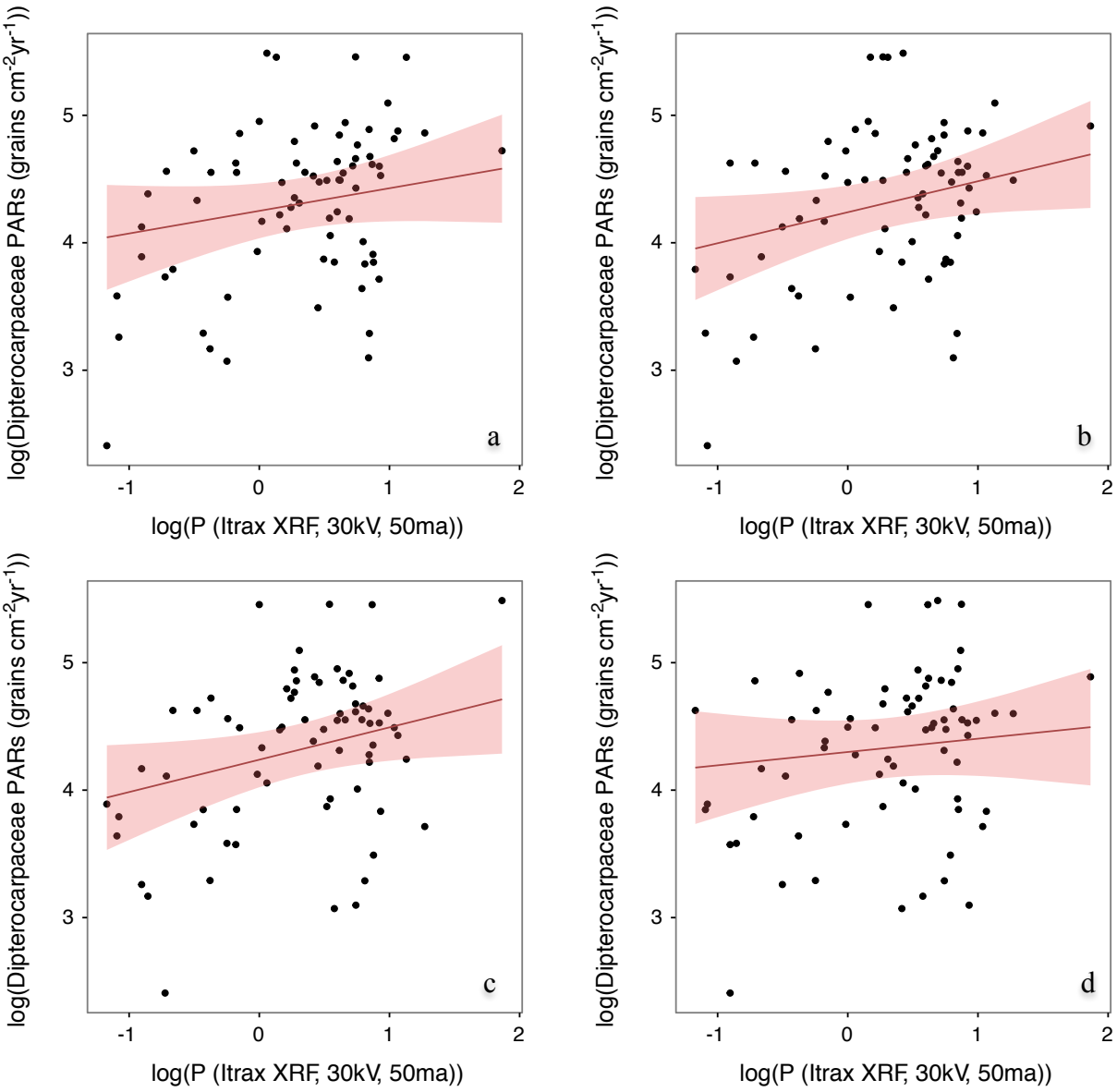


Figure S5 | The relationship between Dipterocarpaceae PARs and phosphorus abundance (P) in the Bulusan sequence over the last 1,400 years according to the best fitted models for different number of lags. a), 1 lag (~20 yrs): log(Dipterocarpaceae PARs) = 4.25 + 0.18*log(P), **b)**, 2 lags (~40 yrs): log(Dipterocarpaceae PARs) = 4.24 + 0.24*log(P), **c)**, (~60 yrs): log(Dipterocarpaceae PARs) = 4.24 + 0.25*log(P), and **d)**, 4 lags (~80 yrs): log(Dipterocarpaceae PARs) = 4.30 + 0.10*log(P). Data plotted with *ggplot2* package (Wickham 2009) in R version 3.2.4 (R Core Team 2013).

Pollen accumulation rates as a biomass proxy

Morphological analysis of fossil pollen is the most commonly used method for reconstructing past plant dynamics. PARs can provide independent data points for each taxon and have therefore been widely used to track the dynamics of individual taxa over time (Bennett and Willis 2001), including their population size (e.g. Magyari *et al.* 2011; Jeffers *et al.* 2012), abundance (e.g. Davis 1969; Bjune and Birks 2008), and biomass (e.g. Mazier *et al.* 2012; Jeffers *et al.* 2015).

A reliable interpretation of the PARs of a particular taxon requires the consideration of the life history traits. Specifically, if a taxon's size at first flowering and its size at full growth are similar, then the sizes of flowering individuals in a population are comparable and PARs can be linked to its absolute abundance (i.e. the number of flowering individuals on a landscape). If, however, a taxon's size at its first flowering and its size at full growth vary greatly, as is the case with Dipterocarp species, then PARs may not reflect absolute abundances because larger individuals will produce more flowers. Biomass is a more appropriate term to use in those cases, as it accounts for both the number of individuals and their size (Seppä *et al.* 2009; Mazier *et al.* 2012; Jeffers *et al.* 2015).

Importantly, previous work has shown that PARs can also be affected by changes in pollen productivity over time, for instance due to changes in environmental conditions (e.g. temperature, precipitation, CO_2 concentration) (Mazier *et al.* 2012). Dipterocarp trees in particular have irregular flowering patterns which have been linked to ENSO-induced drought episodes which take place every 2-7 years. Consequently, changes in flower production rates in response to environmental conditions can influence Dipterocarp PARs even on longer time scales. It is therefore probable that Dipterocarp PARs in the Bulusan sequence reflect both the number and the size of Dipterocarps trees on a landscape (i.e. woody biomass) and their pollen productivity (i.e. reproductive biomass).

In addition, changes in pollen deposition conditions (i.e. taphonomy) can also influence PARs records. For instance, varying water levels can change lake size and shape, and consequently its pollen deposition rate (Bennett and Buck 2016). Similarly, changes in the sedimentation rate due to changing biotic activity or soil erosion intensity can influence the concentration of pollen

in the sediments (Giesecke and Fontana 2008). Moreover, alternating sediment types and drying of the sediments can cause changes in the preservation conditions across the sedimentary sequence, especially with cores spanning long time scales, and this in turn can alter pollen concentrations.

We have minimised these taphonomic effects through a careful choice of the coring site. Bulusan lake is a permanent, medium-sized lake of considerable depth and steep slopes, and hence any past changes in water levels are unlikely to have brought about major modifications in its size and shape. Because Bulusan sediments are uniform, highly organic and relatively young, the chances of differential preservation conditions along the sequence are low, and so are the chances that the robust, high-resolution age-depth model that we have generated for the Bulusan sequence (Figure S1) would inadequately account for any major changes in the sedimentation rates. We are therefore confident that taphonomic factors have not played a major role in shaping PARs in the Bulusan sequence.

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CHAPTER 6: EFFECTS OF ENSO CHANGES ON PIONEER TAXA AND GAP DYNAMICS IN DIPTEROCARP RAINFORESTS

Abstract

While climate projections for this century indicate pronounced changes in El Niño/ Southern Pacific Oscillation (ENSO) dynamics, their consequences for tropical rainforests remain poorly understood. Here we use a suite of palaeoproxies from a 1,400-year-old lacustrine sedimentary sequence from the Philippines to examine the effects of ENSO enhanced drought conditions on gap dynamics in Dipterocarp rainforests. We find that higher hydrogen isotope values of leaf wax alkanes combined with higher macrocharcoal influx rates had a significant positive effect on the pollen accumulation rates (PARs) of pioneer taxa. These results suggest that intensified ENSO-induced drought conditions combined with higher fire intensity had increased the abundance of pioneer taxa at the study site, favouring their dominance in forest gaps. We also show that the magnitude and rate of responses of the pioneer PARs to the enhanced ENSO conditions were taxa-specific, which complicates the prediction of the composition of gap assemblages under such conditions. Our findings indicate that enhanced ENSO regime coupled with increased fire activity would alter gap dynamics in Dipterocarp rainforests.

Introduction

The El Niño/ Southern Pacific Oscillation (ENSO) is the main driver of rainfall variability in Southeast Asia. In particular, El Niño events, which take place every 2-7 years, trigger severe drought episodes across the region. Previous studies have reported the large-scale ecological effects of these events on the region's dominant and most diverse terrestrial ecosystem, the Dipterocarp rainforests (Figure 1a); notably, a severe drought episode can cause the mortality of up to 45% of large trees (i.e. >80 cm d.b.h.) in these forests (Van Nieuwstadt and Sheil 2005). The death of such large trees regularly leads to the creation of forest gaps (Ghazoul and Sheil 2010). While forest gaps are a natural part of the growth cycle in Dipterocarp rainforests and vital for preserving their structural heterogeneity and habitat diversity, they form only a small

portion of the total forest area per year (e.g. ~0.1% at the Lambir Hills National Park in Sarawak) (Ghazoul 2016, page 173).

Climate projections suggest pronounced changes in ENSO dynamics, namely an increased frequency of extreme El Niño events (Latif and Keenlyside 2009; Collins *et al.* 2010). An enhanced ENSO regime is likely to increase the drought-induced mortality of large trees, and, thereby, increase the frequency of forest gaps (Walsh 1996). What remains unclear, however, is how such change in gap dynamics would influence the structure and functioning of Dipterocarp rainforests.

The effects of increasing gap frequency on the structure and functioning of Dipterocarp rainforests will depend heavily on the type of vegetation regeneration in the newly created gaps. According to previous studies, there are two modes of gap regeneration: 1) the regeneration that comes predominately from pre-existing shade-tolerant seedlings and saplings of climax taxa (e.g. Dipterocarp species), characteristic of smaller gaps, and ii) the regeneration that happens primarily through germination of light-demanding taxa from seeds (i.e. pioneer taxa such as *Macaranga*, *Trema*, *Melastoma*) (Whitmore 1988; Ghazoul 2016), prevalent in larger gaps. Climax taxa and pioneer taxa have widely different life-history traits. For instance, climax taxa have medium to high longevity, low flowering frequency, high growth rates, light wood, larger seeds and low root to shoot ratio, while the opposite is true for pioneer taxa (Whitmore 1988; Ashton 2014, page 79). Consequently, a large number of gaps dominated by pioneer taxa could have major consequences for Dipterocarp rainforests, including lower and uneven forest stature, a reduced above ground biomass, and altered flowering and fruiting patterns. In contrast, if the majority of gaps support regeneration by seedlings and saplings of climax species, the gaps could be filled relatively quickly with limited consequences for the overall forest composition and structure. No studies to date have examined which of the two types of gap regeneration, if either, are favoured under enhanced ENSO conditions, despite the far-reaching implications for Dipterocarp rainforest dynamics under climate change.

Fire activity is an important factor to consider when investigating the gap dynamics in Dipterocarp rainforests under enhanced drought conditions. Severe droughts are more likely to lead to fires, which are particularly destructive for smaller stem trees. For instance, a single fire event can cause near complete mortality of trees with <10 cm d.b.h. in Dipterocarp rainforests

(Van Nieuwstadt and Sheil 2005). On the other hand, previous work has demonstrated the positive effects of fire on the establishment and growth of pioneer plants, including pioneer trees, ferns and grasses (Whitmore 1988; Woods 1989; Schulte and Schöne 1996). There are two mechanisms underlying the observed effects. Firstly, fire removes the pre-existing seedlings/ saplings of climax taxa from forest gaps, thereby exposing bare soil and facilitating germination and growth of pioneer taxa (Woods 1989; Ashton 2014). Secondly, regular fire events delay the vegetation succession in forest gaps. In the absence of fire, pioneer tree species can grow quickly to form a new canopy under which they and other pioneer groups, such as herbs and grasses, are unable to regenerate leading to their gradual replacement by shade-tolerant seedlings originating from seeds produced by neighbouring climax trees (Whitmore 1988; Ashton 2014; Ghazoul 2016). Regular fire events remove such pioneer-made canopies, thereby hindering the rise of climax tree species and enabling continuous regeneration of pioneer taxa; however, studies have yet to test if the combination of drought and fire under enhanced ENSO conditions would necessarily give rise to pioneer-dominated gaps.

The composition of the pioneer community is also important for evaluating the effects of changing gap dynamics on Dipterocarp rainforests. Based on their life-history traits (e.g. growth form, nutrient uptake, longevity, reproduction), pioneer taxa can be distinguished into different functional groups, such as trees, herbs, and lianas. As a result, the exact nature and extent of the changes that new gaps will bring about in Dipterocarp rainforests will depend on which, if any, of these pioneer groups will dominate. For example, if the majority of gaps are dominated by herbs, this is likely to bring greater reduction in the overall biomass production and nutrient cycling, and a larger increase in canopy openness, than if the same gaps were dominated by pioneer trees. Previous studies have suggested that it is the severity of the disturbance that shapes the composition of pioneer communities. For instance, communities regenerating on land deforested and cultivated for less than two years tend to be dominated by species of *Trema, Macaranga* and *Mallotus* (Kochummen and Ng 1966), whereas communities regenerating on deforested and severely degraded land are initially dominated by species of *Melastoma, Chromolaena* and *Dicranopteris* (Kochummen and Ng 1977), and later by species of *Adinandra, Ploiarium* and *Rhodamnia* (Sim *et al.* 1992). Furthermore, previous work indicates that fire in logged forests leads to severe canopy loss and gaps covered by grasses (e.g. *Imperata cylindrica*), while burnt primary forest suffers less severe canopy damage and the density of

grasses is relatively low (Woods 1989). Given this information, it is possible that enhanced ENSO conditions will favour some pioneer taxa over others, and pinpointing which taxa these are would help predict the likely composition of forest gap communities under future conditions.

In this study we use palaoecological proxies from a 1,400-years old laminated sedimentary sequence from Bulusan Lake, Philippines (Figure 1b, c), to examine for the first time the gap dynamics in Dipterocarp rainforests under enhanced ENSO conditions. Long-term records of climatic (e.g. stable isotopes) and biological proxies (e.g. fossil pollen, phytoliths) can be used to reconstruct biotic responses to past large-scale climatic changes and provide insights beyond the observational record (Willis and MacDonald 2011; Willis *et al.* 2013). While instrumental data show relatively stable ENSO dynamics over the last few decades, hydrogen isotope values of leaf wax alkanes (δD_{wax}) from the Bulusan sediments indicate that markedly drier conditions have taken place during the latter half of the Little Ice Age, i.e. ~BP 300-50 (BP defined as 'years Before Present', i.e. AD 1950), suggesting an enhanced ENSO regime during this time period (Figure 2) (Prohaska *et al.* in prep, Chapter 3). In addition, macrocharcoal influx rates from the same sequence indicates increased fire activity at Bulusan Lake from ~BP 550-50 (Figure 2) (Prohaska *et al.* In prep., Chapter 4). Hence, the Bulusan sedimentary sequence presents an excellent opportunity to test the effects of heightened ENSO-induced drought conditions on gap dynamics in Dipterocarp rainforests, both in the presence and absence of increased fire activity.

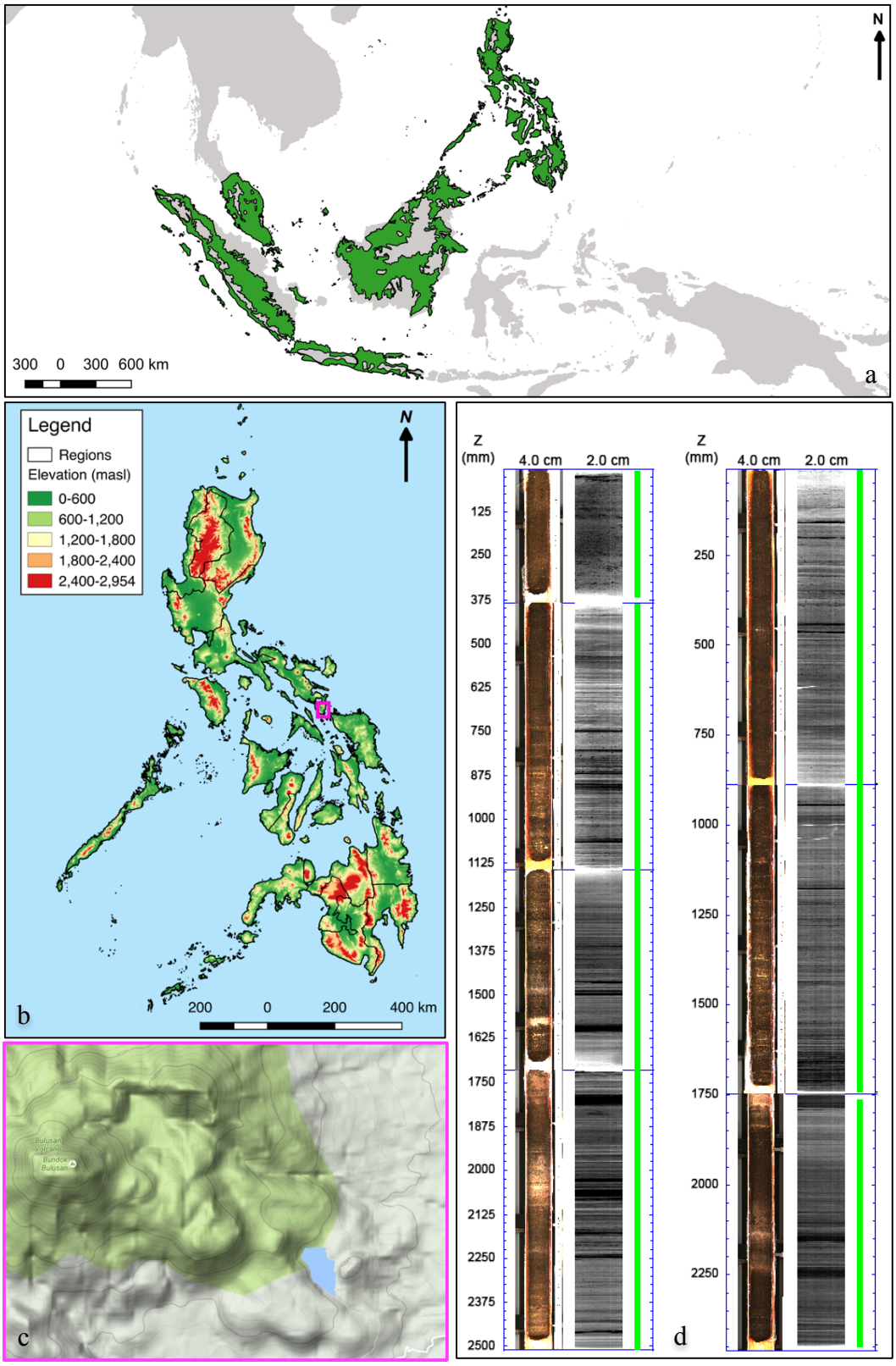


Figure 1 | Geographical and sedimentological features of the Bulusan site. a, Map showing the distribution of Dipterocarp rainforests (in green). Data from Olson et al. (2001), map generated in QGIS version 2.14.3 (Quantum GIS Development Team 2016). **b,** Topographic map of the Philippines showing the location of the study site. Data from PhilGIS (PHILGIS 2016), map generated in QGIS version 2.14.3.**c,** Map showing Bulusan Lake (in blue) within its larger landscape, with Mt Bulusan volcano in the west (in green) (Google 2016). **d,** Optical and radiographic profiles of the Bulusan sediments. The radiograph images depict the level of organic content, with higher values shown as lighter bands. The green line represents measurement validation along the cores. Images generated in ItraxPlot program (Croudace and Rothwell 2015). Figure from Prohaska *et al.* (In prep., Chapter 4).

We focus our analysis on the responses of pioneer taxa identified in the Bulusan pollen record, i.e. *Macaranga, Trema, Calamus,* Poaceae and Polypodiopsida, by generating a continuous record of their fossil pollen accumulation rates (PARs) at bi-decadal resolution. These taxa cover the three main functional types of pioneers: trees (*Macaranga, Trema*), herbs (Poaceae, Polypodiopsida) and lianas (*Calamus*). The pioneer PARs records were then compared to two recently generated records from the same sedimentary sequence – a δD_{wax}-based record of precipitation variability and a macrocharcoal-based record of local fire activity - in order to address the following questions: 1) What is the effect of ENSO enhanced drought conditions on the abundance of pioneer taxa in Dipterocarp rainforests, 2) How does the introduction of increased fire activity change this effect, and 3) Are some pioneer taxa favoured over others under prolonged periods of enhanced ENSO conditions such as the ~BP 300-50 interval?

Materials & Methods

Study site

Bulusan Lake has an area of 0.28 km^2 and is situated at the elevation of 360 m. It consists of two basins: a round basin, and a larger narrow basin, 12 and 24 m deep respectively. The lake is part of the Bulusan Volcanic National Park, a nature reserve which was first established in 1935 at the foot-slopes of Mt Bulusan (Abada Gatumbato *et al.* 2011), an active stratovolcano at the southeast end of the Bicol Volcanic Arc (Delfin *et al.* 1993). Logging, hunting and burning in the park is strictly prohibited, limiting anthropogenic impacts on its ecosystems. The area experiences an aseasonal tropical climate characterised by lack of a dry season (i.e. mean monthly rainfall <100 mm) (PAGASA 2016). Intra-annually, the Bulusan area receives most of its rainfall from the north-eastern monsoon, and inter-annually, its precipitation is strongly linked to ENSO variability.

The vegetation surrounding Bulusan Lake, and up the slope of Mt Bulusan, is classified as Lauan Dipterocarp forest dominated by *Shorea contorta* (Abada Gatumbato *et al.* 2011). Dipterocarp rainforests are dominated by Dipterocarpaceae trees, which can constitute up to 10% of total tree diversity, over 50% of the basal area and nearly 80% of all emergent individuals (Appanah 1985). Dipterocarp trees also shape the reproduction dynamics of these forests. A large number of Dipterocarp species can only reproduce during drought episodes

which are primarily related to El Niño events and thus usually take place every 2-7 years (Ashton *et al.* 1988; Sakai 2002). Their flowering during these drought episodes triggers gregarious, community-wide flowering events, referred to as general flowering, which include many other tree species of Anacardiaceae, Euphorbiaceae, Annonaceae, Fabaceae, Burseraceae, Moraceae and Myristicaceae (Appanah 1985). In addition to *Shorea* and *Dipterocarpus*, other notable large tree genera in the Philippine Dipterocarp rainforests include *Nephelium*, *Dysoxylum*, Drypetes, *Chisocheton*, *Strombosia*, *Pinanga, Leptonychia* and *Ficus* (Co *et al.* 2006). Species from *Litsea, Aglaia, Xanthophyllum* and *Syzygium* dominate in the lower canopy, while *Leea, Praravinia, Lepisanthes, Cyrtandra, Psychotria* and *Maesa* are prominent subcanopy trees. Presently, pioneer plants comprise only a small fraction of the Dipterocarp rainforest community, given that their successful establishment is limited to gaps (Ashton 2014) and these tend to cover only around 1% of total forest area (Ghazoul 2016, page 173). Common pioneer taxa include *Macaranga, Trema, Melastoma, Dillenia, Alstonia, Eupatorim,* Poaceae and Polypodiopsida (Woods 1989; Davies and Ashton 1999; Co *et al.* 2006; Ashton 2014). A plateau covered by monoculture of the grass species *Imperata cylindrica* is located up the slope of Mt Bulusan at 3 km from the Bulusan Lake at 900 m.a.s.l.

Material collection

Two overlapping sedimentary sequences, BUL1 and BUL2, were collected in March 2013 from the smaller basin of Bulusan Lake with a Livingstone Piston corer from an anchored platform. The sediments were sealed in protective plastic containers, shipped to the University of Oxford and stored at 5 °C. The two sedimentary sequences were used to create a continuous, undisturbed composite core (Prohaska *et al.* in prep, Chapter 3). Sediment laminations were mapped using a combination of optical and radiograph images taken with an Itrax Core Scanner at the University of Aarhus in September 2013 (Figure 1d). For more information on the possible origins of the Bulusan laminations, see Prohaska *et al.* In prep. (Chapter 3).

Extraction and processing of fossil samples

Sediment samples were extracted from the top 3.0 m of the composite Bulusan sequence as a continuous series of 4 cm long slices of 1 cm^3 volume, with each slice corresponding to a ~20-year interval. Standardized protocols were used for the extraction and counting of fossil pollen

(Bennett and Willis 2001), and a reference collection of different Dipterocarpaceae pollen types was generated using herbarium samples (Appendix A) and combined with printed and online sources (e.g. Australasian Pollen and Spore Atlas Online Database (APSA Members 2007), Pollen flora of the Philippines (Bulalacao 1997), Pollen Flora of Taiwan (Huang 1972). Five hundred terrestrial pollen grains were counted and identified in each sample. PARs, i.e. the number of pollen grains accumulated over 1 cm^2 of sediment per year, were calculated for each of the identified pioneer taxa following the standard procedures (Stockmarr 1971; Birks and Birks 2004). The PARs were used as a proxy of the absolute abundance of pioneer taxa (i.e. number of flowering individuals) on the landscape surrounding Bulusan Lake. Given that pioneer plants are short-lived, fast growing and regular flowerers whose size at the age of first flowering is relatively similar to their maximum size (Ashton 2014), pioneer PARs are likely to primarily reflect their absolute abundances, though some influence of varying pollen productivity rates over time and in response to changing environmental conditions cannot be excluded.

The δD values of the nC_{29} alkane (δD_{wax}, ‰) and macrocharcoal influx rates (particle $cm^{-2}yr^{-1}$, particle size >150 μm) from the same sequence and of the same sampling resolution as PARs samples were used as proxies of ENSO variability (Prohaska *et al.*, Chapter 3) and local fire activity (Prohaska *et al.*, Chapter 4), respectively. A high-resolution age-depth model was established using 10 $AMS^{14}C$ dates of terrestrial plant material (Table S1 in Supplementary Information) and computed with the *Bacon 2.2* package (Blaauw and Christen 2011; Blaauw and Christen 2015) using R version 3.2.4 (R Core Team 2013) and the IntCal13 radiocarbon calibration curve for the Northern Hemisphere (Reimer 2013) (Figure S1 in Supplementary Information).

Data analysis

Five pioneer taxa were identified in the Bulusan fossil pollen record: *Macaranga*, *Trema*, *Calamus*, Poaceae and Polypodiopsida. The relationship between each of the pioneer taxa of interest and the environmental variables (i.e. precipitation and fire) was determined statistically using the Generalised Linear Least Squares (GLS) while accounting for heteroscedacity with heterogeneous variance structures, and for temporal autocorrelation with an autoregressive-moving-average (ARMA) correlation structure. The models were developed using the nlme

3.1-128 package (Pinheiro et al. 2016) in R version 3.2.4 (R Core Team 2013). The validity of individual models was evaluated using diagnostic tests (Galecki and Burzykowski 2013), and the best fitting model with satisfying diagnostics was selected based on the lowest Akaike Information Criterion (AIC) coefficients with a simpler model selected whenever the difference in AIC coefficients between two models was smaller than 2. Models were considered significant at the 95 % level of confidence. Positive and negative slopes are indicated as (+) or (−), respectively. Prior to the model running, we removed points with zero pollen counts, and in Poaceae, one point was removed from the final model because preliminary analysis identified it as a strong outlier.

The Sequential T-test Analysis of Regime-Shifts algorithm, STARS (Rodionov 2004; Rodionov 2006), with time windows of incremental sizes (5-15 points, ~100-300 years) and a p-value <0.05, was used to detect significant changes in the mean of pioneer PARs values (e.g. Seddon *et al.* 2014). To address uneven spacing of the samples, each time series was sorted into 22-year bins (i.e. maximum sample time span), and then standardized by the mean and standard deviation. Since the STARS algorithm assumes normality and does not explicitly account for autocorrelations, the time series were transformed to normal distribution using Box Cox transformation and passed through a white-noise filter using the ordinary least-squares method outlined in (Rodionov 2006) prior to the application of the STARS algorithm.

Results

PARs dynamics of pioneer taxa

PARs of the five pioneer taxa in the Bulusan record changed substantially over the last 1,400 years, though there was little coherence in PARs dynamics among the taxa (Figure 2). Results from the STARS algorithm showed that *Calamus* experienced a significant decrease in PARs at ~BP 800, followed by an increase at ~BP 500 and finally a large shift to low PARs at ~BP 200 that persisted to the present day. *Macaranga* PARs increased significantly at ~BP 600 and remained at that level for the rest of the record. A significant drop in otherwise stable Polypodiopsida PARs was recorded from ~BP 550-900. Poaceae experienced reduction in its PARs at ~BP 350 followed by a shift to higher PARs levels in the record at ~BP 150 and

continued to today. Finally, *Trema* PARs have been relatively stable during most of the record, until ~BP 200 when they increase to the current level.

Effects of drought and fire on pioneer taxa

The relationship between the δD_{wax} and the PARs of four pioneer taxa, i.e. *Macaranga, Trema,* Poaceae and Polypodiopsida, is significantly influenced by macrocharcoal influx rates (Table 1, Figures 3 and 4). At low values of macrocharcoal influx rates, δD_{wax} values are negatively related to the pollen abundance of the four taxa, while at high macrocharcoal influx levels, the relationship between δD_{wax} and the PARs becomes significantly positive. *Calamus* is an exception to this, as its PARs are not significantly related to either δD_{wax} values, macrocharcoal influx rates or their interaction (Table 1, Figure 3).

Results also show differential responses in PARs among the pioneer taxa to the prolonged period of enhanced ENSO regime ~BP 300-50 (inferred from the δD_{wax} values), though the timing of this precipitation change does not directly coincide with the significant shifts in the PARs values of the pioneer taxa (Figure 5, Tables S2-S6 in Supplementary Information). During the enhanced ENSO interval, *Macaranga* and Polypodiopsida PARs had higher values in comparison to the period before (~BP 1350-300) and after (~BP 50 -present) this interval, with the exception of the period between ~BP 550-300, during which PARs values of these two taxa were not significantly different from the ~BP 300-50 rates (Figure 5). The PARs values of Poaceae and *Trema* showed significant increase only in the second half of the enhanced ENSO period, in comparison to the prior ~800 years, while *Calamus* PARs experienced a significant drop half way through this period (~BP 250) (Figure 5).

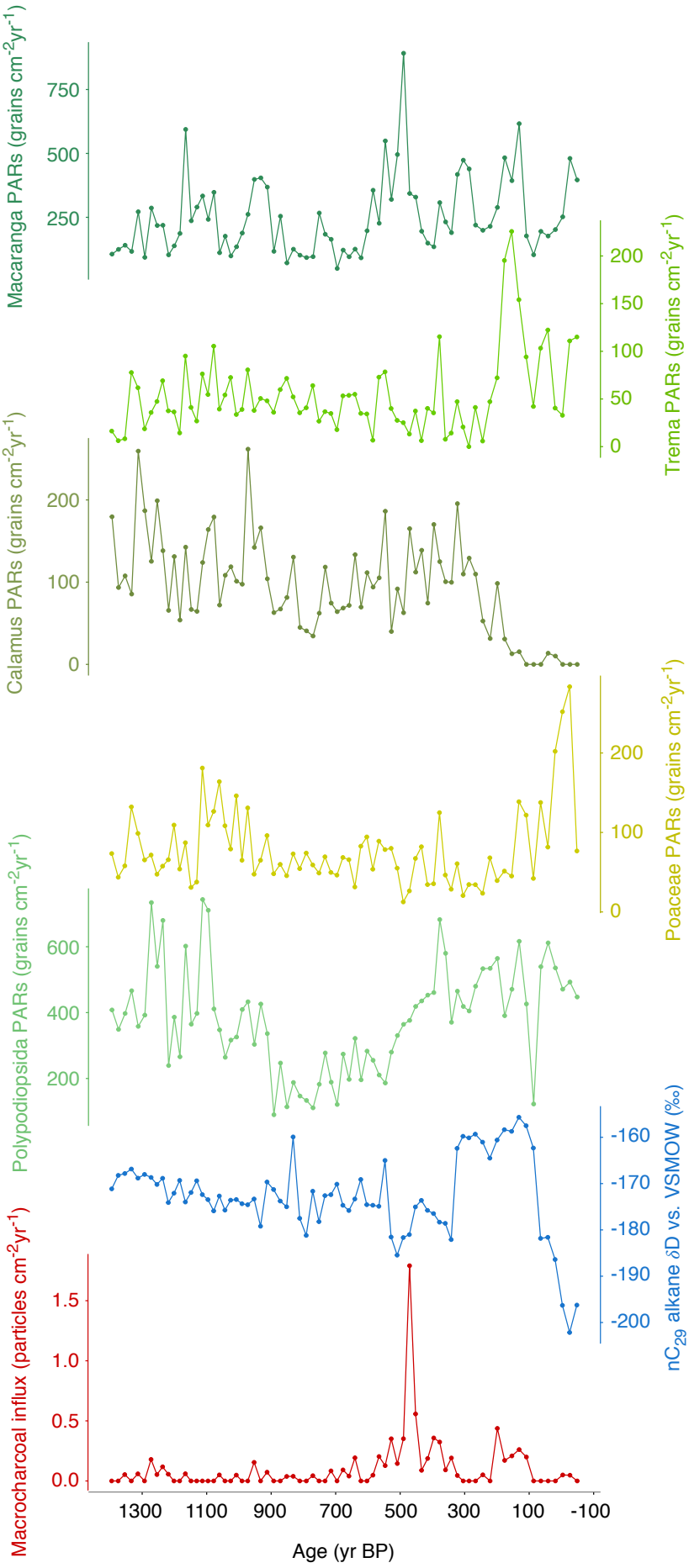


Figure 2 | PARs dynamics of the five identified pioneer taxa in the Bulusan sequence during the last 1,400 years. Data plotted with *ggplot2* package (Wickham 2009) in R version 3.2.4 (R Core Team 2013).

Table 1 | Summary of the best fitted GLS models for the relationship between pioneer PARs dynamics and environmental variables. PARs = pollen accumulation rates (grains $cm^{-2}yr^{-1)}$, char = macrocharcoal influx rates (particles $cm^{-2}yr^{-1}$), δDC_{29} = nC_{29} alkane δD values (‰), time = age (yr BP), : = interaction, SE = standard error.

Taxon	*Macaranga*	*Trema*	*Calamus*	Poaceae	Polypodiopsida
Model Structure	log(PARs) = δDC_{29} + char + δDC_{29} : char	log(PARs) = δDC_{29} + char + δDC_{29} : char	log(PARs) = time + δDC_{29} + char	log(PARs) = δDC_{29} + char + δDC_{29} : char	PARs = δDC_{29} + char + δDC_{29} : char
Fixed effects					
Analysis of variance (F-test/p-value)					
Intercept	2592.63/<0.01	338.32/<0.01	970.33/<0.01	5583.48/<0.01	53.43/<0.01
Time	/	/	4.28/0.04	/	/
δDC_{29}	0.45/0.51	0.19/0.66	1.11/0.29	17.10/<0.01	1.02/0.31
Char	<0.01/0.96	<0.01/0.96	2.28/0.13	1.47/0.23	0.58/0.45
δDC_{29} : char	4.53/0.04	11.25/<0.01	/	9.62/<0.01	6.17/0.01
Coefficients table (coefficient/ SE/p-value)					
Intercept	2.91/1.63/0.08	0.37/2.28/0.87	6.14/1.98/<0.01	-2.91/1.37/0.04	-490.85/442.77/0.27
Time	/	/	0.0008/0.0004/0.02	/	/
δDC_{29}	-0.01/0.01/0.14	-0.02/0.01/0.15	0.01/0.01/0.23	-0.04/0.01/<0.01	-4.95/2.51/0.05
Char	17.04/7.80/0.03	41.53/12.38/<0.01	0.44/0.28/0.12	39.22/12.56/<0.01	5373.29/2084.63/0.01
δDC_{29} : char	0.10/0.04/0.03	0.23/0.07/<0.01	/	0.23/0.07/<0.01	29.70/11.63/0.01
Variance Function (95% CI)	/	/	power(time) -0.16 (-0.44, 0.12)	expon(char) 1.31(0.00, 2.61)	/
Correlation Structure (95% CI)	ARMA (p=0, q=2) 0.42 (0.17, 0.70) 0.42 (0.17, 0.62)	ARMA (p=1, q=1) 0.92 (0.1, 0.99) -0.78 (-0.93, -0.40)	ARMA (p=1, q=1) 0.78 (0.23, 0.95) -0.44 (-0.73, -0.04)	/	ARMA (p=1, q=1) 0.87 (0.48, 0.97) -0.50 (-0.80, -0.08)
Scale (standardised residuals, σ)	0.55 (0.45, 0.67)	0.57 (0.76, 1.02)	1.48 (0.28, 7.77)	0.42 (0.35, 0.51)	149.75 (112.20, 199.86)

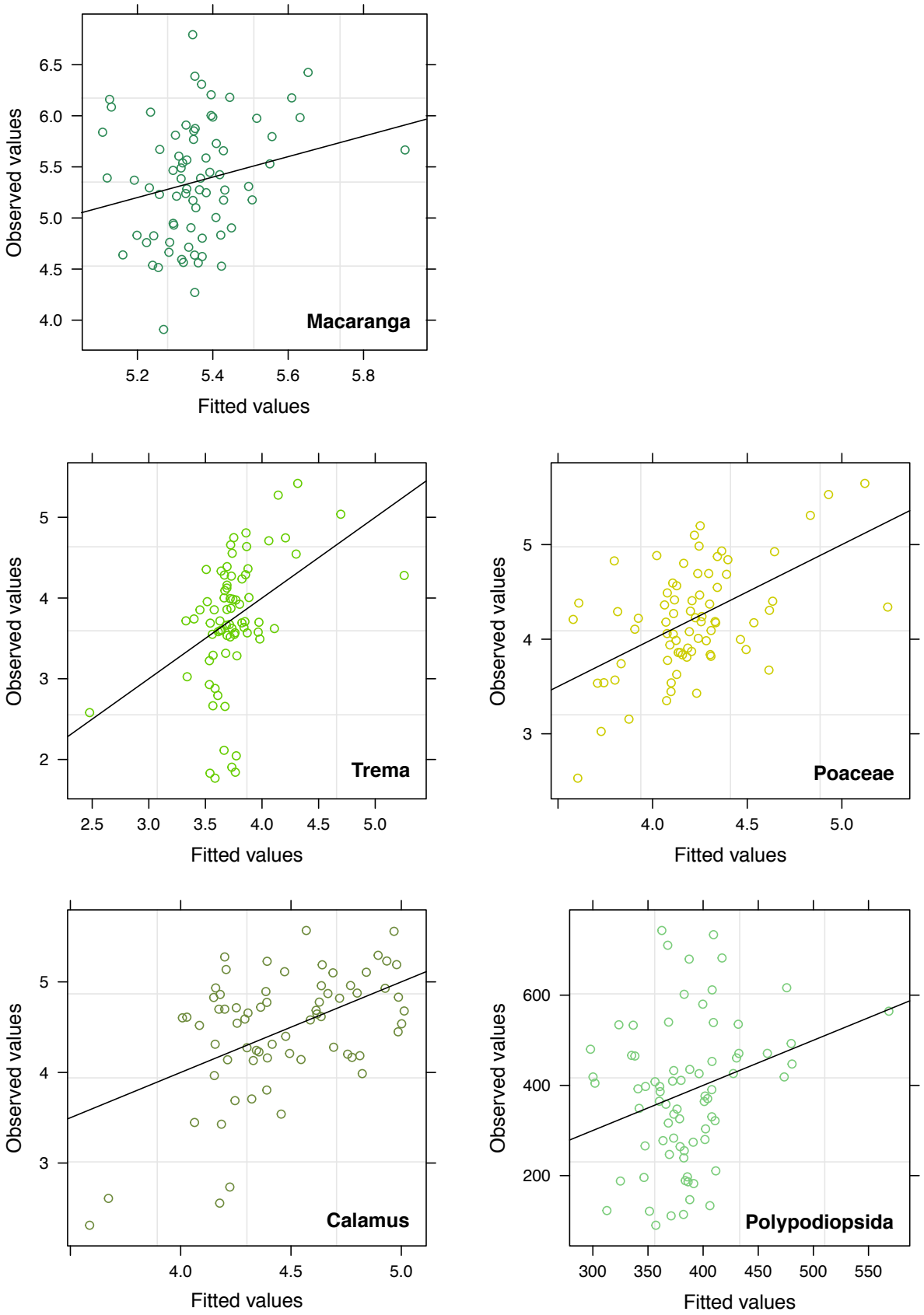


Figure 3 | The relationship between observed values and predicated values of the best fitted GLS model for the examined pioneer taxa. ***Macaranga***, log(PARs) = 2.91 - 0.01*δDC_{29} + 17.12*char + 0.09*δDC_{29} : char; ***Trema***, log(PARs) = 0.38 - 0.02*δDC_{29} + 41.52*char + 0.23*δDC_{29} : char; **Poaceae**, log(PARs) = -2.70 -0.04*δDC_{29} + 36.51*char + 0.21*δDC_{29} : char; and **Polypodiopsida,** PARs = -490.853-5.05 *δDC_{29} + 5306.32 *char + 29.32*δDC_{29} : char. PARs (grains $cm^{-2}yr^{-1}$), char = macrocharcoal influx rates (particles $m^{-2}yr^{-1}$), δDC_{29} = δD values of the nC_{29} alkane (‰), : = interaction. Data plotted with *ggplot2* package (Wickham 2009) in R version 3.2.4 (R Core Team 2013).

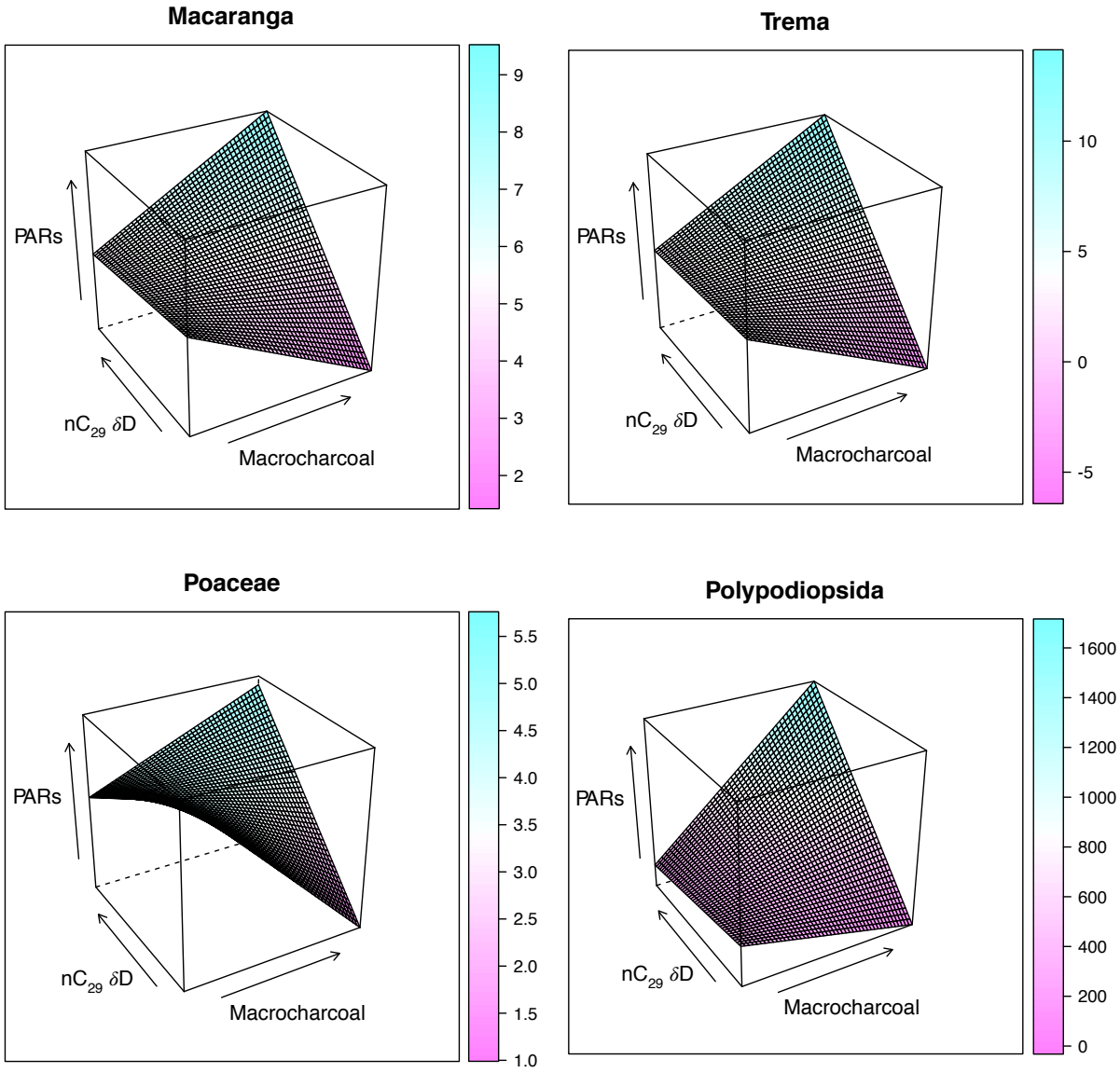


Figure 4 | The relationship between pioneer PARs, δD values of the C_{29} alkane and macrocharcoal influx rates according to the best fitted GLS models. ***Macaranga***, log(PARs) = 2.91 - 0.01*δDC_{29} + 17.12*char + 0.09*δDC_{29} : char; ***Trema***. log(PARs) = 0.38 - 0.02*δDC_{29} + 41.52*char + 0.23*δDC_{29} : char; **Poaceae**, log(PARs) = -2.70 -0.04*δDC_{29} + 36.51*char + 0.21*δDC_{29} : char; and **Polypodiopsida**, PARs = -490.853-5.05 *δDC_{29} + 5306.32 *char + 29.32*δDC_{29} : char. PARs (grains $cm^{-2}yr^{-1}$), char = macrocharcoal influx rates (particles $m^{-2}yr^{-1}$), δDC_{29} = δD values of the nC_{29} alkane (‰), : = interaction. Data plotted with *lattice* package (Sarkar 2008) in R version 3.2.4 (R Core Team 2013).

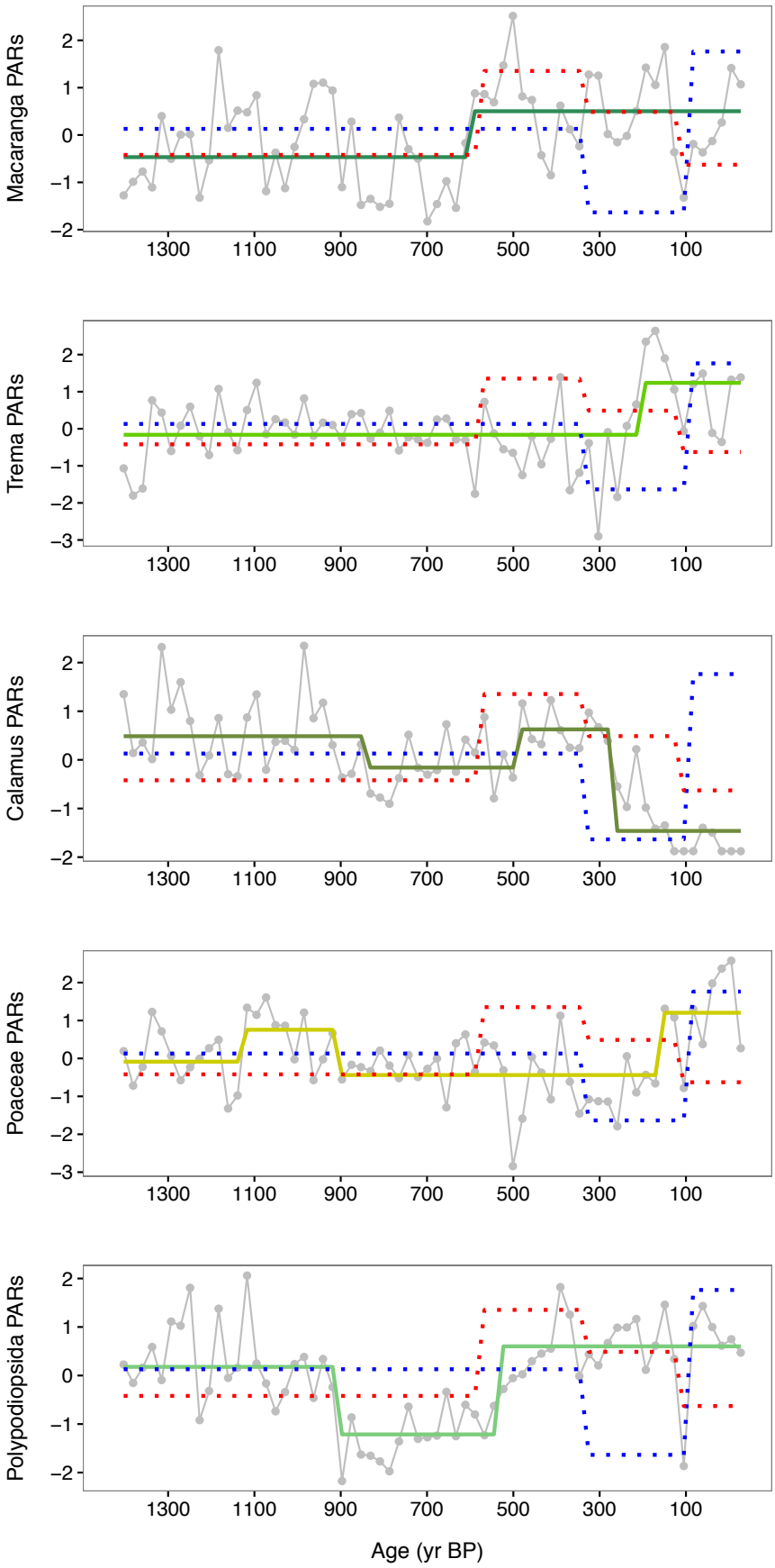


Figure 5 | Significant changes detected in the PARs records of pioneer taxa in the Bulusan sequence. The grey lines depict pioneer PARs after Box Cox transformation and pre-whitening. Green, red and blue lines show significant changes (p-value <0.05) in sample mean of the taxon PARs (grains $cm^{-2}yr^{-1}$), macrocharcoal influx rates (particles $cm^{-2}yr^{-1}$), and nC_{29} alkane δD values (‰), respectively. Time window size is set to 8 data points (~160 yrs). Data plotted with *ggplot2* package (Wickham 2009) in R version 3.2.4 (R Core Team 2013).

Discussion

Our results suggest that the effect of enhanced ENSO-induced drought conditions on the abundance of key pioneer taxa depends heavily on the level of fire activity. Specifically, at low to no fire activity, enhanced drought intensity appears to have a negative effect on pioneer taxa abundance, while high fire activity leads to a positive effect. This would then indicate that enhanced ENSO-induced drought conditions in absence of increased fire activity are likely to promote gap regeneration by climax taxa as opposed to regeneration by pioneer taxa. One potential explanation could be the size of the gaps that such conditions favour. Many large tree species in Dipterocarp rainforests, including the members of the dominant Dipterocarpaceae family, have buttress roots and these structures lend them additional stability and reduce the chance of the tree falling after death (Gale and Barfod 1999; Hall *et al.* 2004). Tree gaps created by the death of such trees are likely to be smaller in size (in comparison to gaps created by tree fall or landslides), thereby favouring vegetation regeneration from pre-existing shade-tolerant seedlings and saplings of climax species and minimising the impact of increasing gap frequency on the structure and functioning of Dipterocarp rainforests. This explanation is supported by Prohaska *et al.* (In prep., Chapter 4), which showed that ENSO-induced drought had no major effect on Dipterocarp PARs at the Bulusan site over the last 1,400 years, suggesting that Dipterocarp species may be able to compensate their increasing mortality rates with higher establishment rates. Many species of Dipterocarps produce a massive number of seeds during a fruiting event (>100,000 seeds per individual) (Ashton 1988) and dispersal of these seeds is generally poor. This, coupled with lack of seed dormancy gives rise to dense layers of Dipterocarp seedlings around the mother trees (Ashton 1969; Curran and Webb 2000; Itoh *et al.* 2003) which can survive in shade conditions for over 10 years while accumulating resources needed for fast growth when conditions become more favourable (i.e. opening of the canopy) (Whitmore and Brown 1996; Brown *et al.* 1999; Delissio *et al.* 2002). Consequently, when the mother tree dies, its seedlings are in an excellent position to make use of the new gap conditions.

Since higher fire levels and enhanced drought conditions combined have a positive effect on the PARs of pioneer species, it is probable that the benefits (e.g. higher establishment rates) can outweigh the detrimental effects of fire (e.g. higher mortality rates) on pioneer populations under such conditions, giving rise to pioneer-dominated gaps. Gap dynamics in Philippine Dipterocarp rainforests may be particularly susceptible to such conditions because they are

regularly exposed to strong typhoons (Co *et al.* 2006) which increase the likelihood of tree falls and often completely defoliate the tree canopy. Consequently, typhoons give rise to both smaller and larger gaps that pioneer species could particularly flourish in during the periods of enhanced drought and fire conditions.

Given the relatively low macrocharcoal influx rates in the Bulusan record (Prohaska *et al.* In prep., Chapter 4), it is hard to identify key drivers of fire activity at the site. Previous work has established positive correlation between ENSO-induced drought and fire (Fuller and Murphy 2006; Langner and Siegert 2009; Wooster *et al.* 2012). However, while macrocharcoal influx rates are overall low enough to assume natural, ENSO-associated fire, the poor concurrence between ENSO-induced drought conditions and increased fire activity in the Bulusan record provide little support to ENSO being the sole driver of fire activity during the last 1,400 years. Similarly, though previous work has shown that past volcanic activity can cause large fires of multi-decadal duration (Wilmshurst and McGlone 1996; Zhao *et al.* 2015), the period of increased fire activity in the Bulusan record does not contain any tephra layers, suggesting that volcanic activity had a minor role in shaping fire patterns at the site. Furthermore, while written accounts of human settlement in the wider Bulusan area trace back to AD 1630 and native burial grounds suggest human presence from the time before Spanish arrival (Abada *et al.* 2011), no archaeological evidence has been found in close vicinity of the site. Finally, the lack of increase in Poaceae pollen in response to increased fire activity in the Bulusan record (Prohaska *et al.* In prep., Chapter 3) makes it difficult to link enhanced burning at the site with agricultural activities. This apparent absence of permanent settlements and agricultural activities at the lake may be due to the rough terrain surrounding it as well as the abundance of low-lying, flat areas in the wider Bulusan area that are more suitable for growing crops. Taken together, these lines of evidence suggest that humans had a limited influence on fire dynamics at the Bulusan site. Nevertheless, the extraction of forest products (firewood, rattan), hunting and fishing had likely taken place at the lake in the past, particularly during more recent times as the resources in more accessible areas became depleted.

These findings have implications for the conservation and management of Dipterocarp rainforests in the face of climate change, especially given that the last few decades have seen a marked increase in the frequency and magnitude of fire events in these forests (Salafsky 1994; Folkins *et al.* 1997; Salafsky 1998; Siegert *et al.* 2001; Huijnen *et al.* 2016). Previous work has

shown that while El Niño related droughts can lead to fire events, they are not the likely cause of the increased fire occurrence (Field and Shen 2008; Langner and Siegert 2009). Instead, the observed trend of increasing fire intensity has been linked primarily to anthropogenic activities such as forest fragmentation and degradation. For instance, at least 80% of the 1997– 1998 ENSO-associated fires across Indonesia (primarily Kalimantan) were caused by logging and agricultural activities (Curran *et al.* 1999). Therefore, it is highly likely that the projected intensification of ENSO coupled with continuous anthropogenic activities will be accompanied by heightened fire activity in the region. Interestingly, the study by Prohaska *et al.* (Chapter 3) suggests that even in presence of stronger fire activity, enhanced ENSO-induced drought conditions may not have a major influence on the biomass dynamics of Dipterocarp trees. This finding combined with the new findings presented here suggests that such climatic conditions can potentially give rise to a rainforest system that is simultaneously dominated by Dipterocarp trees and harbours a large number of pioneer dominated gaps. Such an ecosystem is currently non-existent, and therefore, represents a non-analogue community whose structure and functioning is difficult to foresee. Given the significance of potential changes that enhanced ENSO and increased fire together could bring to Dipterocarp rainforests, development and implementation of effective strategies for minimising fire occurrence and magnitude during future El Niño droughts should be seriously considered in order to preserve the current state of these forests and avoid the rise of novel forest communities.

Our data also indicate that during the prolonged period of enhanced ENSO and fire regime (~BP 300-50) pioneer taxa have experienced significantly different abundance dynamics and, thus, such regime is likely to favour some pioneer taxa over others. Specifically, the significantly higher PARs of *Macaranga* and Polypodiopsida during this time interval suggests favourable conditions for these taxa, while the increase in *Trema* and Poaceae PARs only in the second half of the period and a significant drop *in Calamus* PARs recorded half way through it suggest the conditions have not been particularly suitable for these taxa. It can therefore be inferred that while enhanced drought coupled with increased fire activity may be generally beneficial to the establishment and growth of pioneer taxa, the magnitude and intensity level of these two disturbances during the enhanced ENSO regime ~BP 300-50 was such that it promoted *Macaranga* and Polypodiopsida over *Trema* and Poaceae. Finally, the lack of direct correspondence between the significant shifts in the pioneer PARs records, and the δD_{wax} and

macrocharcoal records suggests that other factors besides precipitation and fire had influenced abundance dynamics of the pioneer taxa during the study period.

Previous studies offer some clues as to the reasons behind the responses of different pioneer taxa observed in the Bulusan records. For instance, an increase in fire frequency can boost the establishment of pioneer trees such as *Macaranga* and *Trema* up to a point, but too frequent burning will eventually remove these taxa from forest gaps and give way to grasses such as *Imperata cylindrica* (Woods 1989). Therefore, the increase in the abundances of *Macaranga* and *Trema* and absence of change in the abundance of grasses during the ~BP 300-50 interval, suggests that fire activity during enhanced ENSO conditions can still be low enough to favour pioneer trees over grasses. On the other hand, the drop in *Calamus* abundance during the enhanced ENSO period, which is a tree climber with strong reliance on climax species, could be attributed to the fire intensity being high enough to reduce the number of climax species in the gaps, thereby removing potential hosts for the *Calamus* species. Finally, the higher performance of *Macaranga* in comparison to *Trema* during the same time interval may be linked to the size of the gaps created under enhanced ENSO conditions. *Trema* species usually germinate but do not survive to reproductive size except in very large gaps (Denslow 1987; Condit *et al.* 2004). Such preference can significantly limit the capacity of *Trema* to respond positively to higher availability of smaller gaps such as those created by standing dead trees. A weak positive response of this taxon in the Bulusan record during the enhanced ENSO regime further supports the idea that these climatic conditions were creating predominately smaller gaps that *Trema* would have difficulty reproducing in. Human activities may have also contributed to differential dynamics of pioneer taxa at the Bulusan site. For instance, there is a long history of *Calamus* (rattan) harvesting in the Philippines (Dransfield *et al.* 2002). Currently, farmers in the vicinity of Bulusan Volcano National Park depend heavily on rattan harvesting (Abada *et al.* 2011), and it is therefore possible that such harvesting was taking place closer to the Bulusan Lake before the park was established in 1935, which would explain the drop in *Calamus* pollen from ~BP 250 onwards. Interestingly, this drop in *Calamus* pollen coincides with an increase in *Trema* and Poaceae pollen (Figure 5), which is indicative of an increase in forest gap sizes, and also possibly caused by the logging and extraction of wood products closer to the lake. These results suggest that while it is improbable that past human activities at the Bulusan site had changed the structure of the Dipterocarp forest, they may have

influenced the composition of its pioneer community. On the whole, the differential responses of pioneer taxa to the prolonged period of enhanced ENSO regime (~BP 300-50) highlight the need for taxa-specific evaluation of the effects of ENSO changes on pioneer plants, both in the presence and absence of human activities, in order to improve predictions of the composition of pioneer communities under future ENSO scenarios.

In conclusion, PARs dynamics of pioneer taxa at the Bulusan site over the last 1,400 years suggests that under low fire activity, enhanced ENSO-induced drought conditions favour forest gaps dominated by climax taxa, while under high fire activity, it is pioneer dominated gaps that are prevalent. Furthermore, our findings indicate that over longer time periods of enhanced ENSO, such as the ~BP 300-50 interval, pioneer plant responses are taxa-specific and related to fire intensity, though human influence should also be taken into account. It can therefore be argued that a combination of enhanced ENSO regime and increased fire activity may give rise to significant changes in the structure and functioning of Dipterocarp rainforests, such as increased canopy openness and reduced biomass production. More research on the dynamics of Dipterocarp rainforests during the previous periods of enhanced ENSO conditions is needed to further our understanding of the potential ecological responses to such conditions and improve predictions of tropical rainforest dynamics in a warming world.

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Supplementary Information

Age-depth modelling

Table S1 | AMS^{14}C dates of the Bulusan sedimentary sequence measured at the NERC Radiocarbon Facility, East Kilbride.

Lab ID	Sample Material	Core Depth (cm)	Age (yr BP)	Error (yr)
SUERC-64001	Terrestrial plant	59	240	±35
SUERC-64002	Terrestrial plant	69	293	±37
SUERC-64003	Terrestrial plant	74	450	±37
SUERC-64005	Terrestrial plant	82	323	±37
SUERC-64004	Terrestrial plant	84	401	±37
SUERC-51111	Terrestrial plant	126	617	±38
SUERC-64006	Terrestrial plant	163	609	±37
SUERC-51112	Terrestrial plant	204.5	1146	±35
SUERC-64010	Terrestrial plant	272	1235	±37
SUERC-64011	Terrestrial plant	342.5	1629	±37

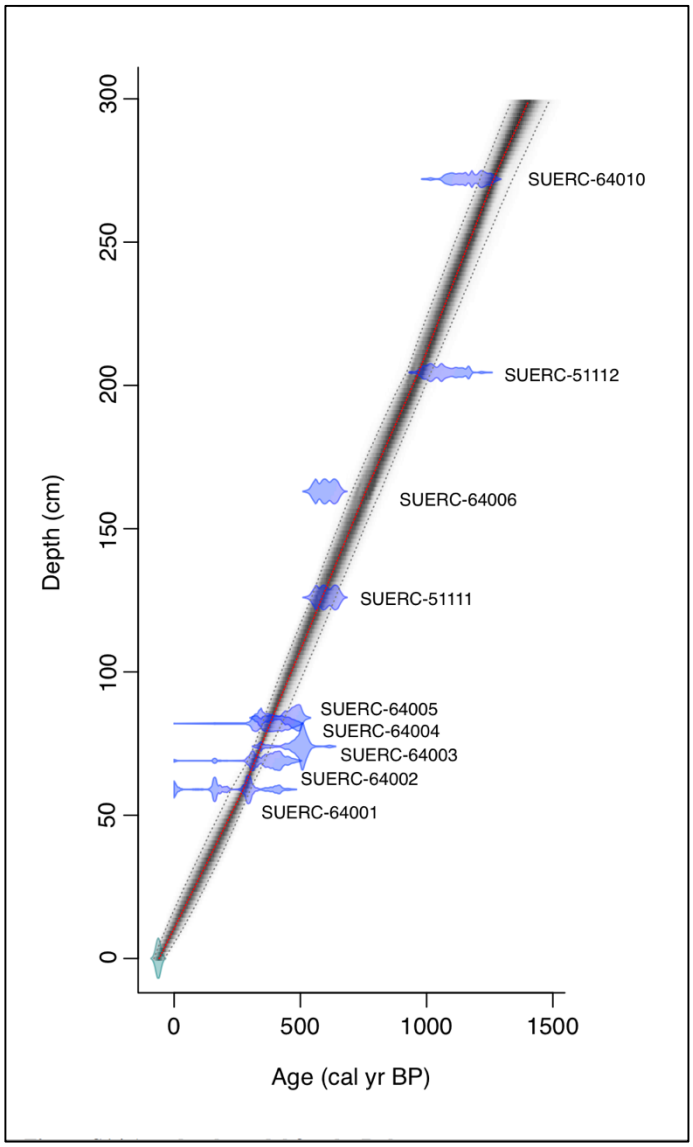


Figure S1 | Age-depth model for the Bulusan sediment sequence constructed in *Bacon 2.2* (Prohaska *et al.* In prep, Chapter 3). Probability distributions for the nine radiocarbon calibrations are shown in blue. SUERC-64011 is not shown here as it lies below the analysed section. The shaded areas represent the 1σ probability age ranges by interpolating between ^{14}C age control points. The red dashed line represent the age model used in further analysis.

Significant changes in pioneer pollen records

For a detailed account of the timing and the significance of the changes in the mean of pollen accumulation rates (PARs) of the five pioneer taxa, detected by the Sequential T-test Analysis of Regime-Shifts algorithm, STARS (Rodionov 2004; Rodionov 2006), please see Tables S2-S6.

Table S2 | The timing and p-values of the significant changes in the mean of *Macaranga* PARs values (grains $cm^{-2}yr^{-1}$) in the Bulusan sequence identified by the STARS algorithm with incremental time window sizes. Increases and decreases in the sample mean are shown in green and red, respectively.

Time window (no. data points)	Change Point 1 (1183 yr BP)	Change Point 2 (1073 yr BP)	Change Point 3 (853 yr BP)	Change Point 4 (589 yr BP)	Change Point 5 (-5 yr BP)
5	4.09E-03	7.70E-02	1.25E-02	3.04E-06	/
6	/	/	/	1.12E-04	/
7	/	/	/	1.12E-04	/
8	/	/	/	1.12E-04	/
9	/	/	/	1.12E-04	/
10	/	/	/	1.12E-04	/
11	/	/	/	1.12E-04	/
12	/	/	/	1.12E-04	3.46E-02
13	/	/	7.40E-04	5.39E-06	3.64E-02
14	/	/	1.32E-03	6.49E-06	3.79E-02
15	/	/	/	5.72E-04	3.79E-02

Table S3 | The timing and p-values of the significant changes in the mean of *Trema* PARs values (grains $cm^{-2}yr^{-1}$) in the Bulusan sequence identified by the STARS algorithm with incremental time window sizes. Increases and decreases in the sample mean are shown in green and red, respectively.

Time window (no. data points)	Change Point 1 (193 yr BP)
5	7.33E-04
6	7.33E-04
7	1.62E-03
8	7.33E-04
9	7.33E-04
10	3.44E-04
11	3.44E-04
12	3.44E-04
13	3.44E-04
14	3.44E-04
15	3.44E-04

Table S4 | The timing and p-values of the significant changes in the mean of *Calamus* PARs values (grains $cm^{-2}yr^{-1}$) in the Bulusan sequence identified by the STARS algorithm with incremental time window sizes. Increases and decreases in the sample mean are shown in green and red, respectively.

Time window (no. data points)	Change Point 1 (831 yr BP)	Change Point 2 (479 yr BP)	Change Point 3 (259 yr BP)	Change Point 4 (193 yr BP)
5	1.71E-02	/	/	2.08E-13
6	1.71E-02	/	/	2.08E-13
7	1.49E-03	3.61E-04	2.33E-09	/
8	1.49E-03	3.61E-04	2.33E-09	/
9	3.41E-04	1.52E-04	2.33E-09	/
10	3.41E-04	1.52E-04	2.33E-09	/
11	3.41E-04	1.52E-04	2.33E-09	/
12	3.41E-04	1.52E-04	2.33E-09	/
13	3.41E-04	1.52E-04	2.33E-09	/
14	4.56E-03	/	/	1.04E-13
15	9.83E-03	/	7.81E-08	/

Table S5 | The timing and p-values of the significant changes in the mean of Poaceae PARs values (grains $cm^{-2}yr^{-1}$) in the Bulusan sequence identified by the STARS algorithm with incremental time window sizes. Increases and decreases in the sample mean are shown in green and red, respectively.

Time window (no. data points)	Change Point 1 (1117 yr BP)	Change Point 2 (897 yr BP)	Change Point 3 (501 yr BP)	Change Point 4 (347 yr BP)	Change Point 5 (149 yr BP)
5	/	/	/	8.91E-04	2.22E-04
6	/	/	/	8.91E-04	2.22E-04
7	1.23E-03	/	/	/	1.78E-03
8	1.44E-02	2.81E-04	/	/	1.49E-03
9	1.44E-02	2.81E-04	/	/	1.49E-03
10	1.44E-02	2.81E-04	/	/	1.49E-03
11	/	/	9.34E-04	/	2.79E-04
12	/	/	9.34E-04	/	2.79E-04
13	/	/	9.34E-04	/	2.79E-04
14	/	/	9.34E-04	/	2.79E-04
15	/	/	9.34E-04	/	2.79E-04

Table S6 | The timing and p-values of the significant changes in the mean of Polypodiopsida PARs values (grains $cm^{-2}yr^{-1}$) in the Bulusan sequence identified by the STARS algorithm with incremental time window sizes. Increases and decreases in the sample mean are shown in green and red, respectively.

Time window (no. data points)	Change Point 1 (897 yr BP)	Change Point 2 (545 yr BP)	Change Point 3 (523 yr BP)	Change Point 4 (501 yr BP)
5	2.10E-08	/	/	2.16E-11
6	2.10E-08	/	/	2.16E-11
7	8.40E-09	/	9.88E-12	/
8	8.40E-09	/	9.88E-12	/
9	8.40E-09	/	9.88E-12	/
10	8.40E-09	/	9.88E-12	/
11	8.40E-09	/	9.88E-12	/
12	8.40E-09	/	9.88E-12	/
13	6.41E-09	1.88E-11	/	/
14	6.41E-09	1.88E-11	/	/
15	6.41E-09	1.88E-11	/	/

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CHAPTER 7: GENERAL DISCUSSION AND CONCLUDING REMARKS

Main Findings

Knowledge of the response of tropical rainforests to large-scale climatic changes in the past, and the associated environmental drivers, is important for predicting and managing the impacts of ongoing climate change. This thesis aimed to provide such knowledge for the lowland rainforests of Southeast Asia, aka Dipterocarp rainforests, through investigation of their vegetation responses to major changes in ENSO dynamics, fire activity and nutrient supply over the last 1,400 years using a wide range of fossil proxies from a Philippine lacustrine sedimentary sequence.

Four central questions were asked in this thesis:

v) What was the direction, magnitude and rate of ENSO changes in the tropical Pacific over the last 1,400 years? (Chapter 3),

vi) How did these ENSO changes influence the biomass dynamics of Dipterocarpaceae taxa, and did the nature and extent of this influence depend on fire intensity? (Chapter 4),

vii) What was the effect of past changes in phosphorus availability on the biomass dynamics of Dipterocarp taxa? (Chapter 5),

viii) What were the responses of pioneer taxa to the changes in ENSO dynamics and fire activity over the last 1,400 years, and what were the consequences of these responses for gap dynamics in Dipterocarp rainforests? (Chapter 6).

Key findings are discussed below in relation to each of these four research questions.

i) What was the direction, magnitude and rate of ENSO changes in the tropical Pacific over the last 1,400 years? (Chapter 3)

Enhanced ENSO regime persisted in the tropical Pacific during the second half of the Little Ice Age (~AD 1650-1900).

To determine past ENSO variability in the tropical Pacific, we generated a new high-resolution hydrological record using the hydrogen isotope composition of terrestrial lipid biomarkers (δD_{wax}) from a 1,400-year old sedimentary sequence from Bulusan Lake, eastern Philippines. The results show a stable period of ~20‰ higher δD_{wax} values from ~AD 1650-1900. Based on the observed modern relationship between monthly measurements of δD precipitation and precipitation amount, a 20‰ increase in δD precipitation would correspond to the reduction of total annual rainfall by ~500-850 mm. Thus, we infer significantly lower precipitation at Bulusan Lake during the second half of the Little Ice Age (LIA), compared to the rest of the examined record.

Given the precipitation sources at the Bulusan site, as well as the direction, timing and magnitude of the precipitation change in the Bulusan record, we reject that the higher δD_{wax} values from ~AD 1650-1900 were caused by changes in the position or latitudinal extent of the Intertropical Convergence Zone (ITCZ). Instead, we propose that a weakening of the Pacific Walker Circulation (PWC) and the establishment of an El Niño-like state were responsible for the observed hydrological changes. While this interpretation is corroborated by tropical Pacific Sea Surface Temperature (SST) records (Cobb *et al.* 2003; Newton *et al.* 2006; Conroy *et al.* 2008; Oppo *et al.* 2009; Conroy *et al.* 2010), other hydrological records from the region provide limited support (Moy *et al.* 2002; Sachs *et al.* 2009; Tierney *et al.* 2010; Rodysill *et al.* 2011; Yan *et al.* 2011; Nelson and Sachs 2016). However, given that most of these hydrological records come from sites where total precipitation is significantly influenced by the ITCZ, we argue that ITCZ-driven changes may be concealing ENSO-driven changes. Consequently, these hydrological records do not conflict with our findings; rather our data reconcile the observed changes in SST with hydrological changes.

The data also show that changes from one ENSO state to the other can occur on decadal timescales and well within the lifetime of a human generation. The shift from weak to strong

ENSO regime recorded at the Bulusan site at ~AD 1650 happened over the period of only ~20 years, as did the subsequent return to the weak regime ~250 years later. This finding is in accordance with regional SST reconstructions. For instance, zonal gradient of tropical Pacific SST, reconstructed using the records from eastern and western equatorial Pacific, shows that the change to a state of weak SST zonal gradient at ~AD 1650, interpreted as El Niño-like conditions, happened over the course of a few decades (Conroy *et al.* 2010). Similarly, the Palmyra record from the central tropical Pacific (Cobb *et al.* 2003) suggests a rapid rise and termination of the marked period of low SST values during the LIA.

The importance of this study is two-fold. Firstly, it shows that, in addition to changes in the ITCZ position, the hydrology of the tropical Pacific region during the last millennium has also been profoundly influenced by notable and rapid changes in the ENSO dynamics. Secondly, it highlights the need to factor in rapid rates of ENSO regime change into future climate projections.

ii) How did these ENSO changes influence the biomass dynamics of Dipterocarpaceae taxa, and did the nature and extent of this influence depend on fire intensity? (Chapter 4)

Past changes in ENSO dynamics had no apparent effect on the biomass dynamics of Dipterocarp trees

To investigate the effects of past ENSO variability on the biomass dynamics of a key tree family of Dipterocarp rainforests, Dipterocarpaceae, I first generated Dipterocarp pollen accumulation rates (PARs) and macrocharcoal influx rates from the Bulusan sedimentary sequence, and used them to approximate the biomass dynamics of Dipterocarp trees and local fire activity, respectively. I combined these with the previously reconstructed hydrological record from the same sedimentary sequence (Chapter 3) to evaluate the importance of changes in δD_{wax} values and macrocharcoal influx rates on Dipterocarp PARs over the study period.

The results show that the changes in δD_{wax} values over the last 1,400 years, including the prolonged period of higher δD_{wax} values between ~AD 1650-1900, had no apparent influence on the Dipterocarp PARs. This indicates that on longer time scales the negative effects of

enhanced ENSO strength, e.g. drought-induced mortality of Dipterocarp trees, can be offset by other mechanisms. We propose two plausible candidates: i) positive effect of enhanced ENSO activity on Dipterocarp flower production and ii) resilience of Dipterocarp woody biomass to enhanced ENSO activity. Given that stronger drought episodes usually result in stronger general flowering events, and that the period between two mass flowering events can be as short as 2 years (Sakai *et al.* 1999), an ENSO regime that brings higher frequency and strength of droughts could increase the occurrence and magnitude of general flowering events. This would subsequently increase Dipterocarp PARs and mask any decreases in Dipterocarp tree biomass, and this effect could be carried long into the future by the surviving individuals given the longevity of Dipterocarp trees (i.e. lifespan of 100s of years). On the other hand, stronger and more frequent general flowering events could have potentially led to stronger and more frequent masting events, increasing the germination success (Toy 1991; Kelly 1994) and expanding the total genetic diversity of the offspring pool. These processes could facilitate the adaptation of Dipterocarp species to the newly established drought regime. Additionally, while enhanced ENSO conditions are likely to increase drought-induced mortality of Dipterocarp trees, they could also potentially facilitate the recruitment of pre-existing Dipterocarp seedlings around the mother trees into the canopy by creating favourable gap conditions (Ghazoul 2016). It is thus possible that the negative effects of ENSO enhanced drought conditions would be offset by the cumulative effect of an increased recruitment rates and a positive selection for individuals with a higher tolerance to drought conditions, boosting the resilience of Dipterocarp woody biomass to enhanced ENSO activity.

There was also no evidence that Dipterocarpaceae PARs were affected by the changes in macrocharcoal influx rates. This suggests that the mechanisms which helped counteract any negative effects of enhanced ENSO regime had not been hindered by increased fire activity. For instance, previous work has demonstrated that while fire can cause almost complete mortality among small stem trees (i.e. <10 cm d.b.h) its effect decreases substantially towards larger tree classes (Van Nieuwstadt and Sheil 2005). Since Dipterocarp seedlings belong to the small stem class of trees only up to 5-10 years of age, our results suggest that the frequency of fire events was lower than that during the study period, allowing Dipterocarp seedlings to grow enough to escape fire-related mortality. Generally low macro- and micro-charcoal influx rates in the Bulusan sedimentary sequence indicate low frequency of fires at both local and regional

scale, and support the idea that fire frequency had little consequence for the survival and growth of Dipterocarp seedlings.

This study pioneers the investigation into the consequences of past ENSO changes on the biomass dynamics of Dipterocarp trees in the lowland tropical rainforests of Southeast Asia and suggests that the consequences may not be as severe as previously suggested.

iii) What was the effect of past changes in phosphorus availability on the biomass dynamics of Dipterocarp taxa? (Chapter 5)

Phosphorus availability has played a major role in the past biomass dynamics of Dipterocarp trees.

To examine how phosphorus availability influences the productivity of Dipterocarp rainforests, we measured the effect of phosphorus abundance (i.e. proxy of phosphorus availability) on Dipterocarp PARs (i.e. proxy for Dipterocarp biomass dynamics) in the Bulusan sedimentary sequence. The Bulusan site is uniquely positioned to address this question because its close proximity to the active Mt Bulusan volcano has caused considerable fluctuations in phosphorus supply over time. We focused on Dipterocarp trees given their major contribution to both the woody and reproduction biomass dynamics of Dipterocarp rainforests (Burgess 1972; Cockburn 1975; Appanah 1985; Sakai *et al.* 1999; Newbery *et al.* 2002).

Results show that phosphorus abundance had a significant positive effect on Dipterocarp PARs in the Bulusan sedimentary sequence with no apparent lags in the changes of Dipterocarp PARs in response to the changes in sediment derived phosphorus. We interpret these findings as an indication that long-term changes in phosphorus availability exert a significant influence on the Dipterocarp biomass dynamics at the landscape scale and discuss the plausible underlying mechanisms: i) an increase in Dipterocarp reproductive biomass (i.e. flower production) and ii) an increase in their woody biomass. Support for the first mechanism comes from the observation that only a portion of reproductively mature Dipterocarp individuals flower in any mass flowering event (Ashton *et al.* 1988; Sakai *et al.* 1999). Phosphorus accumulation was proposed as a decisive factor in the occurrence and magnitude of mast reproduction given the

high phosphorus costs of mass flowering as well as the nutrient poor soils of Southeast Asia (Ichie *et al.* 2005; Ichie and Nakagawa 2011). Therefore, decreasing phosphorus availability at the Bulusan site could have potentially decreased the magnitude and frequency of mass flowering in Dipterocarps, resulting in lower production rates of their pollen. However, the positive effect of sedimentary phosphorus on Dipterocarp PARs may also be indicative of long-term phosphorus limitation to the woody biomass production in Dipterocarp forests. Recent work showed that Dipterocarp trees gain woody biomass faster than otherwise equivalent non-dipterocarp trees (Banin *et al.* 2014). Though experimental work suggests that the effect of phosphorus availability on the rate of woody biomass increment in Dipterocarps is relatively small on annual scale (Mirmanto *et al.* 1999), it is possible that this effect accumulates and becomes notable on multi-decadal scales.

This study is the first to suggest that phosphorus plays an important role in determining the biomass dynamics of Dipterocarp trees over longer time scales. While it is difficult to determine from the pollen record alone what aspect of Dipterocarp biomass is influenced by phosphorus supply, our study highlights the importance of factoring in nutrient constraints to lowland rainforest productivity in future climate-vegetation models.

iv) What were the responses of pioneer taxa to the changes in ENSO dynamics and fire activity over the last 1,400 years, and what were the consequences of these responses for gap dynamics in Dipterocarp rainforests? (Chapter 6)

The effect of ENSO changes on the abundance of pioneer taxa and the associated forest gap dynamics depends heavily on fire activity.

To assess the impact of past ENSO changes on gap dynamics in Dipterocarp rainforests, I generated PARs records for five key pioneer taxa, i.e. *Macaranga, Trema, Calamus,* Poaceae and Polypodiopsida, and compared these to the records of δD_{wax} and macrocharcoal influx rates from the same sequence (see Chapters 2 and 3).

The results suggest that the effect of enhanced ENSO-induced drought conditions on the abundance of pioneer taxa depended heavily on the level of fire activity. Specifically, at low to

no fire activity, enhanced drought intensity appeared to have a negative effect on pioneer taxa abundance, while high fire activity led to a positive effect. Given the findings, it is probable that enhanced ENSO-induced drought conditions in absence of increased fire activity will promote gap regeneration by climax taxa as opposed to regeneration by pioneer taxa. One potential explanation could be the size of the gaps that such conditions favour. Many large tree species in Dipterocarp rainforests, including the members of the dominant Dipterocarpaceae family, remain standing after death due an elaborate system of buttress roots (Gale and Barfod 1999; Hall *et al.* 2004). Consequently, tree gaps created in this way are smaller in size, favouring vegetation regeneration from pre-existing shade-tolerant seedlings/ saplings of climax species. In contrast, a combination of high fire levels and enhanced drought is likely to facilitate the dominance of pioneer taxa even in gaps of smaller size. Firstly, fire removes the pre-existing seedlings of climax taxa from forest gaps, thereby exposing bare soil and facilitating germination and growth of pioneer taxa (Woods 1989; Ashton 2014). Secondly, fire delays the vegetation succession in forest gaps. When fire is absent, pioneer trees can quickly form a canopy under which they and other pioneer groups (e.g. ferns, grasses) are incapable of regenerating which subsequently leads to their replacement by shade-tolerant seedlings of climax species (Whitmore 1998; Ashton 2014). Regular fire removes such pioneer-made canopies and hinders the growth of climax tree species, facilitating the dominance of pioneer taxa.

The data also suggest the prolonged period of enhanced ENSO and fire regime (~AD 1650-1900) had differential effect on the abundance of pioneer taxa, promoting some pioneer taxa more than others. Specifically, the significantly higher abundance of *Macaranga* and Polypodiopsida during this time interval suggests favourable conditions for these taxa, as opposed to *Trema* and Poaceae whose abundance increases only in the second half of the period. It can therefore be argued that the magnitude and intensity level of these two disturbances during the enhanced ENSO regime ~AD 1650-1900 promoted *Macaranga* and Polypodiopsida over *Trema* and Poaceae. Previous studies provide some clues as to the factors possibly underlying these findings. For example, fire intensification can boost the establishment of pioneer trees such as *Macaranga* and *Trema,* but only up to a point after which these taxa give way to grasses such as *Imperata cylindrica* (Woods 1989). Therefore, the increase in the abundances of *Macaranga* and *Trema* and absence of change in the abundance of grasses

recorded during the ~AD 1650-1900 interval points towards fire activity being low enough to favour pioneer trees over grasses. Similarly, higher performance of *Macaranga* in comparison to *Trema* during the same time interval may be linked to the size of the gaps created under enhanced ENSO conditions. *Trema* species usually germinate but do not survive to reproductive size except in very large gaps (Denslow 1987; Condit *et al.* 2004). Such preference can significantly limit the capacity of *Trema* to respond positively to higher availability of smaller gaps such as those created by standing dead trees. Human activities may have also contributed to differential dynamics of pioneer taxa at the Bulusan site. For example, there is a possibility that rattan (*Calamus*) harvesting was happening close to Bulusan Lake before the park was established in 1935, which would explain the drop in *Calamus* pollen from ~AD 1700 onwards. Harvesting of forest products could also explain the increase in *Trema* and Poaceae pollen (Figure 5) during the same time period, indicative of an increase in forest gap size. These findings indicate that while it is unlikely that past human activities had changed the structure of Dipterocarp forest at the Bulusan site, they may have affected the composition of its pioneer community. Taken together, these results highlight the need for taxa-specific evaluation of the effects of ENSO changes on pioneer plants, both in presence and absence of human activities, in order to advance predictions of the composition of pioneer communities under future ENSO conditions.

This study pioneers the examination of gap dynamics in Dipterocarp rainforests under changing ENSO conditions, and highlight the importance of including fire activity and taxa-specific information when predicting the nature and magnitude of pioneer plant responses to future ENSO conditions.

Concluding remarks

This thesis has shown that major ENSO changes have taken place in the tropical Pacific over the last 1,400 years, most notably a period of El-Niño like conditions between the interval ~AD 1650-1900. These changes have had significant impacts on some aspects of Dipterocarp rainforests structure but not others. Surprisingly, the dominant tree family of Dipterocarp rainforests, which has the main role in shaping the biomass production and reproductive

behaviour of these forests, seems to have low sensitivity to enhanced ENSO conditions, including increased drought and fire intensity. This may be due to positive effects of such conditions on the frequency and magnitude of mass flowering and/ or on the rates of seedling recruitment rates in the newly created gaps. In contrast, the biomass dynamics of Dipterocarp trees over the last 1,400 years seems to have been positively influenced by phosphorus availability, although it remains uncertain if this is due to changes in woody biomass or reproductive biomass). Finally, the results suggest that the influence of enhanced ENSO conditions on vegetation regeneration in forest gaps depends heavily on fire intensity – conditions of low to no fire activity seem to promote gaps dominated by climax taxa while high fire frequency favours pioneer dominance. However, differential responses among the pioneer taxa to the prolonged period of enhanced ENSO dynamics highlight the challenge of predicting the composition of these forest gap communities under future ENSO scenarios.

These results have an important bearing for the conservation and management of Dipterocarp rainforests in the face of climate change, especially given that the last few decades have seen a marked increase in the frequency and magnitude of fire events in Dipterocarp rainforests (Salafsky 1994; Folkins *et al.* 1997; Salafsky 1998; Siegert *et al.* 2001; Huijnen *et al.* 2016). Previous work has shown that while El Niño related droughts can lead to fire events, the recent trend of increasing fire intensity is linked primarily to anthropogenic activities such as forest fragmentation and degradation (Curran *et al.* 1999). Therefore, it is highly likely that the projected intensification of ENSO will be accompanied by increased fire activity in the region. According to the findings of this thesis, such environmental conditions could potentially give rise to a novel and thus poorly understood forest type dominated by Dipterocarp trees and pioneer-dominated gaps. Therefore, to ensure the persistence of the current structure and functioning of Dipterocarp rainforests into the future, it is important to develop and implement strategies that can minimise the occurrence and magnitude of fire events in the region.

Future Research Directions

While the new scientific findings presented in this thesis have addressed several important questions about the long-term ecology of Dipterocarp rainforests, they have also opened new

questions with respect to the environmental changes that have influenced this globally important ecosystem and the ecological responses that followed. Most prominent of these questions are discussed below:

1) Provision of more long-term ecological records from Dipterocarp rainforests

While there are several marine sediment records from the Southeast Asian region that reveal the abundance dynamics of Dipterocarpaceae pollen over longer time scales (van der Kaars 1991; van der Kaars and Dam 1995; Wang *et al.* 1999, Sun *et al.* 2000; van der Kaars *et al.* 2000), it is difficult to assume that the pollen is from a particular ecosystem type given the large and uncertain pollen source area of such records and the presence of Dipterocarp species in virtually all of the regional forest types (e.g. peat swamp forests, freshwater swamp forests, montane forests, dry tropical forests). In contrast, lacustrine sediments, particularly those from smaller lakes, have a smaller and more constrained pollen source area (Prentice 1985; Sugita 1993; Sugita 1994), and can therefore limit the vegetation reconstruction to the ecosystem of interest, answering specific questions about its ecology over longer time scales, as demonstrated in this thesis. To the best of our knowledge, the Bulusan sequence is the first lacustrine sediment sequence from Dipterocarp rainforests. More such sediment records, ideally from other parts of the region and of an older age, are needed to establish the generality of our findings as well as to address questions that require wider spatial and temporal coverage, such as the changes in the distribution of different plant taxa during glacial periods. This goal is challenging due to scarcity and inaccessibility of suitable lake sites, but also of utmost importance, given the benefits of such sediment records for advancing our understanding of Dipterocarp forest ecology.

2) Reconstruction of Dipterocarp rainforest responses at higher taxonomic resolution

While fossil pollen morphology remains the most widely used method for reconstructing ancient plant dynamics, it has an important shortcoming; a relatively small number of species produce pollen whose morphological features are distinct enough to allow species-level identification. This is especially true for megadiverse ecosystems such as Dipterocarp rainforests. Consequently, there are limitations to elucidating the effects of past environmental changes on these forests using solely this method. For instance, functional trait analysis – a

particularly potent approach for assessing ecosystem functioning (Díaz and Cabido 2001) - is virtually impossible to perform using fossil pollen data because functional traits are overwhelmingly species-specific.

Ancient DNA (aDNA), i.e. DNA extracted from ancient specimens, is a powerful new proxy for studying late Quaternary environments (Willerslev *et al.* 2003; Willerslev *et al.* 2014). Its main advantage is a high taxonomic resolution, allowing identification of thousands of plant and animal species in the fossil record (Pedersen *et al.* 2014). An approach that combines aDNA analysis of sediments, pollen or macrofossil remains, with classical fossil pollen morphology (Magyari *et al.* 2011; Parducci *et al.* 2012; Pedersen *et al.* 2013) could allow the reconstruction of Dipterocarp rainforest responses at higher taxonomic resolution. Such an approach could examine if changes in ENSO dynamics or nutrient availability cause compositional changes in the Dipterocarp community, e.g. favouring more drought-tolerant species, and what sort of functional consequences would these changes have for Dipterocarp rainforests. Moreover, species-level resolution of palaeoecological data would facilitate the reconstruction of past population dynamics of plant species in Dipterocarp rainforests and allow us to test for the mechanistic relationships between plant populations and environmental variables over long time scales (Jeffers *et al.* 2011; Jeffers *et al.* 2012).

3) Reconstruction of past typhoon variability and its effects on Dipterocarp rainforests

The Philippines are positioned across the typhoon belt, featuring typhoons and strong storms which are especially hazardous for northern and eastern Luzon, including the area of our study site (PAGASA 2016). Presently, the number of tropical storm landfalls in the Philippines varies between 3-6 per year (Kubota and Chan 2009). While Philippine Dipterocarp rainforests are regularly exposed to strong typhoons (Co *et al.* 2006; Yap *et al.* 2016), the consequences of this disturbance for forest structure and functioning are poorly understood. Interestingly, an observational study by Yap *et al.* (2016) demonstrated that a strong typhoon event causes significantly higher tree mortality, but minimal above-ground biomass loss and nearly four times higher recruitment rates, indicating high resilience of Dipterocarp rainforests to the current typhoon regime. However, it would be interesting to examine the ecological consequences of stronger or weaker typhoon regimes than the one these forests currently experience, as well as its synergy with other disturbance types. For instance, typhoons increase

the likelihood of tree falls and often completely defoliate the tree canopy (P. Ashton, pers. comm.), thereby creating both smaller and larger gaps that may be especially favourable for pioneer species during the periods of enhanced drought and fire activity.

Previous studies have used a number of proxies to reconstruct past variability of tropical cyclones, such as historical records (Liu *et al.* 2001), sediment grain size (Liu and Fearn 1993; Woodruff *et al.* 2009), geochemical profiling (Buynevich *et al.* 2004) and stable isotopes (Noren *et al.* 2002), yet no such records have been generated for Southeast Asia to date. Given the large uncertainties when comparing climatic and vegetation records from different regions, particularly for spatially heterogeneous phenomena such as tropical cyclones, it would be beneficial to generate regional records, ideally in the proximity of existing vegetation records. In that regard, it may be possible to produce a typhoon variability record from the Bulusan sediments, for instance, using a ratio of marine to freshwater diatoms (the lake is located ~4 km from the eastern coast) (Nott 2004). Such work would need to be preceded by a proof-of-concept study that would test and calibrate the relationship between different physical, chemical and biotic features of Bulusan sediments and the historic record of Philippine typhoon landfalls in order to identify reliable proxies for this disturbance type.

4) <u>The effect of other plant nutrients on the productivity of Dipterocarp taxa</u>

While phosphorus is considered the main limiting factor on the productivity of tropical rainforests, numerous short-term studies have suggested that other nutrients, namely nitrogen, magnesium, calcium and potassium, also have a notable influence on the growth of Dipterocarp seedlings (Burslem *et al.* 1996; Brearley *et al.* 2003; Vincent and Davies 2003; Paoli *et al.* 2006). Other studies, however, offered no evidence of such relationship (Turner *et al.* 1993; Hattori *et al.* 2013). To the best of our knowledge, no studies to date have examined the individual effects of these other nutrients on the growth of adult Dipterocarp trees over longer time scales. It may be the case that, similarly to phosphorus (Chapter 5), the effect of other nutrients on the biomass dynamics of large tree species may be effectively captured on decadal to centennial time scales.

The challenge will be to find suitable sedimentary sequences to test the effects of the above discussed nutrients. At Bulusan Lake, due to regular deposition of volcanic ash whose main

elements include potassium, magnesium and calcium, it is difficult to assume that the abundance of these elements in the lake's sediments is indicative to their availability in the soil, and this is likely to be true for other sites close to (active) volcanoes. Reconstruction of past nitrogen variability and assessment of its effects on the productivity of plants, however, is more feasible to assess using lake sediments as demonstrated by previous research using stable isotope analysis (Jeffers *et al.* 2011; Jeffers *et al.* 2012; McLauchlan *et al.* 2013). While these previous studies have focused on boreal and temperate ecosystems, there should not be serious barriers to employing the same methods in tropical ecosystems, provided that suitable coring sites are selected. Given its favourable morphological and sedimentary features, Bulusan Lake represents a promising candidate for such future research.

5) Determining the relationship between pollen productivity and biomass dynamics for Dipterocarp trees

A reliable relationship between the number of pollen grains of a particular taxon and the quantity of its vegetative form provides a foundation for quantitative reconstruction of past plant dynamics (Sugita 2007; Hellman *et al.* 2008). This approach has been previously used to translate pollen percentage into local and regional coverage of plant taxa and vegetation types (Bradshaw 1981; Overballe-Petersen *et al.* 2013; Trondman *et al.* 2015), and more recently, to convert pollen accumulation rates (PARs) into absolute units of biomass measurement (i.e. tree volume, m^3 h^{-1}) for reconstructing changes in the biomass production over time (Seppä *et al.* 2009; Mazier *et al.* 2012). The latter application would be particularly useful for quantifying the effect of environmental changes on the biomass production of Dipterocarp trees, as well as to better understand the potential contribution of changing pollen productivity rates on Dipterocarp PARs.

No studies to date have attempted to establish the pollen-vegetation relationship for primary Dipterocarp rainforests, including the Dipterocarpaceae taxa (but see Beuning 1996 for secondary forest information). This task may be particularly challenging, not only due to the high biodiversity and low accessibility, but also because of the irregular flowering patterns which are characteristic for these forests. Capturing full flowering variability of a Dipterocarp rainforest, and especially of its Dipterocarp species, would require studies of modern pollen rain that extend over several years to several decades. While this is a considerably longer time

frame than that of most previous studies, there are some successful examples of multi-decadal measurements from boreal and temperate regions that demonstrate the value and feasibility of such an endeavour (Nielsen *et al.* 2010; Donders *et al.* 2014).

As illustrated above, there are many knowledge gaps on the palaeoecology of Dipterocarp rainforests that future scientific research would need to address. In providing fundamental insights into the vegetation responses of Dipterocarp rainforests to major climatic and environmental changes of the last 1,400 years, this thesis is a first step towards achieving this goal. The work presented here draws from both palaeoecology and modern ecology, using palaeoecological data and modern ecological theory to address some pressing questions about a globally important ecosystem in a changing world.

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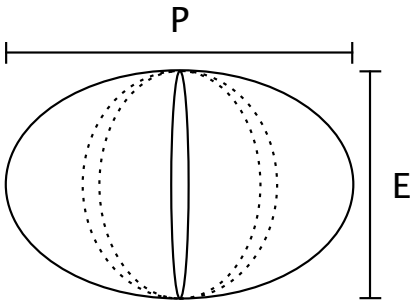
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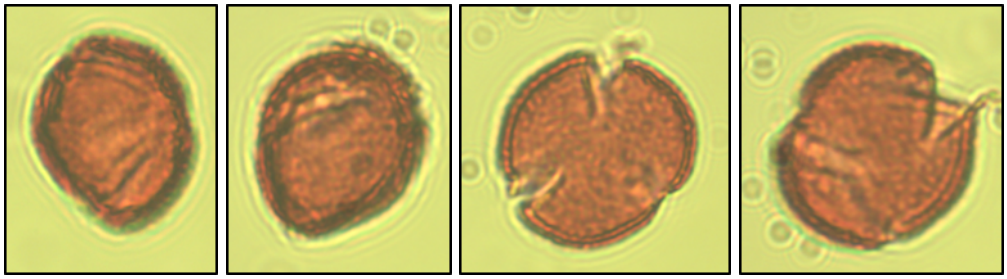
APPENDIX A: DIPTEROCARPACEAE POLLEN REFERENCE COLLECTION



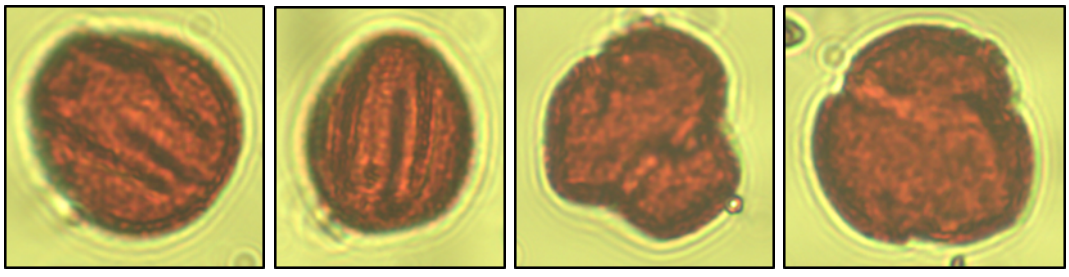
PH = present in the Philippines

ANISOPTERA

Anisoptera costata (PH), E= 16-18 µm, P= 19-23 µm

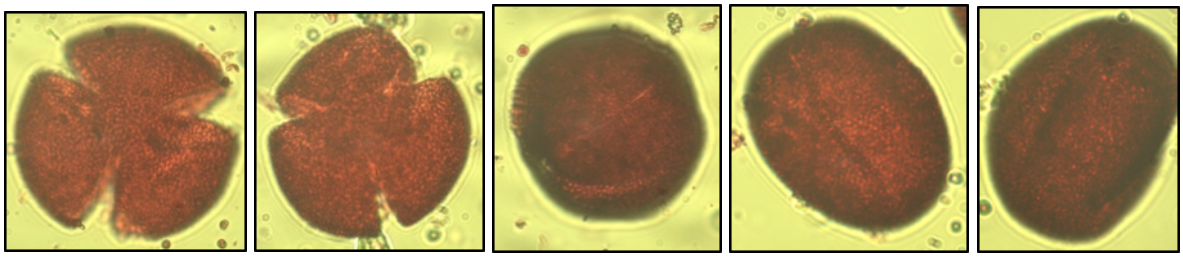


Anisoptera marginata, E= 20-24 µm, P= 15-18 µm

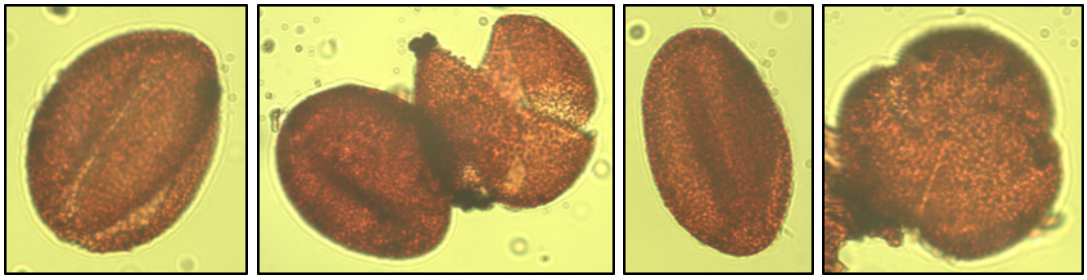


DIPTEROCARPUS

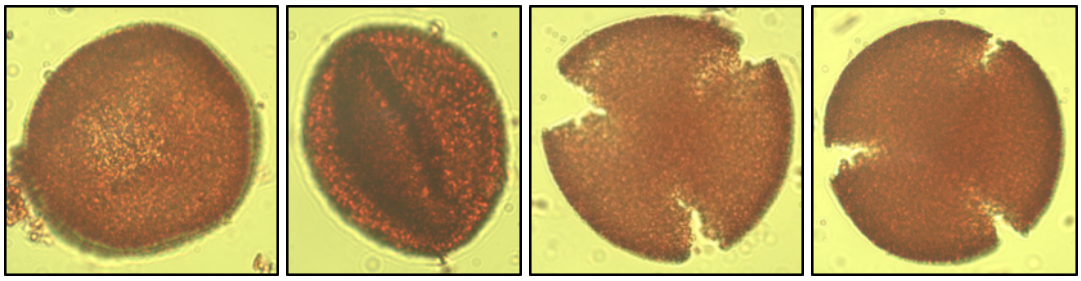
Dipterocarpus criticus, E= 41-53 µm, P= 54-58 µm



Dipterocarpus gracilis (PH), E= 55-62 µm, P= 54-64 µm

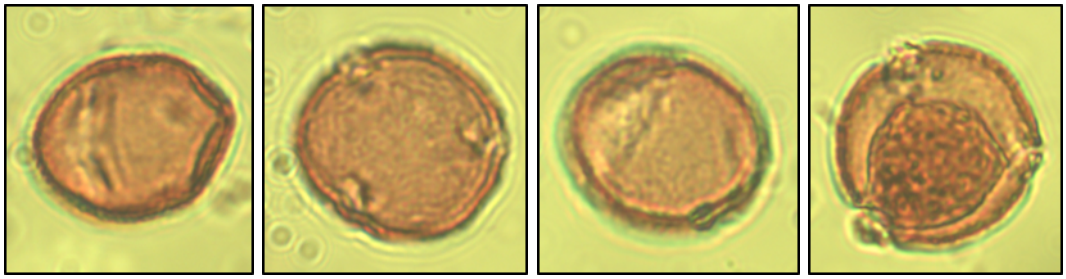


Dipterocarpus kunstleri (PH), E= 59-62 µm, P= 59-64 µm

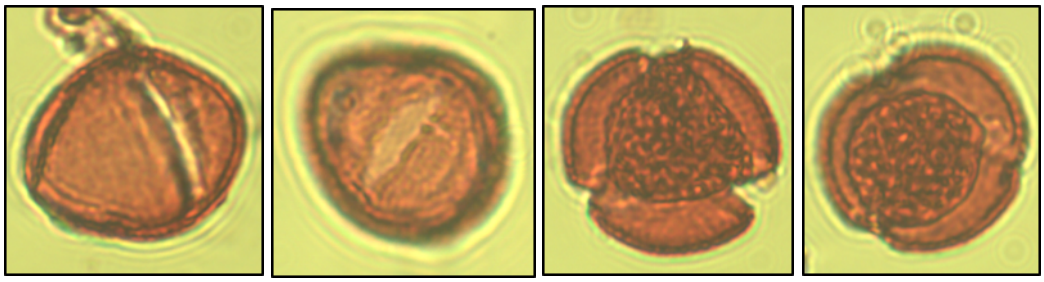


HOPEA

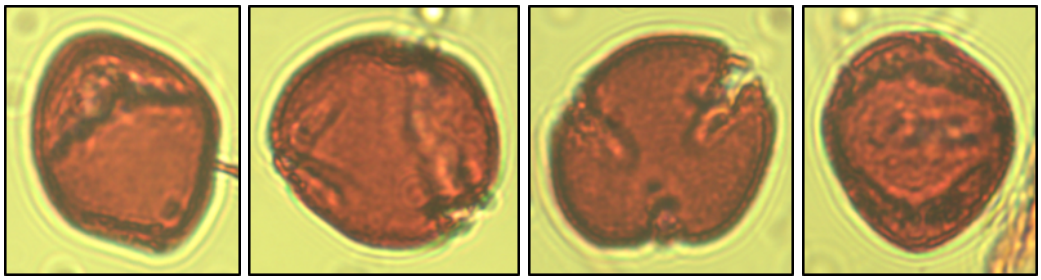
Hopea beccariana, E= 21-24 µm, P= 24-27 µm



Hopea ferruginea, E= 23-26 µm, P= 27-30 µm

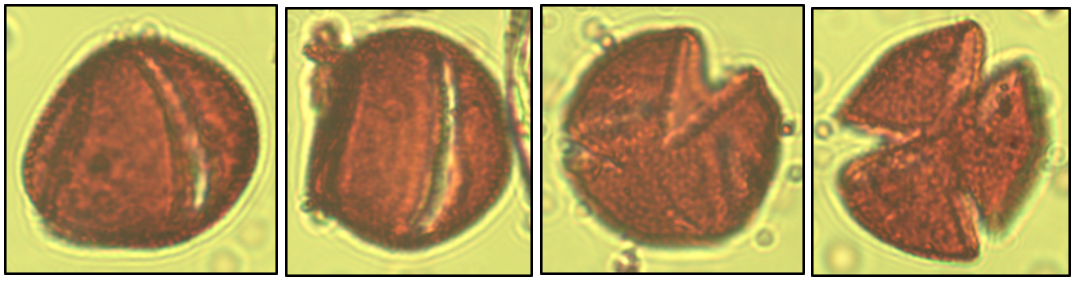


Hopea mengeriana, E= 22-25 µm, P= 28-30 µm

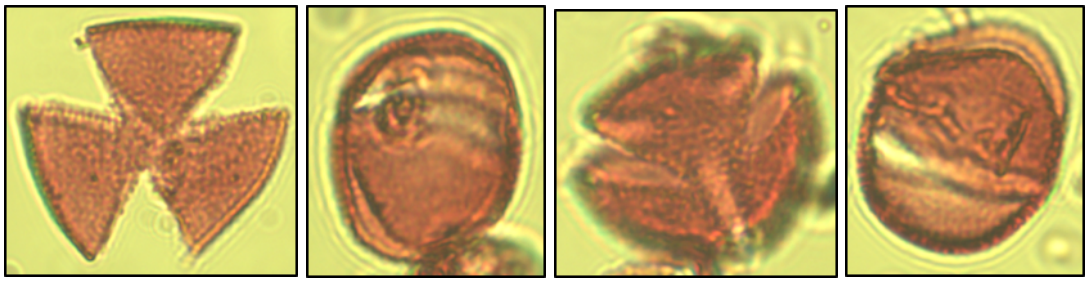


PARASHOREA

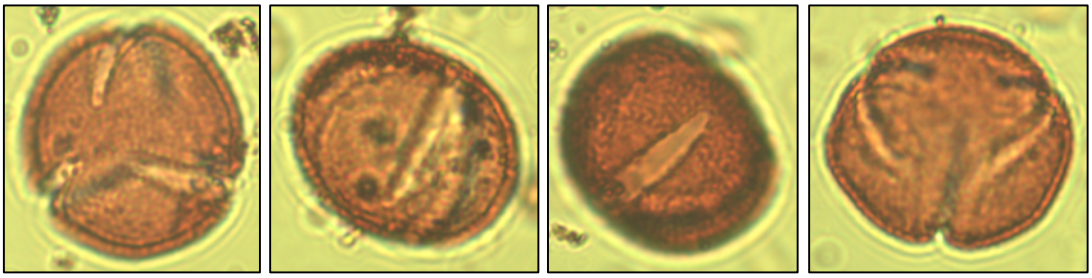
Parashorea malaanonan (PH), E= 16-20 µm, P= 19-22 µm



Parashorea smythsiensis, E= 15-17 µm, P= 19-21 µm

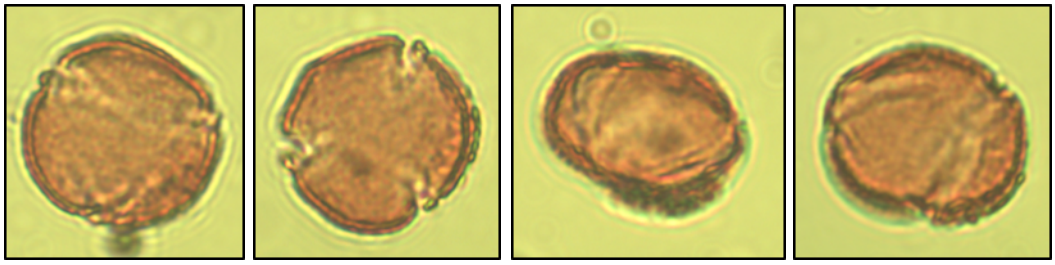


Parashorea tomentosa (PH), E= 16-17 µm, P= 19-21 µm

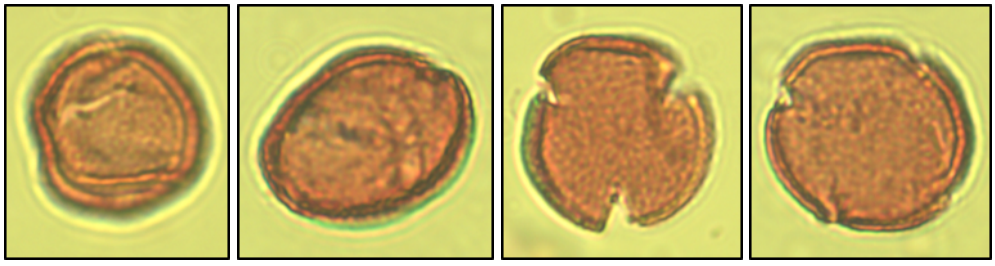


SHOREA

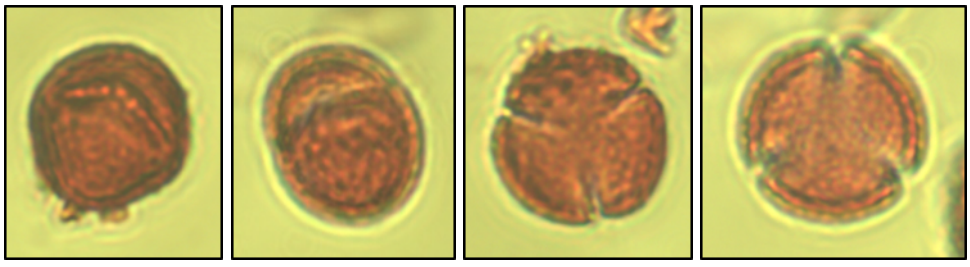
Shorea guiso (PH), E= 14-16 µm, P= 17-19 µm



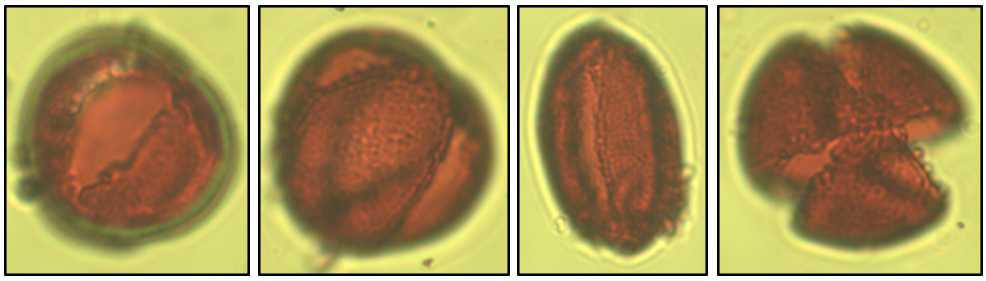
Shorea ovata (PH), E= 15-16 µm, P= 18-19 µm



Shorea seminis (PH), E= 14-15 µm, P= 15-17 µm

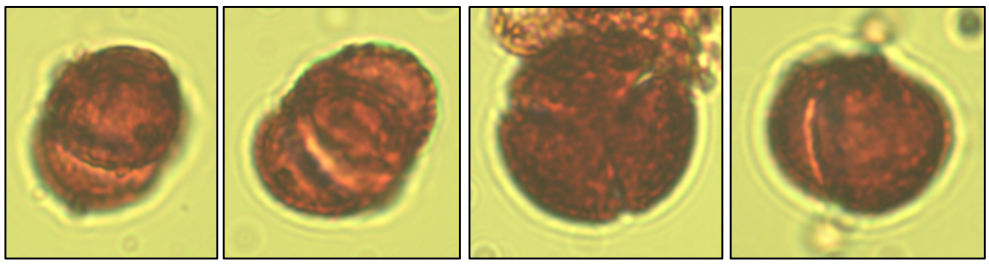


Shorea virescens (PH), E= 17-22 µm, P= 21-23 µm

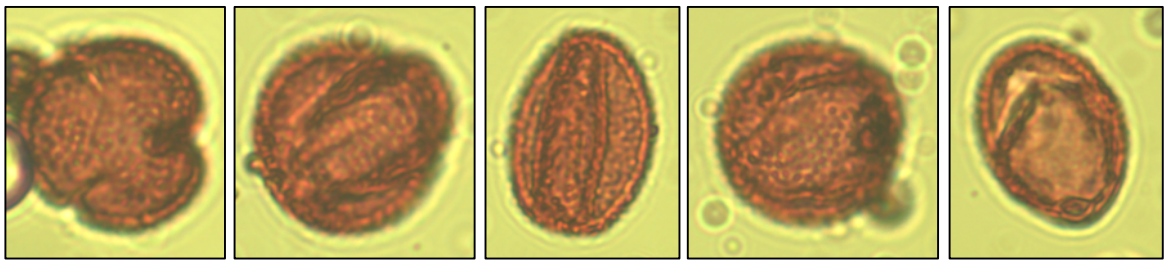


VATICA

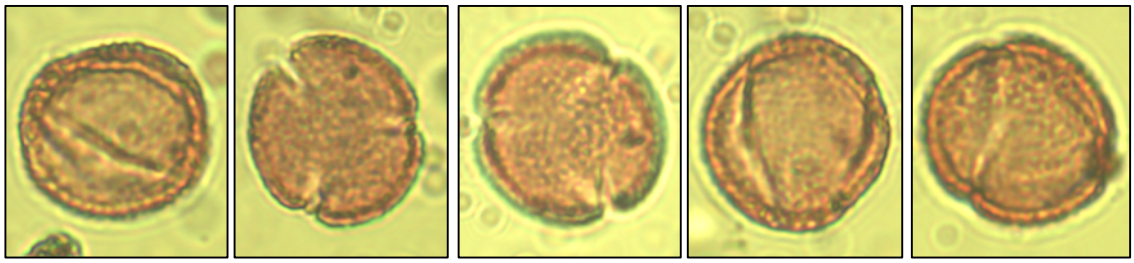
Vatica mangachapoi (PH), E= 13-14 µm, P= 15-17 µm



Vatica rassak (PH), E= 14-19 µm, P= 17-19 µm



Vatica umbonata (PH), E= 17-19 µm, P= 17-18 µm



APPENDIX B: BULUSAN POLLEN DIAGRAMS

The two pollen diagrams presented here contain the main plant taxa identified in the Bulusan sedimentary sequence. Pollen abundance of a particular taxon is expressed as a percentage of the total terrestrial pollen grains (%) (Figure B1) and as pollen accumulation rates, PARs (grains $cm^{-2}yr^{-1}$) (Figure B2). The diagrams were produced using the *rioja* package (Juggins *et al.* 2013) in the R version 3.2.4 (R Core Team 2013).

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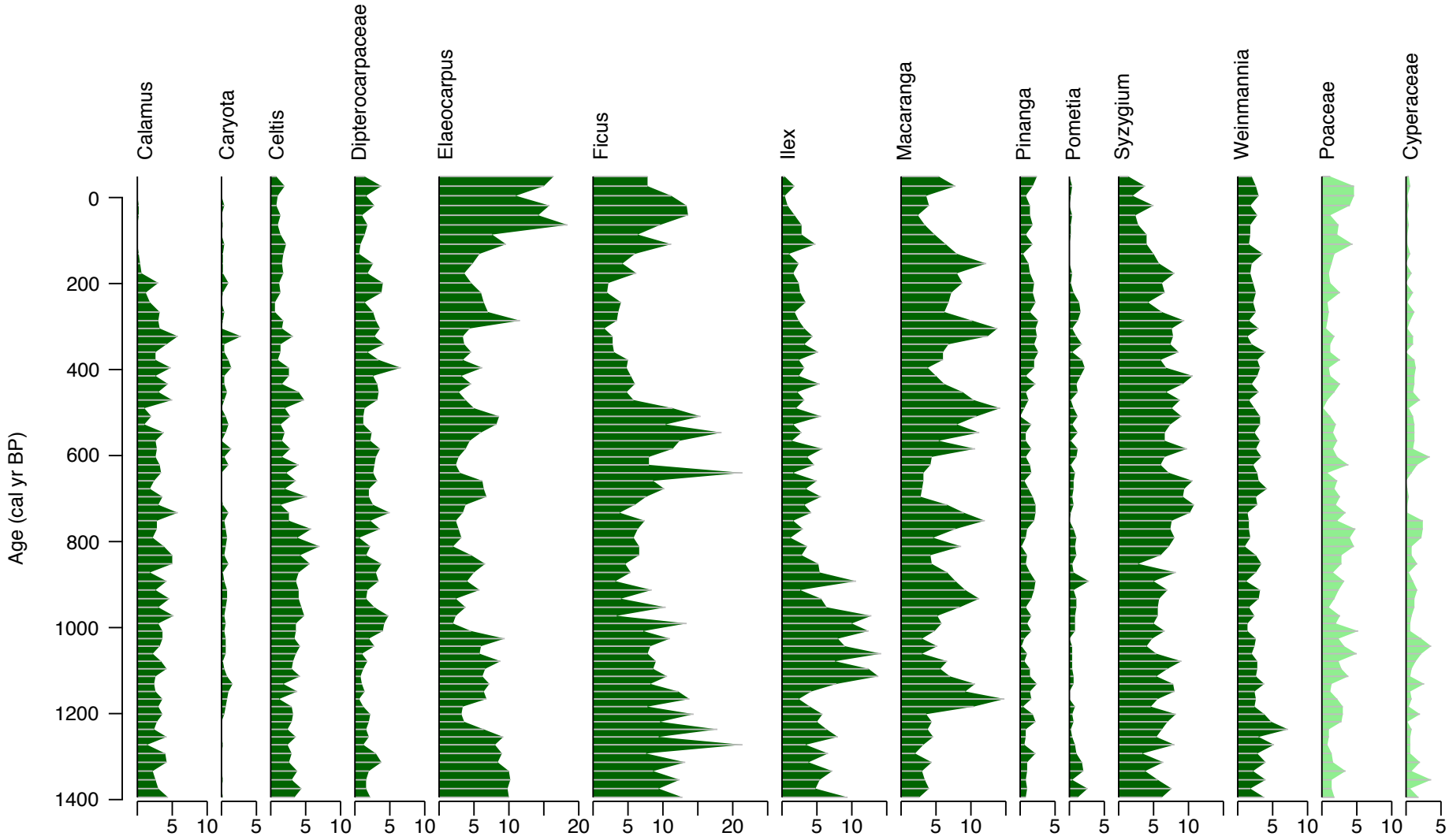


Figure B1 | Pollen abundance of a particular taxon is expressed as a percentage of the total terrestrial pollen grains (%). The diagram was generated using the *rioja* package (Juggins *et al.* 2013) in the R version 3.2.4 (R Core Team 2013).

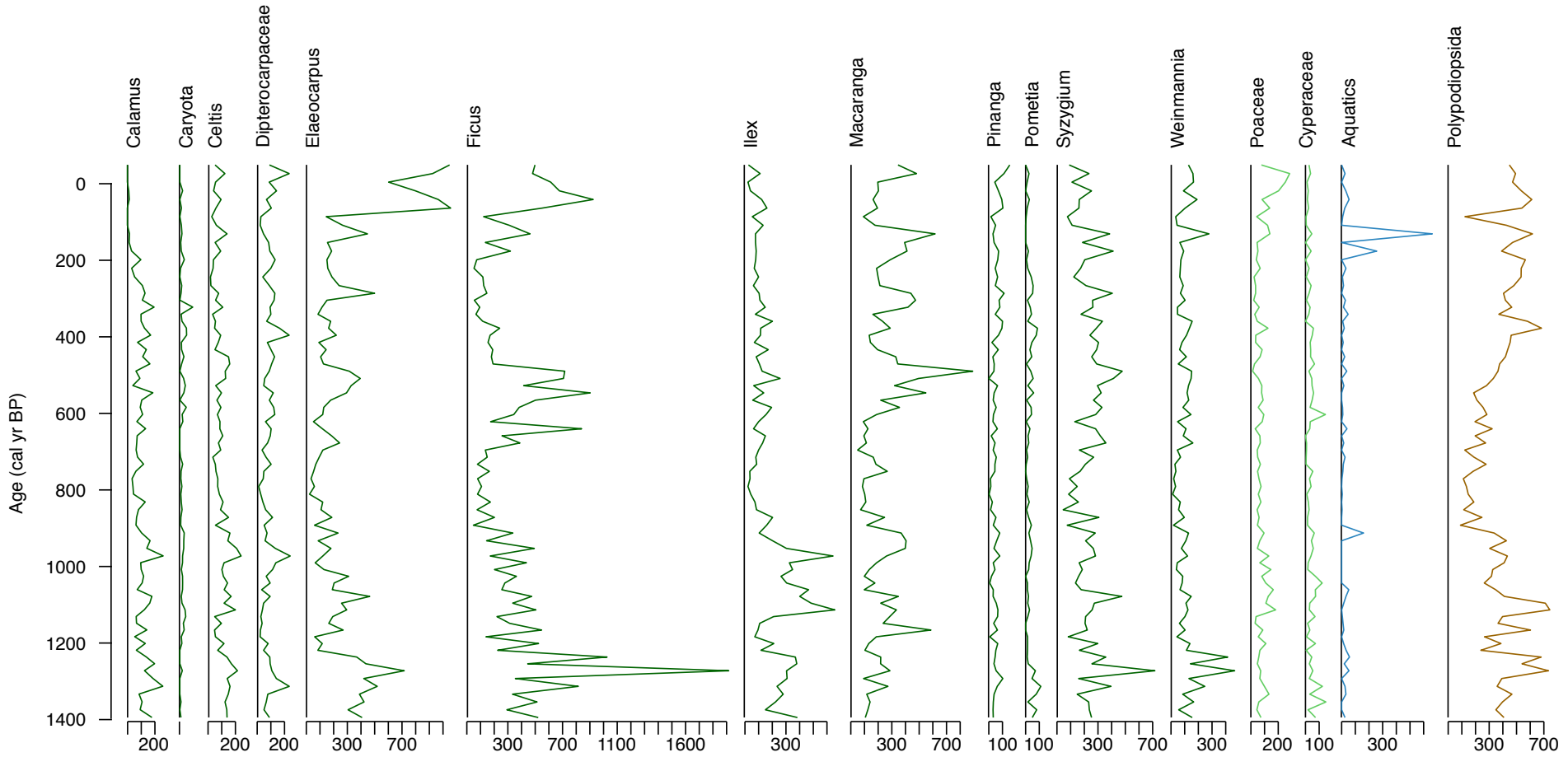


Figure B2 | Pollen abundance of a particular taxon is expressed as pollen accumulation rates, PARs (grains $cm^{-2}yr^{-1}$). The diagram was generated using the *rioja* package (Juggins *et al.* 2013) in the R version 3.2.4 (R Core Team 2013).