Long-term ecological responses of a lowland dipterocarp forest to climate changes and nutrient availability

Ana Prohaska[1,2,7] (iD), Alistair W. R. Seddon[3,4] (iD), Oliver Rach[5] (iD), Andrew Smith[6] (iD), Dirk Sachse[5] (iD) and Katherine J. Willis[1] (iD)

[1]Department of Biology, University of Oxford, South Parks Road, Oxford, OX1 3RB, UK; [2]Department of Zoology, University of Cambridge, Downing St, Cambridge, CB2 3EJ, UK; [3]Department of Biology, University of Bergen, Bergen, NO-5020, Norway; [4]Bjerknes Centre for Climate Research, University of Bergen, Bergen, NO-5020, Norway; [5]Section 4.6: Geomorphology, Organic Surface Geochemistry Lab, Centre for Geosciences, GFZ-German Research, Telegrafenberg, Potsdam, 14473, Germany; [6]National Environmental Isotope Facility, British Geological Survey, Keyworth, Nottingham, NG12 5GG, UK; [7]Present address: Globe Institute, University of Copenhagen, Copenhagen, 1350, Denmark

Author for correspondence:
Ana Prohaska
Email: ana.prohaska@sund.ku.dk

Summary

- Understanding the long-term impact of projected climate change on tropical rainforests is critical given their central role in the Earth's system. Palaeoecological records can provide a valuable perspective on this problem. Here, we examine the effects of past climatic changes on the dominant forest type of Southeast Asia – lowland dipterocarp forest.
- We use a range of proxies extracted from a 1400-yr-old lacustrine sedimentary sequence from north-eastern Philippines to determine long-term vegetation responses of lowland dipterocarp forest, including its dominant tree group dipterocarps, to changes in precipitation, fire and nutrient availability over time.
- Our results show a positive relationship between dipterocarp pollen accumulation rates (PARs) and leaf wax hydrogen isotope values, which suggests a negative effect of drier conditions on dipterocarp abundance. Furthermore, we find a positive relationship between dipterocarp PARs and the proxy for phosphorus availability, which suggests phosphorus controls the productivity of these keystone trees on longer time scales. Other pollen taxa show widely varying relationships with the abiotic factors, demonstrating a high diversity of plant functional responses.
- Our findings provide novel insights into lowland dipterocarp forest responses to changing climatic conditions in the past and highlight potential impacts of future climate change on this globally important ecosystem.

Introduction

Lowland tropical rainforests make up the most productive terrestrial biome and cover nearly 10% of Earth's land surface (Saatchi *et al.*, 2011). As such, they represent a key component of the models predicting Earth's capacity to combat increasing levels of CO_2 (Bonan & Levis, 2010; Huntingford *et al.*, 2013). Yet the nature and extent to which climate and nutrient availability influence the productivity and reproduction of tropical rainforests remain poorly resolved (Cleveland *et al.*, 2011). This is particularly true for the lowland tropical rainforests of Southeast Asia that once covered much of peninsular Malaysia, Sumatra, Java, Borneo and the Philippines (Appanah, 1985) but which presently occupy only 30% of their original range following record-high rates of deforestation (Sodhi *et al.*, 2004; Wilcove *et al.*, 2013). These forests are ecologically unique among tropical rainforests in that they engage in interannual mass flowering, and are overwhelmingly dominated by a single plant family, Dipterocarpaceae which is overwhelmingly composed of canopy and emergent trees. Dipterocarp trees (dipterocarps) constitute up to 10% of total tree diversity, over 50% of the basal area and nearly 80% of all emergent trees in these forests (Appanah, 1985). Consequently, the lowland tropical rainforests of Southeast Asia are often referred to as lowland dipterocarp forests. Lowland dipterocarp forests are aseasonal and thus markedly differ from seasonal dipterocarp forest found in Cambodia, Myanmar and parts of Thailand, which experience seasonal drought and burning, characterised by a more open (woodland-like) canopy and a significant grass cover (Ashton & Seidler, 2014).

Observational studies have shown that drought and fire events can exert a large influence on the ecological processes in lowland dipterocarp forests on annual scales. Severe drought events in the region, of which El Niño–Southern Oscillation (ENSO) is the main driver, lead to increased mortality for most tree species in lowland dipterocarp forests, with large trees being particularly susceptible. For instance, in a single drought event in 1998, large trees (i.e. > 80 cm dbh) made up > 45% of total stem mortality in lowland dipterocarp forests (Van Nieuwstadt & Sheil, 2005).

Furthermore, fire events, which are more likely to occur during severe droughts, can cause near-total mortality of smaller trees (Van Nieuwstadt & Sheil, 2005). The resulting increase in tree mortality can lead to higher occurrence of forest gaps, which presently form only a small portion of the total area (Ghazoul & Sheil, 2010). It has therefore been hypothesised that long-term changes in the magnitude and frequency of drought and fire events, associated with the changes in ENSO activity projected for this century, will profoundly alter the structure of lowland dipterocarp forests (Whitmore, 1988; Ghazoul, 2016).

By contrast, other work has suggested that El Niño-induced drought events play a key role in the reproduction of lowland dipterocarp forests because they trigger mass flowering events (Sakai *et al.*, 2006). Most dipterocarp species reproduce only during such events. For example, > 60% of *c.* 200 dipterocarp species in North Borneo were observed to flower during a single strong El Niño drought event in 1955 (Woods, 1956), and almost 50% of the mature dipterocarp individuals have been shown to flower during mass flowering years (Burgess, 1972; Cockburn, 1975). Mass flowering of dipterocarp is often accompanied by heavy flowering of many other plant species, including members of other prominent families of lowland dipterocarp forests such as Anacardiaceae, Euphorbiaceae, Annonaceae, Fabaceae, Burseraceae, Moraceae and Myristicaceae (Appanah, 1985). Seedlings of many dipterocarp tree species can survive in shade for > 10 yr 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. An alternative hypothesis, therefore, is that rather than a decline in dipterocarp tree abundance, stronger El Niño-related drought regimes predicted for this century will instead lead to stronger/more frequent flowering and masting events, boosting the reproduction of lowland dipterocarp forests, which may lead to an increase in dipterocarp tree abundance if seedling recruitment is not hindered by drier conditions.

In addition to drought and fire, understanding nutrient limitations in lowland dipterocarp forests is essential for predicting their responses to current and future disruptions in nutrient cycling (Sala *et al.*, 2000; Boisvenue & Running, 2006; Hou *et al.*, 2018). Phosphorus is a primary plant macronutrient with particularly low concentrations in tropical soils and it is thus widely assumed to be the main limiting nutrient to the productivity of lowland tropical rainforests (Vitousek, 1984) (in contrast to nitrogen (N) that is believed to be generally abundant due to biological nitrogen fixation (Jenny, 1950; Cleveland *et al.*, 1999; Galloway *et al.*, 2004)). However, evidence of phosphorus limitation is scarce and comes predominantly from short-term experimental studies at stand-level (Vitousek *et al.*, 1993; Mirmanto *et al.*, 1999; Newbery *et al.*, 2002; Davidson *et al.*, 2004; Wright *et al.*, 2011; Alvarez-Clare *et al.*, 2013; Cunha *et al.*, 2022) and at the level of individual trees (Burslem *et al.*, 1996; Gunatilleke *et al.*, 1997; Lawrence, 2003; Yavitt & Wright, 2008), and from observational studies across soil nutrient gradients (Vitousek *et al.*, 1992; Santiago *et al.*, 2004; Santiago & Mulkey, 2005; Baltzer *et al.*, 2008; Fyllas *et al.*, 2009). However, a large portion of the biomass production in a tropical rainforest stand is carried out by large trees (Rutishauser *et al.*, 2010; Slik *et al.*, 2010,

2013) according to a hypothesis by Vitousek (1984), and it is the large trees in a tropical rainforest that are most limited by phosphorus availability. Thus, understanding the response of a lowland dipterocarp forest to phosphorus availability is not possible without understanding the response of its large trees, which overwhelmingly belong to the Dipterocarpaceae family.

Given the long life span (multicentennial) and generation time (multidecadal) of large rainforest trees, predicting future responses of tropical rainforests, such as lowland dipterocarp forests, to changing conditions is extremely challenging. However, distinct changes in precipitation amount, some of which linked to ENSO dynamics, along with changing fire intensity and nutrient availability, have been recorded over the past millennia (Cobb *et al.*, 2003, 2013; Conroy *et al.*, 2008; Overpeck & Cole, 2010; Marlon *et al.*, 2013; McLauchlan *et al.*, 2013; Prohaska *et al.*, 2023). Comparing palaeoclimate records with fossil pollen and other fossil proxies that capture plant responses to these changes therefore holds great potential for understanding and predicting the effects of future climate change on lowland dipterocarp forests.

Here, we set out to answer three main questions: (1) How do prolonged drought conditions influence lowland dipterocarp forests; (2) how is this forest type affected by changes in fire activity over longer time scales; and (3) what is the response of lowland dipterocarp forests, and particularly its large trees, to changing nutrient availability? To address these questions, we use a range of palaeo-proxies from a 1400-yr-old laminated sedimentary sequence from Bulusan Lake in the north-eastern Luzon, Philippines (Fig. 1a–c). We generate bi-decadal pollen accumulation rates (PARs, grains $cm^{-2}\,yr^{-1}$; Davis & Deevey, 1964; Giesecke & Fontana, 2008) and use the PARs as an independent proxy of past plant abundance. Unlike the more widely used percentage pollen values, PARs of a particular pollen type that is associated with a specific plant taxon (hereafter pollen taxon) provide independent estimates of its quantity on a landscape and have therefore been widely used to reconstruct the dynamics of individual plant taxa and as well as vegetational communities over time (Bennett & Willis, 2001; Jeffers *et al.*, 2011, 2012; for more details about the analysis and interpretation of PARs, see Supporting Information Notes S1). We also generate a record of carbon isotope values of leaf wax alkanes ($\delta^{13}C_{wax}$, ‰) from the same sequence and use nC_{29} alkane $\delta^{13}C$ values (hereafter $\delta^{13}C_{wax}$ record) as an independent proxy of the vegetation cover, specifically the ratio of C_3 vegetation (trees and grasses) to C_4 vegetation (grasses; Collister *et al.*, 1994). We examine the response of individual dipterocarp forest plant taxa, including the dominant dipterocarps, and the overall forest vegetation cover, to a range of abiotic factors. These independent variables, representing climatic and nutrient variability in the Bulusan sequence, are reconstructed from three main sources: a recently generated record of hydrogen isotope values of leaf wax alkanes (δD_{wax}, ‰) as a proxy record of precipitation variability (Prohaska *et al.*, 2023); fossil macrocharcoal influx rates (particles $cm^{-2}\,yr^{-1}$) as a proxy record of local fire activity (Clark, 1988; Mooney & Tinner, 2010); and stable nitrogen isotope composition of bulk sediments ($sed\delta^{15}N$, ‰) and phosphorus concentration of bulk sediments ($sedP_{conc}$, XRF counts per second; Croudace *et al.*, 2006) as proxy records of
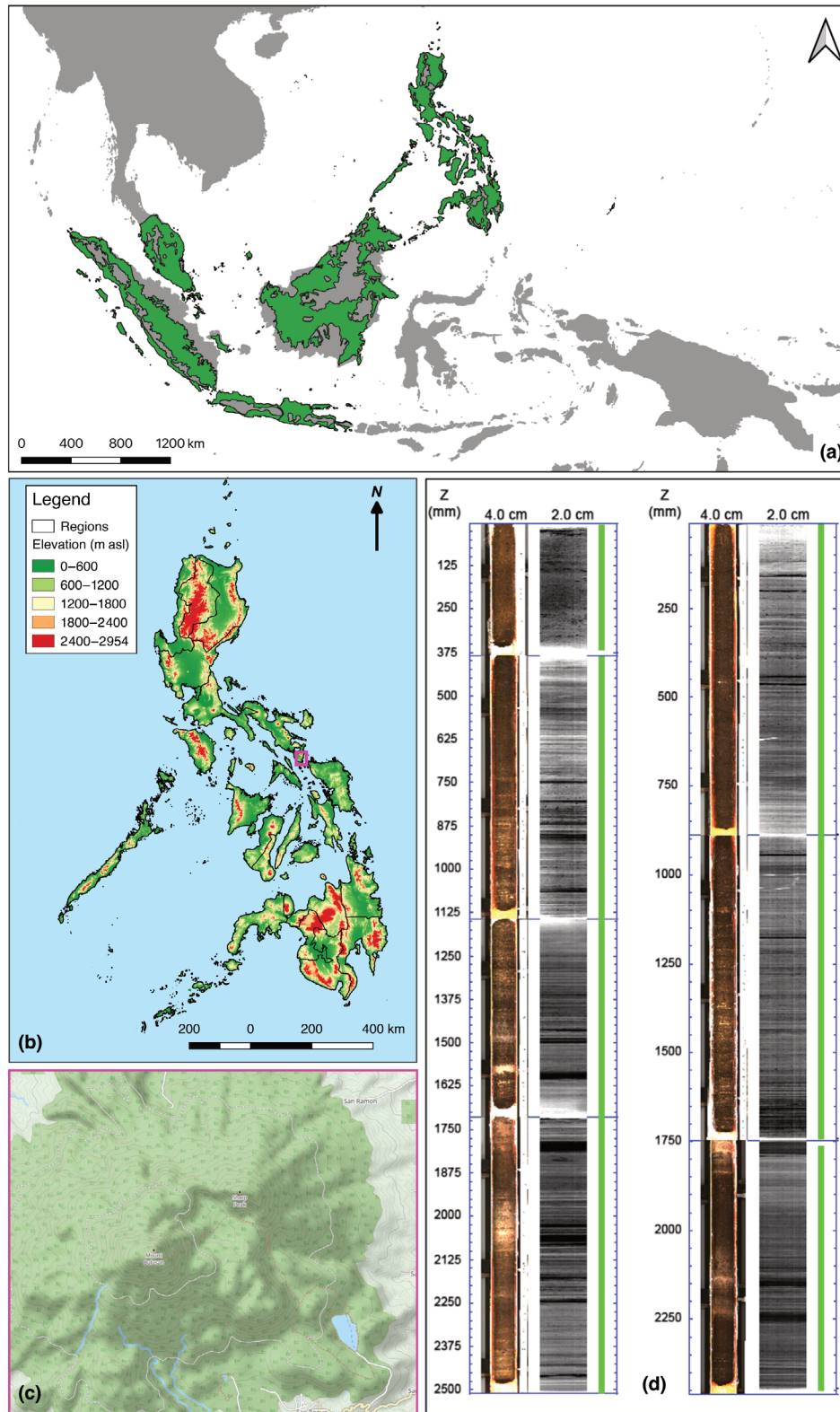
Fig. 1 Geographical location and sedimentary record from the Bulusan site. (a) Map showing the geographic distribution of lowland dipterocarp forests (shaded in green). Data from Olson *et al*. (2001), map generated in Q~GIS~ v.3.10.14 (QGIS Development Team, 2020). (b) Topographic map of the Philippines showing the location of the study site (magenta window) (Prohaska *et al*., 2023). Data from PhilGIS (2017), map generated in Q~GIS~ v.3.10.14 (QGIS Development Team, 2020). (c) Map showing Bulusan Lake (in blue) within the larger landscape, with Mt Bulusan volcano to the northwest (OpenStreetMap, 2023). (d) Optical and radiographic profiles of the two overlapping sedimentary sequences, BUL1 and BUL2, obtained from the Bulusan Lake (Prohaska *et al*., 2023). 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 were generated in the ITRAXP~LOT~ program (Croudace & Rothwell, 2015).

nitrogen and phosphorus availability, respectively. We use generalised additive models (GAMs) to examine the temporal trends in Bulusan palaeo-records and to evaluate the relationship between PARs and abiotic factors at Bulusan.

Materials and Methods

Study site

The Philippines is the world's second-largest archipelago, encompassing over 7600 islands and covering an approximate total land area of 300 000 km^2. The Philippines has a humid equatorial climate. Temperatures are generally high, averaging *c.* 27°C throughout the year. Average annual rainfall is also high, but it greatly varies geographically, decreasing from east to west. The north-eastern Luzon has a dominant rainfall season occurring during autumn and is a member of the global 'Autumn Monsoon precipitation' region (Ramesh *et al.*, 2021). ENSO is the main driver of interannual rainfall variability at Bulusan, resulting in reduced precipitation during El Niño years and increased precipitation during La Niña years (Prohaska *et al.*, 2023).

Bulusan Lake is a 0.28 km^2 lake lying at 360 m asl on the foothills of Mt Bulusan, a stratovolcano at the southeast end of the Bicol Volcanic Arc (Delfin *et al.*, 1993; Fig. 1c). The lake consists of two basins: a smaller 12 m deep round basin and a larger 24 m deep narrow basin. The two basins have no inlets or outlets and comprise a closed system fed primarily by precipitation and groundwater. The waters of Bulusan Lake are of clear, bright green colour and no floating or submerged vegetation has been recorded at the lake. The lake is part of the Bulusan Volcano National Park, a nature reserve that was first established in 1935, and where logging and hunting activities are strictly regulated (Abada Gatumbato *et al.*, 2011). Fine loamy clay with low sand content has been formed throughout the Bulusan area, which originated from andesitic rocks. Soils are generally well drained and have relatively low fertility (Abada Gatumbato *et al.*, 2011).

The lowland dipterocarp forests of the Philippine Archipelago represent a biodiversity hotspot thanks to a large number of endemic species (Merril, 1926; Myers *et al.*, 2000) and have experienced intensive logging and agricultural expansion that has removed 97% of primary forests (Liu *et al.*, 1993; Shively & Pagiola, 2004). The remaining forests are considered highly vulnerable to projected climate change (Pang *et al.*, 2021), making the Philippines one of the global priority areas for conservation efforts (Myers *et al.*, 2000).

The lowland dipterocarp forests in the eastern region of the Philippines can be described as a mixed dipterocarp forest type. However, their species richness is relatively lower compared with the forests of the same type found in western regions of Southeast Asia. The lowland dipterocarp forest surrounding Bulusan Lake is classified as Lauan Dipterocarp forest, dominated by dipterocarp tree *Shorea contorta* S. Vidal (Abada Gatumbato *et al.*, 2011). In addition to *Shorea*, other notable large tree genera in the Bulusan dipterocarp forest include dipterocarp trees *Vatica* and *Parashorea*, as well as *Pterocarpus*, *Dracontomelon*, *Agathis* and *Ficus* (Abada Gatumbato *et al.*, 2011). Genera such as *Litsea*, *Aglaia*, *Artocarpus*

and *Syzygium* dominate in the lower canopy, while *Elaeocarpus*, *Leea* and *Bischofia* are prominent subcanopy trees. Palm genera such as *Pinanga*, *Caryota*, *Areca* and locally harvested *Calamus* (rattans) are also present. Common pioneer taxa include *Macaranga*, *Trema*, *Melastoma*, *Dillenia*, *Alstonia*, Poaceae and Polypodiopsida (Woods, 1989; Davies & Ashton, 1999; Co *et al.*, 2006; Ashton & Seidler, 2014). Pioneer plants normally comprise only a small fraction of the lowland dipterocarp forest vegetation because their successful establishment is limited to gaps, which cover only *c.* 1% of total forest area (Ghazoul, 2016).

Collection and dating of lake sediments

Two overlapping sedimentary sequences, BUL1 and BUL2, were collected as 1 m cores in March 2013 from the smaller basin of Bulusan Lake with a Livingstone Piston corer from an anchored platform. The sediments were shipped to the University of Oxford and stored at 5°C. The two sedimentary sequences were used to create a continuous, undisturbed composite sequence using laminations present throughout the sequence, which were detected with high-resolution optical and radiographic imaging using an ITRAX Core Scanner (Fig. 1d). For a more detailed description of Bulusan sediments, see Methods S1 and S2. All proxy records in this study come from the two sedimentary sequences and are constrained by a high-resolution age-depth model (Fig. S1; Prohaska *et al.*, 2023) based on AMS^{14}C dates from terrestrial plant macrofossils (Table S1; see Methods S3 for details about the age-depth modelling).

Extraction and processing of fossil proxies

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 *c.* 20-yr interval according to the age-depth modelling output. Standard protocols were used for the extraction and counting of fossil pollen (Bennett & Willis, 2001), and a reference collection of pollen types from the region was generated using herbarium samples and combined with printed and online sources (e.g. Australasian Pollen and Spore Atlas Online Database (APSA Members, 2007), Pollen flora of the Philippines (Jagudilla-Bulalacao, 1997), Pollen Flora of Taiwan (Huang, 1972)). Five hundred terrestrial pollen grains were counted in each sample and identified to the lowest taxonomic level possible. PARs were calculated as the number of pollen grains deposited in 1 cm^2 of sediment per year according to the standard procedures (Stockmarr, 1971) and used to infer changes in the abundance of pollen taxa, associated with particular plant taxa, over time. For obtaining fossil macrocharcoal influx rates as a proxy of local fire activity, we calculated the total number of macrocharcoal particles (> 150 μm) deposited in 1 cm^2 of sediment per year (Clark, 1988; Mooney & Tinner, 2010).

n-Alkane palaeohydrological and palaeovegetation records

Subsampling of Bulusan sediments for the *n*-alkane analysis was identical to that for the fossil pollen analysis. For detailed

description of extraction, identification and quantification of higher leaf wax n-alkanes (nC$_{23-33}$ homologues) and the compound-specific hydrogen isotope measurement and evaluation, see Prohaska *et al.* (2023).

Compound-specific stable carbon isotope ratios of the aliphatic fraction were measured at the German Research Centre for Geosciences in Potsdam using a Thermo Fisher Delta V Plus Isotope Ratio Mass Spectrometer coupled to a Thermo Fisher TraceGC 1310 gas chromatograph (Thermo Fisher Scientific, Waltham, MA, USA). The samples were measured on a 30 m DB5-MS column with an inner diameter of 0.25 mm and a film thickness of 0.25 µm, with the following GC-temperature program: (1) temperature was held for 2 min at 70°C; (2) temperature was increased to 150°C at a rate of 15°C min^{-1}; (3) oven temperature was increased to 320°C at 5°C min^{-1}; and (4) the final temperature was held for 10 min. A standard containing nC$_{16}$ to nC$_{30}$ alkanes with known δD values (mix A6, 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 normalisation of δD values to the Vienna Standard Mean Ocean Water (VSMOW) scale. The alkane standard mix was measured with the same temperature program as the samples. Samples and standards were measured in duplicates. The mean standard deviation of all measured samples for the nC$_{23}$, nC$_{25}$, nC$_{27}$, nC$_{29}$, nC$_{31}$ and nC$_{33}$ alkanes ($n = 41–65$) was *c.* 0.3‰, 0.3‰, 0.2‰, 0.1‰, 0.1‰ and 0.3‰, respectively.

δD$_{wax}$ from lacustrine sediments has been widely used as palaeohydrological proxies over a range of geological timescales (Sachse *et al.*, 2012). Prohaska *et al.* (2023) demonstrated that δD of precipitable water (δD$_{pw}$) values in the Bulusan record are isotopically enriched, and rainfall is reduced, during El Niño years relative to La Niña years. This relationship to ENSO enables the use of Bulusan δD$_{wax}$ to make inferences about precipitation changes in the area and the associated water stress to its vegetation. Previous studies have also established that δ^{13}C$_{wax}$ values of higher plant n-alkanes reflect their carbon fixation pathway (Collister *et al.*, 1994) and can thus be used to track changes in C$_3$/C$_4$ composition of vegetation over time (e.g. Schefuss *et al.*, 2003; Castañeda *et al.*, 2009; Garcin *et al.*, 2014), particularly the widely abundant and ubiquitous nC$_{27-31}$ alkanes.

Bulk sediment nitrogen isotope composition

Bulk sediment samples from the Bulusan cores were analysed for δ^{15}N, along with percentage carbon, percentage nitrogen and δ^{13}C, at the Godwin laboratory for Palaeoclimate Research, Department of Earth Sciences, University of Cambridge. The subsampling for the nitrogen isotope analysis followed the same procedure as that for the fossil pollen analysis. The dried and homogenised samples were carefully weighed into a tin capsule (*c.* 10 mg), sealed and loaded into the autosampler. The samples were analysed using a Costech Elemental Analyser attached to a Thermo DELTA V mass spectrometer in continuous flow mode. Reference standards from IAEA in Vienna were also run at intervals throughout the sequence and these values were used to

calibrate to the international standards for ^{14}N/^{15}N (δ^{15}N air) and ^{12}C/^{13}C (δ^{13}C VPDB). Precision of analyses is ±0.5% for C and N, and better than 0.1‰ for δ^{13}C and δ^{15}N. McLauchlan *et al.* (2007) demonstrated a strong correlation between changes in nitrogen availability for trees in a catchment area, inferred from the δ^{15}N values of tree rings, and changes in the δ^{15}N of lake sediments, supporting the use of the latter as a proxy for terrestrial nitrogen availability.

Bulk sediment phosphorus concentration

We conducted a high-resolution analysis of major and trace chemical elements, including phosphorus, in the Bulusan sedimentary sequence using the ITRAX Core Scanner (Croudace *et al.*, 2006) at Aarhus University, Denmark. The cores 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 generated using a charge-coupled line camera. The count time for each measurement was 30 s to ensure that minor elements are well detected. The X-ray beam used to irradiate the cores is 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 reflects relative abundance or concentration of the element in the sediment. The relative concentration of phosphorus in bulk lake sediments (sedP$_{conc}$) can be used as a proxy of phosphorus availability in the surrounding soil (further details provided in Notes S2).

Generalised additive modelling

The temporal trends in mean and variance of the generated PARs records were estimated using GAMs following Simpson (2018). Generalised additive models can be used to estimate trends in mean and variance as smooth functions of time using automatic smoothness selection methods that objectively determine the complexity of the fitted trend (Hastie & Tibshirani, 1986, 1990; Wood, 2017). Generalised additive models are particularly powerful for analysing palaeoenvironmental time series because they allow to estimate complex, nonlinear trends and to identify time intervals of significant change. Two GAM models were applied in R v.3.6.3 (R Development Core Team, 2020) using the MGCV package v.1.8-41 (Wood, 2018): generalised additive model (gam) that accounts for heteroscedasticity and generalised additive mixed model (gamm+car(1)) that accounts for autocorrelation between temporally adjacent samples. In both GAM models, we used Tweedie distribution to limit predicted values to positive numbers. We checked whether the size of the basis expansion is sufficient by fitting a different number of basis functions (k) using gam.check function. For the gam models, we accounted for heteroscedasticity that may have arisen due to variation in sedimentation rates over time. The fitted GAM smoother was considered significant at *P*-value < 0.05. Both gamm+car(1) and gam models for individual PAR datasets were plotted with confidence intervals that were generated using the critical value from the t-distribution.

We also used GAMs to assess the effect of abiotic factors (δD_{wax}, macrocharcoal influx rates, sedimentary $\delta^{15}N$ and P_{conc}) on the abundance of pollen taxa associated with specific plant taxa (PARs) and on the composition of vegetation cover ($\delta^{13}C_{wax}$). Macrocharcoal influx rates were transformed using square root function to reduce the effect of a small number of disproportionately large values (log function not used due to many zero values). Two GAMs were applied as described above. In both GAMs, we used a Gamma distribution to limit predicted PAR values to positive numbers (Tweedie family was also attempted but the models did not converge over similar ρ values). Since the Gamma family does not support zero values, these were removed from PAR datasets before the analysis. In the macrocharcoal influx rates and sedP$_{conc}$ datasets, two points identified by preliminary analysis as strong outliers were removed before modelling. For the $\delta^{13}C_{wax}$ record, we used a Gaussian distribution. Both gam and gamm+car(1) models included the four abiotic factors as explanatory variables and were compared according to their Akaike Information Criterion (AIC) coefficients. The best 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. Explanatory variables were considered significant at the 95% level of confidence. To evaluate the impact of removing zero values from the PAR records, we also run GAMs based on the Quasi-Poisson family that showed similar results (the results are provided in Notes S3; Table S2; Fig. S2). Where a model with log link for Gamma and/or Quasi-Poisson distribution could not converge, square root (sqrt hereafter) or identity links were used instead, and the converging model with the lowest AIC value was selected.

Results

Temporal dynamics of Bulusan palaeo-records

Fire, precipitation and nutrient availability dynamics The δD_{wax} record covering the past 1400 yr shows an abrupt increase in δD_{wax} values at Bulusan c. 1630 AD sustained till c. 1900, indicative of significantly drier conditions during this time (Prohaska et al., 2023; Fig. 2a). Furthermore, our new record of fossil macrocharcoal influx rates from Bulusan site shows that this period was accompanied by increased fire activity in comparison with the more recent times, though there was a period of even higher fire activity preceding it (1400–1600 AD; Fig. 2b). Nitrogen isotopic values show limited variability over the last 1400 yr, apart from a pronounced increase at c. 1000 AD, indicating a decrease in nitrogen availability to plants at Bulusan at that time. This was followed by a modest decrease in $\delta^{15}N$ (an increase in nitrogen availability) to present-day levels from c. 1250 (Fig. 2c). By contrast, the record of sedP$_{conc}$ varied extensively at Bulusan over the same period, with notable peaks at c. 900 AD and c. 1700 AD, and troughs at c. 750 AD and c. 1200 AD (Fig. 2d).

Plant abundance dynamics based on PARs Dipterocarpaceae PARs exhibited relatively large fluctuations throughout the Bulusan record (Fig. 2h). Notably, Dipterocarpaceae PARs declined and remained low during the 1630–1900 AD period of reduced precipitation. However, the PARs also exhibited at least two comparable declines in abundance before this, specifically during 1100–1300 AD and 700–900 AD, despite relatively stable precipitation during these time periods. Furthermore, during the most intense fire period recorded in the Bulusan record, 1400–1600 AD, Dipterocarpaceae PARs were at some of their highest levels. Finally, the peaks and troughs of Dipterocarpaceae PARs correspond closely to the peaks and troughs in sedP$_{conc}$. As a result, it is difficult to discern based on the analysis of temporal trends alone the relative contribution of precipitation, fire and nutrient variability to the dynamics of Dipterocarpaceae PARs at Bulusan over the last 1400 yr.

Other pollen taxa show widely divergent PAR trends over the last 1400 yr (as shown in Fig. 2). For instance, Calamus, Pometia and Syzygium show a decrease in PAR values during the 1630–1900 AD period while Ficus and Trema show the opposite. Furthermore, Macaranga, Pometia and Syzygium show a distinct increase in PAR values during the peak in charcoal values between 1400 and 1600 AD, while the PAR values of Calamus, Caryota and Pometia closely follow the P$_{conc}$ changes over time. Finally, Ilex PARs drop significantly c. 1000 AD and remain low to present times and Polypodiopsida experience pronounced reduction in PAR values between 1000 and 1400 AD. One common theme among several pollen taxa is a pronounced change in PARs within the last couple of centuries, specifically a post-1900 AD increase in PARs of Elaeocarpus, Trema, Pinanga and Poaceae, and a post-1800 AD decrease in PARs of Calamus and Caryota. Overall, our results reveal a complex set of temporal dynamics across different plant taxa. The PARs are based on pollen counts which are shown as percentages in the pollen diagram in Fig. S3.

Vegetation cover dynamics based on $\delta^{13}C_{wax}$ Values of $\delta^{13}C$ of nC_{29} alkane in the Bulusan record range from -35.6‰ to -27.8‰. In tropical settings, C_3 (trees and shrubs) and C_4 (grasses) vegetation produces waxes with average $\delta^{13}C_{wax}$ values of -35‰ and -18‰, respectively (Garcin et al., 2014). Bulusan $\delta^{13}C_{wax}$ values are therefore well within the range of C_3 vegetation (Fig. 2t), suggesting that forest cover dominated the surrounding landscape throughout the last 1400 yr. Nevertheless, the Bulusan record also shows a marked and abrupt rise in $\delta^{13}C_{wax}$ values close to 1500 AD, which closely coincides with the peak in the fossil macrocharcoal influx rate values.

Detailed diagnostics of the best-fitted GAMs of temporal dynamics of Bulusan palaeo-records are reported in Tables S3 and S4, and statistically significant periods of change detected in the GAMs are shown in Notes S4 and Fig. S4.

Responses of Dipterocarp forest vegetation to environmental drivers

Dipterocarpaceae PARs Our results suggest that on a bi-decadal scale the changes in Dipterocarpaceae PARs are associated with both precipitation and phosphorus availability. Specifically, the best-fitted GAM model yielded a significant positive effect (P-value < 0.05) of the δD_{wax} values and sedP$_{conc}$ values on
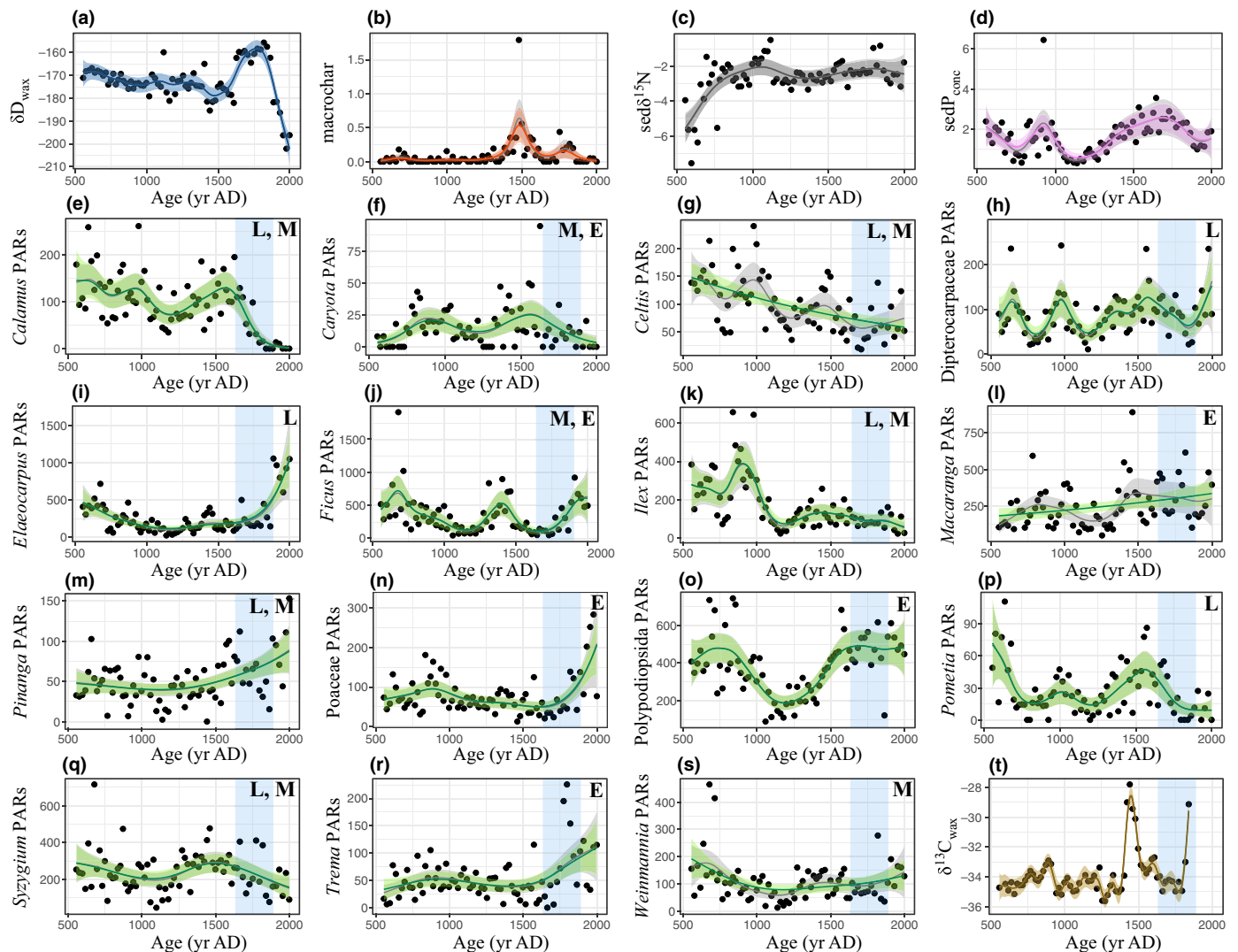
Fig. 2 Temporal trends in mean and variance for the palaeo-records from Bulusan Lake according to the best-fitted generalised additive models (GAMs). (a–d) abiotic factors, (e–s) pollen taxa, (t) vegetation cover. For the two models shown, the colour fit is the result of a GAM with a continuous-time AR(1) process estimated using Restricted Maximum Likelihood smoothness selection (gamm+car(1) ~s(Age, k), while the grey fit is that of a simple GAM with Generalised Cross-Validation-based smoothness selection (gam ~s(Age, k)). The fitted GAM smoother is overall significant (P-value < 0.05). The shaded bands around the estimated trends represent c. 95% across-the-function confidence intervals. PARs, pollen accumulation rates (grains cm^{-2} yr^{-1}); macro-char, macrocharcoal influx rates (particles m^{-2} yr^{-1}); $\delta^{13}C_{wax}$, $\delta^{13}C$ values of the nC_{29} alkane (‰); δD_{wax}, δD values of the nC_{29} alkane (‰); sed$\delta^{15}N$, $\delta^{15}N$ values of bulk sediment (‰); sedP$_{conc}$, phosphorus concentration of bulk sediment (XRF counts per second); s, smooth functions; Age, age of the samples measured as calibrated years AD; k, number of basis functions; L , late-successional taxa; M, mid-successional taxa, E, early-successional taxa. Vertical blue shading in the PAR panels represents the 1630–1900 AD period of significantly drier conditions inferred from the δD_{wax} record, (a). Data were analysed using the MGCV package v.1.8-41 (Wood, 2018) and plotted with the GGPLOT2 package v.3.4.1. (Wickham, 2016) in R v.3.6.3 (R Development Core Team, 2020).

Dipterocarpaceae PARs (Table 1; Fig. 3, detailed model outputs of the best-fitted GAMs are provided in Tables S5, S6). This suggests that on multidecadal scales the dipterocarp abundance is inversely associated with ENSO-mediated drought but positively associated with phosphorus availability.

Surprisingly, we found no evidence that Dipterocarpaceae PARs were significantly affected by the changes in fossil macro-charcoal influx rates (the best-fitted GAM yielded a nonsignificant effect (P-value > 0.05); Table 1), suggesting lack of relationship between dipterocarp abundance and fire activity. Similarly, the best-fitted GAM yielded a nonsignificant effect (P-value > 0.05) of sed$\delta^{15}N$ on Dipterocarpaceae PARs (Table 1),

consistent with the lack of relationship between nitrogen availability and dipterocarp abundance.

Other pollen taxa Other pollen taxa show a wide variety of relationships to the climatic and nutritional conditions at Bulusan (Tables 1, S2; Fig. 3). We find a significant negative relationship between the δD_{wax} and the PARs of *Elaeocarpus* and *Pinanga*, suggesting a detrimental impact of drought on the abundance of these taxa. Interestingly, *Calamus* PARs exhibit unimodal relationship to the δD_{wax}, indicating that while moderate drought conditions have a positive effect on *Calamus* abundance, the opposite is the case at more extreme drought conditions. None of

Table 1 Summary of results of the best-fitted generalised additive models (GAMs) for describing the effects of abiotic factors on plant taxa abundance and vegetation composition at Bulusan.

Plant taxa abundance and vegetation composition	Abiotic factors			
	δD_{wax}	sqrt (macrochar)	sedδ^{15}N	sedP$_{conc}$
Pollen taxa				
Calamus PARs (L, M)	VAR	•	•	POS
Caryota PARs (M, E)	•	•	•	POS
Celtis PARs (L, M)	•	•	•	•
Dipterocarpaceae PARs (L)	NEG	•	•	POS
Elaeocarpus PARs (L)	NEG	•	•	•
Ficus PARs (M, E)	•	VAR	•	•
Ilex PARs (L, M)	•	NEG	•	•
Macaranga PARs (E)	•	POS	•	•
Pinanga PARs (L, M)	NEG	•	•	POS
Poaceae PARs (E)	VAR	•	•	•
Polypodiopsida PARs (E)	•	POS	•	•
Pometia PARs (L)	•	POS	VAR	POS
Syzygium PARs (L, M)	•	POS	•	•
Trema PARs (E)	•	•	POS	•
Weinmannia PARs (M)	•	POS	•	•
Vegetation cover				
$\delta^{13}C_{wax}$	VAR	•	•	•

General model formula: PARs ~ $s(\delta D_{wax})$ + s(sqrt(macrochar)) + s(sedδ^{15}N) + s(sedP$_{conc}$), distribution family = Gamma, smoothing parameter estimation method = Restricted Maximum Likelihood (REML); and $\delta^{13}C_{wax}$ ~ $s(\delta D_{wax})$ + s(sqrt(macrochar)) + s(sedδ^{15}N) + s(sedP$_{conc}$), distribution family = Gaussian, smoothing parameter estimation method = REML. The fit is considered significant at P-value < 0.05. Data were analysed using the MGCV package v.1.8-41 (Wood, 2018). PARs, pollen accumulation rates (grains cm^{-2} yr^{-1}); macrochar, macrocharcoal influx rates (particles m^{-2} yr^{-1}); $\delta^{13}C_{wax}$, δ^{13}C values of the nC$_{29}$ alkane (‰); δD_{wax}, δD values of the nC$_{29}$ alkane (‰); sedδ^{15}N, δ^{15}N values of bulk sediment (‰); sedP$_{conc}$, phosphorus concentration of bulk sediment (XRF counts per second); s, smooth functions; L, late-successional taxa; M, mid-successional taxa; E, early-successional taxa; POS, significant positive relationship; NEG, significant negative relationship; VAR, significant varying relationship; •, no significant relationship.

the taxa exhibited an altogether positive relationship to δD_{wax}, suggesting a predominantly negative effect of drier conditions on the dipterocarp forest vegetation. Furthermore, the PARs of *Macaranga*, *Pometia*, Polypodiopsida, *Syzygium* and *Weinmannia* show a significant positive relationship (P-value < 0.05) with macrocharcoal influx rates, consistent with a significant effect of fire activity on the abundance of these taxa. While PARs of nearly all pollen taxa in the Bulusan record exhibited no significant

relationship to sedδ^{15}N, the PARs of one-third of taxa showed a positive relationship with sedP$_{conc}$ (*Calamus*, *Caryota*, *Pinanga*, *Pometia*, along with Dipterocarpaceae).

Vegetation cover based on plant leaf waxes Our results show a unimodal relationship between $\delta^{13}C_{wax}$ and δD_{wax} values (Fig. 3b), where the relationship is positive at the lower and higher ends of δD_{wax} values (wet and dry conditions) and negative at intermediate δD_{wax} values (moderate conditions). This indicates that moderate conditions had a positive effect on C$_3$ vegetation (trees and shrubs) while extremely wet and dry conditions lead to an increase in C$_4$ plants (grasses). Furthermore, we found no significant effect of fossil macrocharcoal influx rates on $\delta^{13}C_{wax}$, despite the overlap of the peaks in both records *c.* 1500 AD (Fig. 2b,t). Similarly, our results show a lack of significant relationship between nutrient availability and overall vegetation cover.

Discussion

Our results show pronounced changes in precipitation, fire activity and nutrient availability at Bulusan Lake over the last 1400 yr. We also show that responses to these changes have varied greatly across the plant taxa considered in this study, and that this variation does not seem to be strongly associated with the successional stage they inhabit (Table 1). This is in accordance with previously reported short-term observational studies (Apgaua *et al.*, 2015; Maréchaux *et al.*, 2015, 2019).

Dipterocarp trees have a low tolerance to prolonged drought conditions

We originally postulated that an increase in drought intensity and/or frequency over longer time scales will either negatively affect dipterocarps through increased mortality and reduced growth, or positively affect dipterocarps by triggering stronger/more frequent masting. Our results suggest that on multidecadal to multicentennial time scales, drought has an overall negative impact on dipterocarps, which is consistent with the first hypothesis. These results are in line with observational studies that found dipterocarp trees in aseasonal lowland dipterocarp forests to have particularly low tolerance to drought on annual time scales. For instance, Nakagawa *et al.* (2000) found that during drought events the mortality of dipterocarp tree species can increase up to 30 times, as opposed to 2–11 times for other plant families.

Fig. 3 Modelled effects of abiotic factors on plant taxa abundance and C$_3$/C$_4$ vegetation composition at Bulusan. Plots of generalised additive model (GAM) smooth functions from the best-fitted models for describing the changes in pollen accumulation rates of individual pollen taxa (proxy for plant taxa abundance) and δ^{13}C values of the nC$_{29}$ alkane (proxy for C$_3$/C$_4$ vegetation composition). General model formula: PARs ~ $s(\delta D_{wax})$ + s(sqrt (macrochar)) + s(sedδ^{15}N) + s(sedP$_{conc}$), distribution family = Gamma, smoothing parameter estimation method = Restricted Maximum Likelihood (REML); and $\delta^{13}C_{wax}$ ~ $s(\delta D_{wax})$ + s(sqrt(macrochar)) + s(sedδ^{15}N) + s(sedP$_{conc}$), distribution family = Gaussian, smoothing parameter estimation method = REML. PARs, pollen accumulation rates (grains cm^{-2} yr^{-1}); macrochar, macrocharcoal influx rates (particles m^{-2} yr^{-1}); $\delta^{13}C_{wax}$, δ^{13}C values of the nC$_{29}$ alkane (‰); δD_{wax}, δD values of the nC$_{29}$ alkane (‰); sedδ^{15}N, δ^{15}N values of bulk sediment (‰); sedP$_{conc}$, phosphorus concentration of bulk sediment (XRF counts per second); s, smooth functions. The tick marks on the x-axis are observed data points. The y-axis represents the partial effect of each variable. The dotted lines indicate the 95% confidence intervals. Asterisks denote significance levels: *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$. Data were analysed and plotted using the MGCV package v.1.8-41 (Wood, 2018) in R v.3.6.3 (R Development Core Team, 2020).
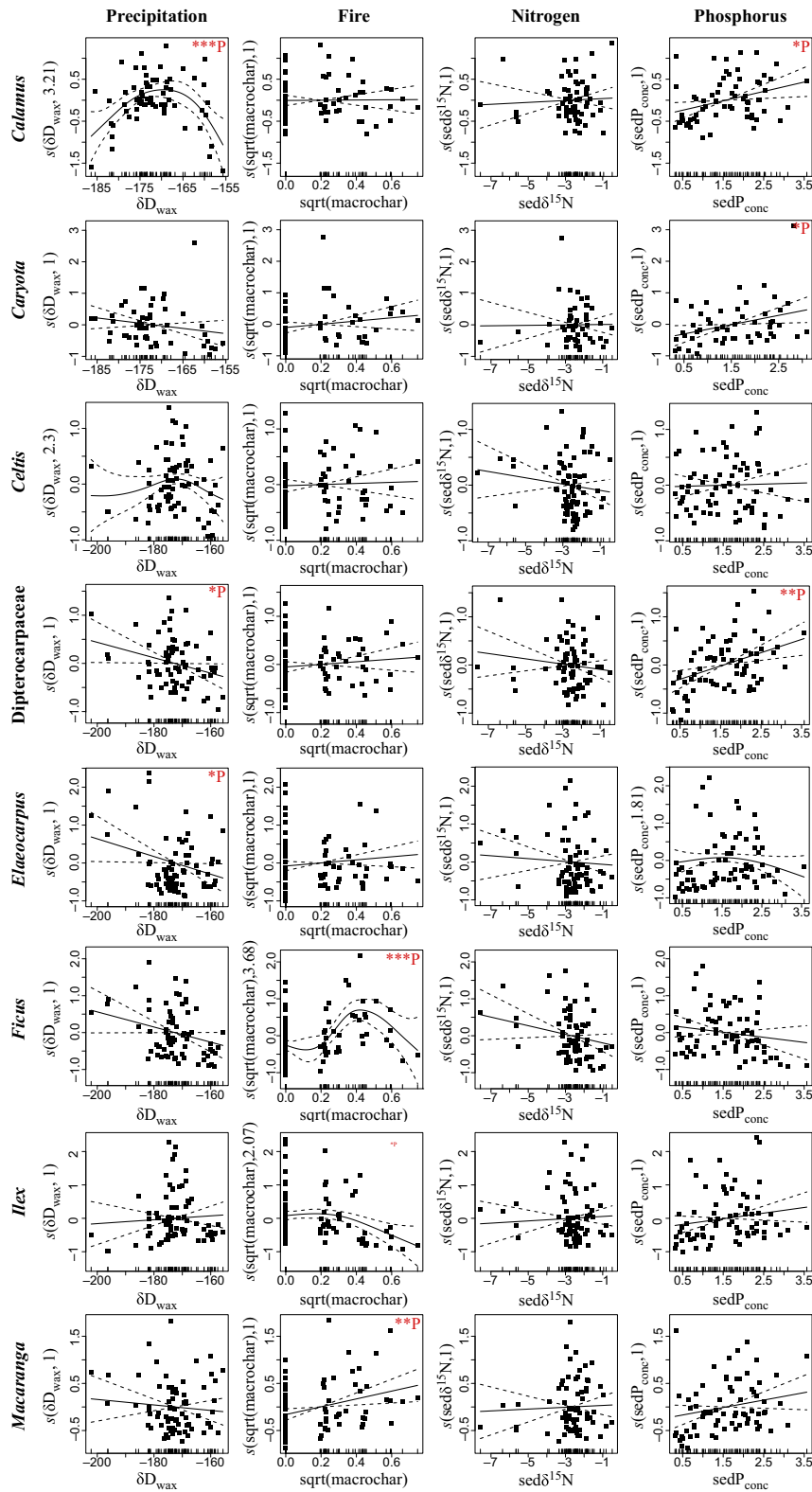
Previous research also has established a positive link between ENSO conditions and dipterocarp tree flower production; stronger El Niño drought events usually result in stronger general flowering events where the period between two mass flowering events can be as short as 2 yr (Sakai *et al.*, 2006). Furthermore, Van Der Kaars *et al.* (2009) showed that the higher frequency of El Niño events over the last 250 yr was accompanied by higher concentration of Dipterocarpaceae pollen in the marine core
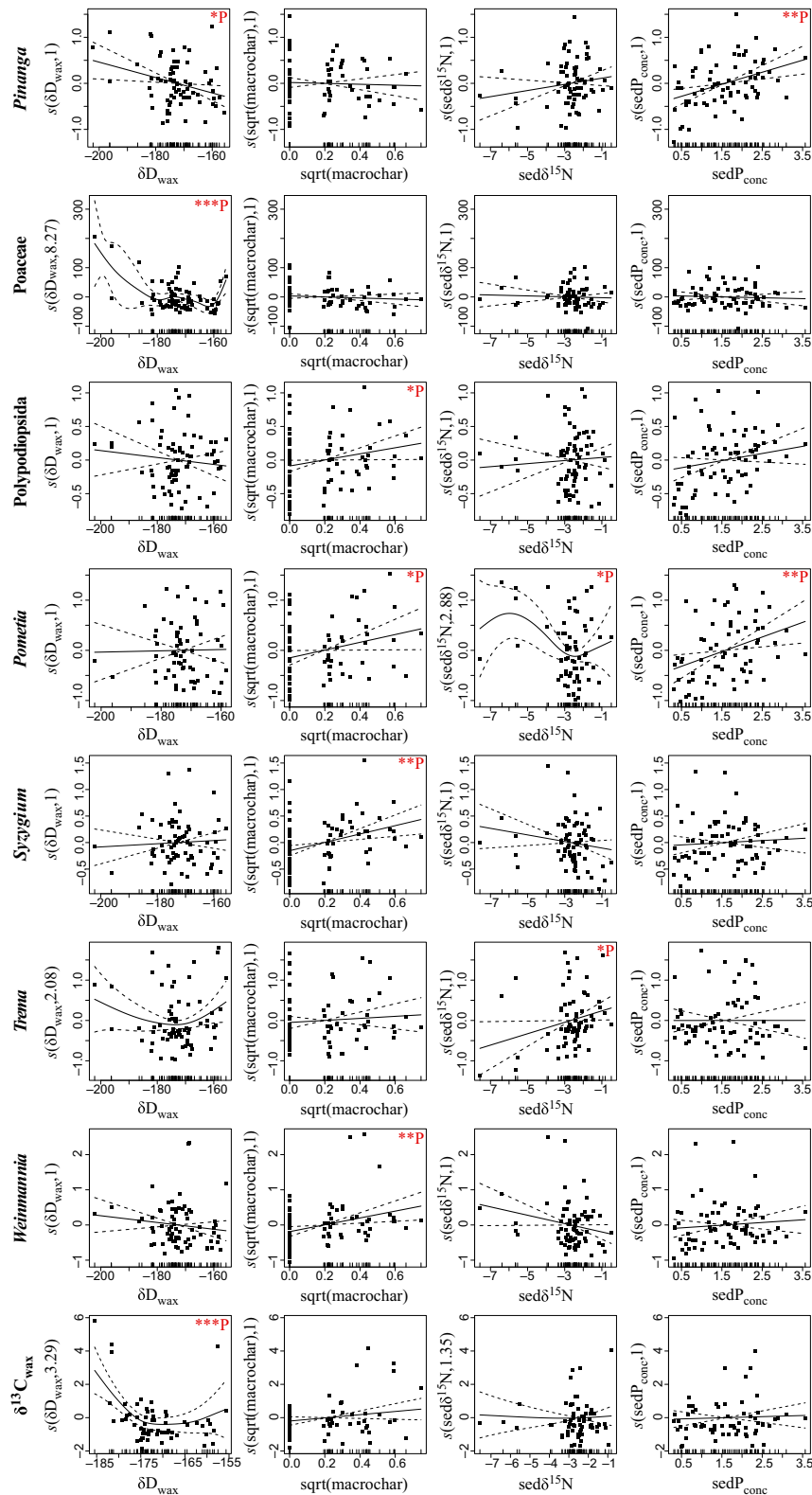
Fig. 3 (Continued)

from Kau Bay, Indonesia. However, our results indicate that any positive effects of the associated drought conditions on dipterocarp pollen production had been surpassed by their negative effects on the recruitment, growth and/or survival of dipterocarp trees. While the negative effect of extremely wet conditions may seem counterintuitive at first, it could be explained by the

dependence of dipterocarp forest reproduction on ENSO-induced drought events; low frequency of such events may have led to reduced reproduction of mass flowering tree taxa, which in long-term translated to reduced abundance of those taxa, and hence a relatively higher proportion of grasses (though still a low proportion considering $\delta^{13}C_{wax}$ values in the Bulusan record never approach the values characteristic of vegetation cover dominated by C_4 plants). Nevertheless, the positive relationship between $\delta^{13}C_{wax}$ and δD_{wax} at the high end of δD_{wax} values highlights the negative effect of more dry conditions on dipterocarp forest vegetation, possibly through an increased tree mortality and subsequent opening of the canopy that favours establishment of grasses.

Limited fire activity has a positive influence on dipterocarp forest plant taxa

Our results suggest a lack of relationship between fire activity and dipterocarp abundance. This indicates that the mechanisms which led to the (mass) flowering of Dipterocarp trees were uninhibited during the periods when fire activity was higher. Most dipterocarp species belong to the largest tree category (i.e. > 80 cm dbh) and observation studies suggested that such large trees are rarely affected by fire (Van Nieuwstadt & Sheil, 2005). Our results support this understanding.

The apparent positive effect of fire activity on pioneers such as *Macaranga*, *Weinmannia* and Polypodiopsida at our site is in accordance with a number of observational studies which have reported positive effects of fire on the establishment and growth of pioneer plants (Whitmore, 1988; Woods, 1989; Schulte & Schöne, 1996). One explanation of this relationship is that 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 & Seidler, 2014). On the contrary, the surprising lack of negative relationship between PARs and fossil macrocharcoal influx rates among other plant taxa at Bulusan (with the exception of *Ilex*) may be partly explained by a limited fire activity at Bulusan Lake and its wider area, as suggested by the relatively low macrocharcoal and microcharcoal counts, respectively (Fig. S5; Notes S5; Methods S4). Consequently, fire events at Bulusan may have not been severe enough to stifle growth and reproduction of plant taxa with a low tolerance to fire.

The lack of a significant effect of macrocharcoal influx rates on $\delta^{13}C_{wax}$, suggesting limited influence of fire activity on dipterocarp forest vegetation cover, can be explained by the generally low macrocharcoal influx rates, along with generally low $\delta^{13}C_{wax}$ values, at Bulusan over the last 1400 yr (apart from the 1500 AD event), suggestive of a low fire activity in the area and the dominance of C_3 (tree) cover.

Phosphorus is a limiting nutrient for Dipterocarp trees on decadal time scales

Our results show a positive relationship between phosphorus and several plant taxa in dipterocarp forest, including the dominant

Dipterocarpaceae family. Banin *et al.* (2014) found that dipterocarp trees gain woody biomass faster than otherwise equivalent, neighbouring nondipterocarp trees, demonstrating that dipterocarp growth is an important contributor to the overall woody biomass production in a lowland dipterocarp forests (Paoli *et al.*, 2008). Though experimental work suggests that the effect of phosphorus availability on the rate of woody biomass increase in dipterocarp trees is relatively small on an annual scale (Mirmanto *et al.*, 1999), it is possible that this effect compounds on multidecadal scales, especially for large trees. For instance, observational studies of biomass production in dipterocarp forest 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 (Paoli *et al.*, 2005, 2008; Paoli & Curran, 2007).

On the contrary, the positive relationship between Dipterocarpaceae PARs and sedP_{conc} 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. Ichie *et al.* (2005a,b) showed the high phosphorus cost of mass flowering and subsequent mast fruiting for dipterocarp species (Ichie *et al.*, 2005a,b; Ichie & Nakagawa, 2013). Therefore, accumulation of phosphorus has been put forward as a potentially decisive factor in the magnitude and frequency of dipterocarp reproduction events on the prevailingly nutrient poor soils of Southeast Asia (Ichie & Nakagawa, 2013). Given this evidence, decreasing phosphorus availability at the Bulusan site could have potentially decreased the frequency and/or magnitude of mass flowering in dipterocarp trees, resulting in lower production rates of their pollen. Since dipterocarp pollen production rates may be dependent not only on the tree abundance, but also on climatically mediated flowering rates, future research would benefit from using independent proxies for dipterocarp tree abundance, such ancient DNA or taxa specific biomarkers, to separate the two signals.

The lack of significant relationship between sedP_{conc} and overall tree cover ($\delta^{13}C_{wax}$) suggests a portion of the plant taxa in lowland dipterocarp forests may not be influenced by phosphorus availability. Nevertheless, a positive relationship between PARs and sedP_{conc} in one-third of plant taxa considered in this study (*Calamus*, *Caryota*, *Pinanga*, *Pometia*, along with Dipterocarpaceae) provides further support to phosphorus being a major limiting nutrient for plant taxa in lowland dipterocarp forests and its aboveground biomass production.

Among the various factors that can influence phosphorus variability in lake sediments, the distinct features of Bulusan Lake and its surrounding area, along with the geochemical and isotopic composition of the Bulusan sediment sequence (Methods S5; Notes S2; Figs S6–S8), suggest that the primary cause behind the observed fluctuations is the solubility of phosphorus resulting from the acidification of soil through volcanic ash deposition. The active Mt Bulusan volcano, located *c.* 4 km from the lake, has historically experienced frequent eruptions of acidic silica-rich ash. These volcanic ashes can lower soil pH and reduce the

solubility of various forms of phosphorus, including phosphates. We postulate that during periods of volcanic ash deposition in the Bulusan region, the pH of the surrounding soils had decreased, resulting in decreased solubility of phosphates and their reduced availability for plants, as well as reduced transport of phosphates via rainfall to the lake.

Impacts of recent human activities on dipterocarp forests at Bulusan

While our study did not directly consider the impact of historical human activities, we note a pronounced post-1900 AD increase in PARs of *Elaeocarpus*, *Trema*, *Pinanga* and Poaceae that coincides with the onset of more intense anthropogenic activities in the area, including moderate logging and charcoal-making, in the areas surrounding the Bulusan Lake (Abada Gatumbato *et al.*, 2011). While land-use change leading to a more open environment is a possible explanation to the recent PAR changes in these predominantly pioneer taxa, it is not included directly in our analysis due to lack of independent records for these activities. Interestingly, these activities appear not to have had a notable effect on dipterocarp abundance, as their PARs continue an upward trajectory, suggesting that the logging and clearing activities may not have removed a large number of mature dipterocarp trees. An alternative hypothesis, mutually nonexclusive to the previous hypothesis, is that the flowering rates of dipterocarps has increased, possibly in response to an increased frequency of extreme El Niño events (Gergis & Fowler, 2009; Wang *et al.*, 2019). Similarly, the post-1800 AD decrease in PARs of *Calamus* and *Caryota* may be at least partially linked to anthropogenic activities, that is harvesting for materials and food that have been documented in this area (Abada Gatumbato *et al.*, 2011). Further indirect support for an effect of recent anthropogenic activities on dipterocarp forest vegetation at Bulusan comes from the $\delta^{13}C_{wax}$ record also shows a marked and abrupt rise in values post-1800 AD, suggesting an increase in the proportion of C_4 vegetation to C_3 vegetation. Relatively low macrocharcoal rates post-1800 suggest fire activity is unlikely to be behind these vegetation changes. This is in contrast to the 1500 AD peak in $\delta^{13}C_{wax}$, which closely coincides with the peak in the fossil macrocharcoal influx rates values. The peak in the macrocharcoal influx rates *c.* 1500 AD is not accompanied by a peak in the microcharcol influx rates, suggesting this was primarily a local fire event, such as those caused by human activities. However, lack of additional charcoal records from nearby areas hinders investigation into spatial and temporal autocorrelation of fire activity in the broader landscape. Since the information of the types, extent and severity of human activities in the Bulusan area is sparse, further data are needed to test these hypotheses and determine the origins of recent changes in vegetation cover.

Implications for conservation and management

Our findings have implications for the conservation and management of lowland dipterocarp forests under future climate change.

Projected drought risk in 1.5°C and 2°C warmer climate scenarios show robust drying in the mean state across many regions by the end of the 21st century, including Southeast Asia (Lehner *et al.*, 2017; Cook *et al.*, 2020). Our results suggest that a stronger drought regime could have profound impacts on the composition, structure and functioning of lowland dipterocarp forests, primarily through a negative impact on the abundance of dipterocarp trees. As giant, old-growth trees with a very complex canopy, and wide base forming an extensive buttressing, dipterocarp trees embody the concept of tropical mega-trees (Pinho *et al.*, 2020). Recent studies highlighted the unique ecological roles of mega-trees such as building the emergent forest layer, providing unique microhabitats inside their canopy and acting as a key source of food and nesting sites. Furthermore, tropical mega-trees are disproportionately large contributors to forest productivity, aboveground biomass and carbon stocks (Slik *et al.*, 2013; Stephenson *et al.*, 2014; Lutz *et al.*, 2018). The importance of dipterocarp trees for the ecological integrity of lowland dipterocarp forests is further amplified through their biomass dominance (Appanah, 1985; Paoli *et al.*, 2008) and mass flowering behaviour (Burgess, 1972; Cockburn, 1975; Appanah, 1985; Sakai *et al.*, 1999), which profoundly shape pollination and food production patterns in these forests. While it has been hypothesised that a stronger drought regime may also increase the frequency and strength of mass flowering, our results suggest that a positive effect of drought is unlikely to offset its negative impacts, for example increased tree mortality. Given the vulnerability of dipterocarp trees to severe drought, and the projected increase in the frequency and intensity of drought in their geographic range (Amnuaylojaroen & Chanvichit, 2019; Pörtner *et al.*, 2022), along with endangered status of most dipterocarp species (Bartholomew *et al.*, 2021), ensuring sustainable land-use practices in the remaining dipterocarp forest is paramount to their long-term survival. This is particularly true for the Philippine dipterocarp forests which have been reduced to only 3% of their historical range, and mostly consist of small and isolated fragments (Heaney & Regalado, 1998; Tumaneng-Diete *et al.*, 2005).

The last few decades have also seen a marked increase in the frequency and magnitude of fire events in dipterocap forests (Salafsky, 1994, 1998; Folkins *et al.*, 1997; Siegert *et al.*, 2001; Huijnen *et al.*, 2016). The observed trend has been linked to the compounding effects of more severe El Niño events (van der Werf *et al.*, 2004; Wooster *et al.*, 2012; Chen *et al.*, 2017; Nurdiati *et al.*, 2022) and anthropogenic activities such as forest fragmentation and degradation (Curran *et al.*, 1999; Chapman *et al.*, 2020). Therefore, it is highly likely that a future intensification of ENSO coupled with anthropogenic activities will result in heightened fire activity in the region. Our study suggests that the dipterocarp forest at Bulusan experienced limited fire activity over the last 1400 yr and that none of the considered plant taxa have been negatively affected by it. Notably, the single period of markedly higher fire activity in the Bulusan record *c.* 1500 AD covering a period of *c.* 200 yr closely overlaps with a significant increase in the C_4 vegetation, suggesting that increased fire activity may favour increase in grass cover.

Furthermore, our results show that fire activity has a positive influence on several pioneer taxa at Bulusan on multidecadal scales. Hence, our results concur with observational studies (Whitmore, 1988; Ghazoul, 2016) which found that periods of higher fire activity lead to larger prevalence of plant pioneers in forest floor gaps created by burning, increased canopy openness and a reduced aboveground biomass, and suggest such changes can persist over longer time scales. Given the long-term negative effects that severe drought and fire may have on lowland dipterocarp forests, strategies for minimising fire occurrence and magnitude, particularly during droughts, should be prioritised to prevent further degradation of these globally important forests.

Our understanding of the nutrient cycles that underlie the productivity of tropical rainforests world-wide remains limited. The prevalent view of primary tropical rainforests is that they inhabit infertile soils, where most of the nutrients are tied in the living matter, and their high production relies on fast and efficient nutrient cycling (Cleveland et al., 2011). However, our study shows that the availability of key limiting nutrients, namely phosphorus, to tropical forest plants can vary considerably on multidecadal to centennial scales (in line with studies on nitrogen availability in higher latitudes; e.g. Jeffers et al., 2011, 2012; McLauchlan et al., 2017) and that this variation affects various plant taxa including dipterocarp trees, thus possibly playing a key role in shaping the productivity of lowland dipterocarp forests. This finding raises important questions for the conservation and management of lowland dipterocarp forests that can be further tested with palaeoecological data. For instance, if phosphorus availability has a significant positive influence on the growth and/ or reproduction of large tropical trees, then all else being equal, are tropical rainforests growing on more fertile soils more resilient to drought and other environmental perturbations on longer time scales? Our study is the first to link changes in pollen accumulation rates to the changes in availability of phosphorus on a scale of hundreds to thousands of years, demonstrating the suitability of palaeo-records for studying the long-term effects of nutrient limitation on the tropical rainforest biome in tandem to the long-term effect of climate change. This knowledge could vastly improve current models of global climate-vegetation dynamics under warming scenarios given the central role of the tropical rainforest biome in regulating Earth's climate and biogeochemical cycles (Brown & Lugo, 1982; Melillo et al., 1993; Cleveland et al., 1999; Bonan, 2008; Fleischer et al., 2019).

Acknowledgements

Competing interests

None declared.

Author contributions

AP initiated and designed the study and conducted the fieldwork. AP planned the sampling scheme and headed the generation and analysis of data with assistance from AWRS, AS, OR and DS. AP, KJW and DS acquired financial support. All authors participated in interpreting the results and writing the manuscript, with AP taking the lead.

ORCID

Ana Prohaska https://orcid.org/0000-0001-5459-6186
Oliver Rach https://orcid.org/0000-0003-3547-2182
Dirk Sachse https://orcid.org/0000-0003-4207-0309
Alistair W. R. Seddon https://orcid.org/0000-0002-8266-0947
Andrew Smith https://orcid.org/0000-0002-7658-6234
Katherine J. Willis https://orcid.org/0000-0002-6763-2489

Data availability

All data needed to appraise the conclusions in the paper are given in the Main Text and the Supporting Information. Pollen and charcoal counts, and isotopic and ITRAX measurements are available at: https://doi.org/10.5061/dryad.2ngf1vhst.

References

Abada Gatumbato E, Carandang W, Pampolina N, Mallar NA, Narvadez S. 2011. *Final report: physical and geopolitical characteristics, biological resources, socio-cultural and economics conditions and institutional arrangements/governance of the Bulusan Volcano Natural Park*. Quezon City, Philippines: Resources, Environment and Economics Center for Studies.

Alvarez-Clare S, Mack MC, Brooks M. 2013. A direct test of nitrogen and phosphorus limitation to net primary productivity in a lowland tropical wet forest. *Ecology* 94: 1540–1551.

Amnuaylojaroen T, Chanvichit P. 2019. Projection of near-future climate change and agricultural drought in Mainland Southeast Asia under RCP8.5. *Climatic Change* 155: 175–193.

Apgaua DMG, Ishida FY, Tng DYP, Laidlaw MJ, Santos RM, Rumman R, Eamus D, Holtum JAM, Laurance SGW. 2015. Functional traits and water transport strategies in lowland tropical rainforest trees. *PLoS ONE* **10**: e0130799.

Appanah S. 1985. General flowering in the climax rain forests of south-east Asia. *Journal of Tropical Ecology* **1**: 225–240.

APSA Members. 2007. *The Australasian pollen and spore atlas v.1.0.* Canberra, Australia: Australian National University. [WWW document] URL http://apsa.anu.edu.au/ [accessed 5 October 2013].

Ashton PS, Givnish TJ, Appanah S. 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *The American Naturalist* **132**: 44–66.

Ashton PS, Seidler R. 2014. *On the forests of tropical Asia: lest the memory fade.* Richmond, UK: Royal Botanic Gardens Kew.

Baltzer JL, Davies SJ, Bunyavejchewin S, Noor NSM. 2008. The role of desiccation tolerance in determining tree species distributions along the Malay–Thai Peninsula. *Functional Ecology* **22**: 221–231.

Banin L, Lewis SL, Lopez-Gonzalez G, Baker TR, Quesada CA, Chao K-J, Burslem DFR, Nilus R, Salim KA, Keeling HC et al. 2014. Tropical forest wood production: a cross-continental comparison. *Journal of Ecology* **102**: 1025–1037.

Bartholomew D, Barstow M, Randi A, Cicuzza D, Hoo PK, Juiling S, Khoo E, Kusumadewi Y, Majapaum R, Maryani AM et al. 2021. *The Red List of Bornean endemic dipterocarps.* Richmond, UK: BGCI.

Bennett KD, Willis KJ. 2001. Pollen. In: Small JP, Birks HJB, Last WM, Bradely RS, Alverson K, eds. *Developments in paleoenvironmental research. Tracking environmental change using lake sediments, vol. 3.* Dordrecht, the Netherlands: Springer, 5–32.

Boisvenue C, Running SW. 2006. Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. *Global Change Biology* **12**: 862–882.

Bonan GB. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* **320**: 1444–1449.

Bonan GB, Levis S. 2010. Quantifying carbon-nitrogen feedbacks in the Community Land Model (CLM4). *Geophysical Research Letters* **37**: L07401.

Brown S, Lugo AE. 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. *Biotropica* **14**: 161–187.

Burgess PF. 1972. Studies on the regeneration of the hill forests of the Malay Peninsula: the phenology of Dipterocarps. *Malaysian Forester* **35**: 103–123.

Burslem DFRP, Grubb PJ, Turner IM. 1996. Responses to simulated drought and elevated nutrient supply among shade-tolerant tree seedlings of lowland tropical forest in Singapore. *Biotropica* **28**: 636–648.

Castañeda IS, Mulitza S, Schefuss E, Lopes dos Santos RA, Sinninghe Damsté JS, Schouten S. 2009. Wet phases in the Sahara/Sahel region and human migration patterns in North Africa. *Proceedings of the National Academy of Sciences, USA* **106**: 20159–20163.

Chapman S, Syktus J, Trancoso R, Salazar A, Thatcher M, Watson JEM, Meijaard E, Sheil D, Dargusch P, McAlpine CA. 2020. Compounding impact of deforestation on Borneo's climate during El Niño events. *Environmental Research Letters* **15**: 084006.

Chen Y, Morton DC, Andela N, van der Werf GR, Giglio L, Randerson JT. 2017. A pan-tropical cascade of fire driven by El Niño/Southern Oscillation. *Nature Climate Change* **7**: 906–911.

Clark JS. 1988. Particle motion and the theory of charcoal analysis: source area, transport, deposition, and sampling. *Quaternary Research* **30**: 67–80.

Cleveland CC, Townsend AR, Schimel DS, Fisher H, Howarth RW, Hedin LO, Perakis SS, Latty EF, Von Fischer JC, Elseroad A et al. 1999. Global patterns of terrestrial biological nitrogen (N₂) fixation in natural ecosystems. *Global Biogeochemical Cycles* **13**: 623–645.

Cleveland CC, Townsend AR, Taylor P, Alvarez-Clare S, Bustamante MMC, Chuyong G, Dobrowski SZ, Grierson P, Harms KE, Houlton BZ et al. 2011. Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis. *Ecology Letters* **14**: 939–947.

Co LL, LaFrankie J, Lagunzad D, Pasion K, Consunji H, Bartolome N, Yap S, Tongco M, Ferreras U, Davies S et al. 2006. *Forest trees of Palanan, Philippines: a study in population ecology.* Diliman, Philippines: Center for Integrative and Development Studies, University of the Philippines.

Cobb KM, Charles CD, Cheng H, Edwards RL. 2003. El Niño/Southern Oscillation and tropical Pacific climate during the last millennium. *Nature* **424**: 271–276.

Cobb KM, Westphal N, Sayani HR, Watson JT, Di Lorenzo E, Cheng H, Edwards RL, Charles CD. 2013. Highly variable El Niño–Southern Oscillation throughout the Holocene. *Science* **339**: 67–70.

Cockburn PF. 1975. Phenology of dipterocarps in Sabah. *Malaysian Forester* **38**: 160–170.

Collister JW, Rieley G, Stern B, Eglinton G, Fry B. 1994. Compound-specific δ¹³C analyses of leaf lipids from plants with differing carbon dioxide metabolisms. *Organic Geochemistry* **21**: 619–627.

Conroy JL, Overpeck JT, Cole JE, Shanahan TM, Steinitz-Kannan M. 2008. Holocene changes in eastern tropical Pacific climate inferred from a Galápagos lake sediment record. *Quaternary Science Reviews* **27**: 1166–1180.

Cook BI, Mankin JS, Marvel K, Williams AP, Smerdon JE, Anchukaitis KJ. 2020. Twenty-first century drought projections in the CMIP6 forcing scenarios. *Earth's Future* **8**: e2019EF001461.

Croudace IW, Rindby A, Rothwell RG. 2006. ITRAX: description and evaluation of a new multi-function X-ray core scanner. *Geological Society, London, Special Publications* **267**: 51–63.

Croudace IW, Rothwell RG. 2015. Micro-XRF studies of sediment cores: applications of a non-destructive tool for the environmental sciences. In: Croudace IW, Rothwell RG, eds. *Developments in paleoenvironmental research, vol. 17.* Dordrecht, the Netherlands: Springer, 25–102.

Cunha HFV, Andersen KM, Lugli LF, Santana FD, Aleixo IF, Moraes AM, Garcia S, Di Ponzio R, Mendoza EO, Brum B et al. 2022. Direct evidence for phosphorus limitation on Amazon forest productivity. *Nature* **608**: 558–562.

Curran LM, Caniago II, Paoli GD, Astianti D, Kusneti M, Leighton M, Nirarita CE, Haeruman H. 1999. Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science* **286**: 2184–2188.

Davidson EA, de Carvalho CJR, Vieira ICG, Figueiredo RO, Moutinho P, Ishida FY, dos Santos MTP, Guerrero JB, Kalif K, Sabá RT. 2004. Nitrogen and phosphorus limitation of biomass growth in a tropical secondary forest. *Ecological Applications* **14**: 150–163.

Davies SJ, Ashton PS. 1999. Phenology and fecundity in 11 sympatric pioneer species of Macaranga (Euphorbiaceae) in Borneo. *American Journal of Botany* **86**: 1786–1795.

Davis MB, Deevey ES Jr. 1964. Pollen accumulation rates: estimates from late-glacial sediment of Rogers Lake. *Science* **145**: 1293–1295.

Delfin FG, Panem CC, Defant MJ. 1993. Eruptive history and petrochemistry of the Bulusan volcanic complex: implications for the hydrothermal system and volcanic hazards of Mt. Bulusan, Philippines. *Geothermics* **22**: 417–434.

Fleischer K, Rammig A, De Kauwe MG, Walker AP, Domingues TF, Fuchslueger L, Garcia S, Goll DS, Grandis A, Jiang M et al. 2019. Amazon forest response to CO₂ fertilization dependent on plant phosphorus acquisition. *Nature Geoscience* **12**: 736–741.

Folkins I, Chatfield R, Baumgardner D, Proffitt M. 1997. Biomass burning and deep convection in southeastern Asia: results from ASHOE/MAESA. *Journal of Geophysical Research: Atmospheres* **102**: 13291–13299.

Fyllas NM, Patiño S, Baker TR, Bielefeld Nardoto G, Martinelli LA, Quesada CA, Paiva R, Schwarz M, Horna V, Mercado LM et al. 2009. Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate. *Biogeosciences* **6**: 2677–2708.

Galloway JN, Dentener FJ, Capone DG, Boyer EW, Howarth RW, Seitzinger SP, Asner GP, Cleveland CC, Green PA, Holland EA et al. 2004. Nitrogen cycles: past, present, and future. *Biogeochemistry* **70**: 153–226.

Garcin Y, Schefuß E, Schwab VF, Garreta V, Gleixner G, Vincens A, Todou G, Séné O, Onana J-M, Achoundong G et al. 2014. Reconstructing C₃ and C₄ vegetation cover using n-alkane carbon isotope ratios in recent lake sediments from Cameroon, Western Central Africa. *Geochimica et Cosmochimica Acta* **142**: 482–500.

Gergis JL, Fowler AM. 2009. A history of ENSO events since A.D. 1525: implications for future climate change. *Climatic Change* **92**: 343–387.

Ghazoul J. 2016. *Dipterocarp biology, ecology, and conservation.* Oxford, UK: Oxford University Press.

Ghazoul J, Sheil D. 2010. *Tropical rain forest ecology, diversity, and conservation.* Oxford, UK: Oxford University Press.

Giesecke T, Fontana SL. 2008. Revisiting pollen accumulation rates from Swedish lake sediments. *Holocene* **18**: 293–305.

Gunatilleke CVS, Gunatilleke IAUN, Perera GAD, Burslem DFRP, Ashton PMS. 1997. Responses to nutrient addition among seedlings of eight closely related species of *Shorea* in Sri Lanka. *Journal of Ecology* **85**: 301–311.

Hastie T, Tibshirani R. 1986. Generalized additive models. *Statistical Science* **1**: 297–310.

Hastie TJ, Tibshirani RJ. 1990. *Generalised additive models*. Boca Raton, FL, USA: Chapman & Hall/CRC.

Heaney LR, Regalado JC. 1998. *Vanishing treasures of the Philippine rain forest*. Chicago, IL, USA: The Field Museum.

Hou E, Chen C, Luo Y, Zhou G, Kuang Y, Zhang Y, Heenan M, Lu X, Wen D. 2018. Effects of climate on soil phosphorus cycle and availability in natural terrestrial ecosystems. *Global Change Biology* **24**: 3344–3356.

Huang T-C. 1972. *Pollen flora of Taiwan*. Taipei, Taiwan: National Taiwan University, Botany Department Press.

Huijnen V, Wooster MJ, Kaiser JW, Gaveau DLA, Flemming J, Parrington M, Inness A, Murdiyarso D, Main B, van Weele M. 2016. Fire carbon emissions over maritime southeast Asia in 2015 largest since 1997. *Scientific Reports* **6**: 26886.

Huntingford C, Zelazowski P, Galbraith D, Mercado LM, Sitch S, Fisher R, Lomas M, Walker AP, Jones CD, Booth BBB et al. 2013. Simulated resilience of tropical rainforests to CO_2-induced climate change. *Nature Geoscience* **6**: 268–273.

Ichie T, Kenta T, Nakagawa M, Sato K, Nakashizuka T. 2005a. Resource allocation to reproductive organs during masting in the tropical emergent tree, *Dipterocarpus tempehes*. *Journal of Tropical Ecology* **21**: 237–241.

Ichie T, Kenzo T, Kitahashi Y, Koike T, Nakashizuka T. 2005b. How does *Dryobalanops aromatica* supply carbohydrate resources for reproduction in a masting year? *Trees* **19**: 704–711.

Ichie T, Nakagawa M. 2013. Dynamics of mineral nutrient storage for mast reproduction in the tropical emergent tree *Dryobalanops aromatica*. *Ecological Research* **28**: 151–158.

Jagudilla-Bulalacao L. 1997. *Pollen flora of the Philippines*. Manila, Philippines: National Museum, Philippines and National Research Council of the Philippines – Department of Science and Technology TAPI-SPU, RFG Casa Imprenta.

Jeffers ES, Bonsall MB, Brooks SJ, Willis KJ. 2011. Abrupt environmental changes drive shifts in tree–grass interaction outcomes. *Journal of Ecology* **99**: 1063–1070.

Jeffers ES, Bonsall MB, Watson JE, Willis KJ. 2012. Climate change impacts on ecosystem functioning: evidence from an *Empetrum* heathland. *New Phytologist* **193**: 150–164.

Jenny H. 1950. Causes of the high nitrogen and organic matter content of certain tropical forest soils. *Soil Science* **69**: 63.

Lawrence D. 2003. The response of tropical tree seedlings to nutrient supply: meta-analysis for understanding a changing tropical landscape. *Journal of Tropical Ecology* **19**: 239–250.

Lehner F, Coats S, Stocker TF, Pendergrass AG, Sanderson BM, Raible CC, Smerdon JE. 2017. Projected drought risk in 1.5°C and 2°C warmer climates. *Geophysical Research Letters* **44**: 7419–7428.

Liu DS, Iverson LR, Brown S. 1993. Rates and patterns of deforestation in the Philippines: application of geographic information system analysis. *Forest Ecology and Management* **57**: 1–16.

Lutz JA, Furniss TJ, Johnson DJ, Davies SJ, Allen D, Alonso A, Anderson-Teixeira KJ, Andrade A, Baltzer J, Becker KML et al. 2018. Global importance of large-diameter trees. *Global Ecology and Biogeography: A Journal of Macroecology* **27**: 849–864.

Maréchaux I, Bartlett MK, Sack L, Baraloto C, Engel J, Joetzjer E, Chave J. 2015. Drought tolerance as predicted by leaf water potential at turgor loss point varies strongly across species within an Amazonian forest. *Functional Ecology* **29**: 1268–1277.

Maréchaux I, Saint-André L, Bartlett MK, Sack L, Chave J. 2019. Leaf drought tolerance cannot be inferred from classic leaf traits in a tropical rainforest. *Journal of Ecology* **108**: 1030–1045.

Marlon JR, Bartlein PJ, Daniau A-L, Harrison SP, Maezumi SY, Power MJ, Tinner W, Vanniére B. 2013. Global biomass burning: a synthesis and review of Holocene paleofire records and their controls. *Quaternary Science Reviews* **65**: 5–25.

McLauchlan KK, Craine JM, Oswald WW, Leavitt PR, Likens GE. 2007. Changes in nitrogen cycling during the past century in a northern hardwood forest. *Proceedings of the National Academy of Sciences, USA* **104**: 7466–7470.

McLauchlan KK, Gerhart LM, Battles JJ, Craine JM, Elmore AJ, Higuera PE, Mack MC, McNeil BE, Nelson DM, Pederson N et al. 2017. Centennial-scale reductions in nitrogen availability in temperate forests of the United States. *Scientific Reports* **7**: 7856.

McLauchlan KK, Williams JJ, Craine JM, Jeffers ES. 2013. Changes in global nitrogen cycling during the Holocene epoch. *Nature* **495**: 352–355.

Melillo JM, David A, Kicklighter DW, Moore B, Vorosmarty CJ, Schloss AL. 1993. Global climate change and terrestrial net primary production. *Nature* **363**: 234–240.

Merril ED. 1926. *An enumeration of Philippine flowering plants, vol. I–IV*. Manila, Philippines: Bureau of Printing.

Mirmanto E, Proctor J, Green J, Nagy L, Suriantata. 1999. Effects of nitrogen and phosphorus fertilization in a lowland evergreen rainforest. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **354**: 1825–1829.

Mooney SD, Tinner W. 2010. The analysis of charcoal in peat and organic sediments. *Mires and Peat* **7**: 1–18.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858.

Nakagawa M, Tanaka K, Nakashizuka T, Ohkubo T, Kato T, Maeda T, Sato K, Miguchi H, Nagamasu H, Ogino K et al. 2000. Impact of severe drought associated with the 1997–1998 El Niño in a tropical forest in Sarawak. *Journal of Tropical Ecology* **16**: 355–367.

Newbery DM, Chuyong GB, Green JJ, Songwe NC, Tchuenteu F, Zimmermann L. 2002. Does low phosphorus supply limit seedling establishment and tree growth in groves of ectomycorrhizal trees in a central African rainforest? *New Phytologist* **156**: 297–311.

Nurdiati S, Sopaheluwakan A, Septiawan P. 2022. Joint pattern analysis of forest fire and drought indicators in southeast Asia associated with ENSO and IOD. *Atmosphere* **13**: 1198.

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'amico JA, Itoua I, Strand HE, Morrison JC et al. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience* **51**: 933.

OpenStreetMap. 2023. *Bulusan Lake*. Satellite image. [WWW document] URL https://www.openstreetmap.org/#map=14/12.7676/124.0801&layers=C [accessed 14 July 2023].

Overpeck JT, Cole JE. 2010. El Niño/Southern Oscillation and changes in the zonal gradient of tropical Pacific sea surface temperature over the last 1.2 ka. *PAGES News* **18**: 32–34.

Pang SEH, De Alban JDT, Webb EL. 2021. Effects of climate change and land cover on the distributions of a critical tree family in the Philippines. *Scientific Reports* **11**: 276.

Paoli GD, Curran LM. 2007. Soil nutrients limit fine litter production and tree growth in mature lowland forest of southwestern Borneo. *Ecosystems* **10**: 503–518.

Paoli GD, Curran LM, Slik JWF. 2008. Soil nutrients affect spatial patterns of aboveground biomass and emergent tree density in southwestern Borneo. *Oecologia* **155**: 287–299.

Paoli GD, Curran LM, Zak DR. 2005. Phosphorus efficiency of Bornean rain forest productivity: evidence against the unimodal efficiency hypothesis. *Ecology* **86**: 1548–1561.

PhilGIS. 2017. *Philippine GIS datasets*. [WWW document] URL http://philgis.org/gis-data [accessed 20 February 2017].

Pinho BX, Peres CA, Leal IR, Tabarelli M. 2020. Critical role and collapse of tropical mega-trees: a key global resource. *Advances in Ecological Research* **62**: 253–294.

Pörtner H-O, Roberts DC, Tignor M, Poloczanska ES, Mintenbeck K, Alegría A, Craig M, Langsdorf S, Löschke S, Möller V et al. 2022. *IPCC, 2022: climate change 2022: impacts, adaptation, and vulnerability. Contribution of working group II to the sixth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge, UK; New York, NY, USA: Cambridge University Press.

Prohaska A, Seddon A, Meese B, Willis K, Chiang J, Sachse D. 2023. Abrupt change in tropical Pacific climate mean state during the Little Ice Age. *Communications Earth & Environment* 4: 227.

QGIS Development Team. 2020. *QGIS geographic information system, v.3.10.14.* Open Source Geospatial Foundation Project. [WWW document] URL https://www.qgis.org [accessed 15 February 2023].

R Development Core Team. 2020. *R: a language and environment for statistical computing, v.3.6.3.* Vienna, Austria: R Foundation for Statistical Computing. [WWW document] URL https://www.r-project.org/ [accessed 10 March 2022].

Ramesh N, Nicolas Q, Boos WR. 2021. The globally coherent pattern of autumn monsoon precipitation. *Journal of Climate* 34: 5687–5705.

Rutishauser E, Wagner F, Herault B, Nicolini E-A, Blanc L. 2010. Contrasting above-ground biomass balance in a Neotropical rain forest. *Journal of Vegetation Science* 21: 672–682.

Saatchi SS, Harris NL, Brown S, Lefsky M, Mitchard ETA, Salas W, Zutta BR, Buermann W, Lewis SL, Hagen S et al. 2011. Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences, USA* 108: 9899–9904.

Sachse D, Billault I, Bowen GJ, Chikaraishi Y, Dawson TE, Feakins SJ, Freeman KH, Magill CR, McInerney FA, Van Der Meer MTJ. 2012. Molecular paleohydrology: interpreting the hydrogen-isotopic composition of lipid biomarkers from photosynthesizing organisms. *Annual Review of Earth and Planetary Sciences* 40: 221–249.

Sakai S, Harrison RD, Momose K, Kuraji K, Nagamasu H, Yasunari T, Chong L, Nakashizuka T. 2006. Irregular droughts trigger mass flowering in aseasonal tropical forests in Asia. *American Journal of Botany* 93: 1134–1139.

Sakai S, Momose K, Yumoto T, Nagamitsu T, Nagamasu H, Hamid AA, Nakashizuka T. 1999. Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. *American Journal of Botany* 86: 1414–1436.

Sala OE, Chapin FS 3rd, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A et al. 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774.

Salafsky N. 1994. Drought in the rain forest: effects of the 1991 El Nio-Southern Oscillation event on a rural economy in West Kalimantan, Indonesia. *Climatic Change* 27: 373–396.

Salafsky N. 1998. Drought in the rain forest, part II an update based on the 1994 ENSO event. In: Markham A, ed. *Potential impacts of climate change on tropical forest ecosystems.* Dordrecht, the Netherlands: Springer, 461–463.

Santiago LS, Kitajima K, Joseph Wright S, Mulkey SS. 2004. Coordinated changes in photosynthesis, water relations and leaf nutritional traits of canopy trees along a precipitation gradient in lowland tropical forest. *Oecologia* 139: 495–502.

Santiago LS, Mulkey SS. 2005. Leaf productivity along a precipitation gradient in lowland Panama: patterns from leaf to ecosystem. *Trees* 19: 349–356.

Schefuss E, Schouten S, Jansen JHF, Sinninghe Damsté JS. 2003. African vegetation controlled by tropical sea surface temperatures in the mid-Pleistocene period. *Nature* 422: 418–421.

Schulte A, Schöne D. 1996. *Dipterocarp forest ecosystems: towards sustainable management.* Singapore: World Scientific Publishing.

Shively G, Pagiola S. 2004. Agricultural intensification, local labor markets, and deforestation in the Philippines. *Environment and Development Economics* 9: 241–266.

Siegert F, Ruecker G, Hinrichs A, Hoffmann AA. 2001. Increased damage from fires in logged forests during droughts caused by El Niño. *Nature* 414: 437–440.

Simpson GL. 2018. Modelling palaeoecological time series using generalised additive models. *Frontiers in Ecology and Evolution* 6: 149.

Slik JWF, Aiba S-I, Brearley FQ, Cannon CH, Forshed O, Kitayama K, Nagamasu H, Nilus R, Payne J, Paoli G et al. 2010. Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests. *Global Ecology and Biogeography: A Journal of Macroecology* 19: 50–60.

Slik JWF, Paoli G, McGuire K, Amaral I, Barroso J, Bastian M, Blanc L, Bongers F, Boundja P, Clark C et al. 2013. Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Global Ecology and Biogeography: A Journal of Macroecology* 22: 1261–1271.

Sodhi NS, Koh LP, Brook BW, Ng PKL. 2004. Southeast Asian biodiversity: an impending disaster. *Trends in Ecology & Evolution* 19: 654–660.

Stephenson NL, Das AJ, Condit R, Russo SE, Baker PJ, Beckman NG, Coomes DA, Lines ER, Morris WK, Rüger N et al. 2014. Rate of tree carbon accumulation increases continuously with tree size. *Nature* 507: 90–93.

Stockmarr JE. 1971. Tables with spores used in absolute pollen analysis. *Pollen and Spores* 13: 615–621.

Tumaneng-Diete T, Ferguson IS, MacLaren D. 2005. Log export restrictions and trade policies in the Philippines: bane or blessing to sustainable forest management? *Forest Policy and Economics* 7: 187–198.

Van Der Kaars S, Tapper N, Cook EJ. 2009. Observed relationships between El Niño-Southern Oscillation, rainfall variability and vegetation and fire history on Halmahera, Maluku, Indonesia. *Global Change Biology* 16: 1705–1714.

Van Nieuwstadt MGL, Sheil D. 2005. Drought, fire and tree survival in a Borneo rain forest, East Kalimantan, Indonesia. *Journal of Ecology* 93: 191–201.

Vitousek PM. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65: 285–298.

Vitousek PM, Aplet G, Turner D, Lockwood JJ. 1992. The Mauna Loa environmental matrix: foliar and soil nutrients. *Oecologia* 89: 372–382.

Vitousek PM, Walker LR, Whiteaker LD, Matson PA. 1993. Nutrient limitations to plant growth during primary succession in Hawaii Volcanoes National Park. *Biogeochemistry* 23: 197–215.

Wang B, Luo X, Yang YM, Sun W, Cane MA, Cai W, Yeh SW, Liu J. 2019. Historical change of El Niño properties sheds light on future changes of extreme El Niño. *Proceedings of the National Academy of Sciences, USA* 116: 22512–22517.

van der Werf GR, Randerson JT, Collatz GJ, Giglio L, Kasibhatla PS, Arellano AF Jr, Olsen SC, Kasischke ES. 2004. Continental-scale partitioning of fire emissions during the 1997 to 2001 El Niño/La Niña period. *Science* 303: 73–76.

Whitmore TC. 1988. *Tropical rain forests of the Far East, 2nd edn.* Oxford, UK: Oxford University Press.

Wickham H. 2016. *GGPLOT2: elegant graphics for data analysis, 2nd edn.* New York, NY, USA: Springer-Verlag.

Wilcove DS, Giam X, Edwards DP, Fisher B, Koh LP. 2013. Navjot's nightmare revisited: logging, agriculture, and biodiversity in southeast Asia. *Trends in Ecology & Evolution* 28: 531–540.

Wood SN. 2017. *Generalized additive models: an introduction with R, 2nd edn.* New York, NY, USA: Chapman and Hall/CRC.

Wood SN. 2018. *mgcv: Mixed GAM computation vehicle with GCV/AIC/REML smoothness estimation and GAMMs by REML/PQL.* R package v.1.8-41. [WWW document] URL http://cran.r-project.org/web/packages/mgcv/index.html [accessed 1 November 2022].

Woods GHS. 1956. The Dipterocarp flowering season in North Borneo. *Malaysian Forester* 19: 193–201.

Woods P. 1989. Effects of logging, drought, and fire on structure and composition of tropical forests in Sabah, Malaysia. *Biotropica* 21: 290.

Wooster MJ, Perry GLW, Zoumas A. 2012. Fire, drought and El Niño relationships on Borneo (Southeast Asia) in the pre-MODIS era (1980–2000). *Biogeosciences* 9: 317–340.

Wright SJ, Yavitt JB, Wurzburger N, Turner BL, Tanner EVJ, Sayer EJ, Santiago LS, Kaspari M, Hedin LO, Harms KE et al. 2011. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology* 92: 1616–1625.

Yavitt JB, Wright SJ. 2008. Seedling growth responses to water and nutrient augmentation in the understorey of a lowland moist forest, Panama. *Journal of Tropical Ecology* 24: 19–26.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Age-depth model for the Bulusan sedimentary sequence.

Fig. S2 Modelled effects of abiotic factors on plant taxa abundance at Bulusan using generalised additive models with a Quasi-Poisson distribution.

Fig. S3 Pollen diagram of the sedimentary sequence from Bulusan Lake.

Fig. S4 Significant periods of change in the key palaeo-records from Bulusan Lake derived from the best-fitted generalised additive model trends.

Fig. S5 Microcharcoal influx rates in relation to macrocharcoal influx rates in the Bulusan record.

Fig. S6 Principal component analysis results of the abundance dynamics of main geochemical elements and the magnitude of magnetic susceptibility in the Bulusan sedimentary sequence.

Fig. S7 Comparison of the record of bulk sediment phosphorus concentrations with the records of volcanic trace elements concentrations, magnetic susceptibility values and bulk sediment phosphate oxygen isotope values from the Bulusan sedimentary sequence.

Fig. S8 Comparison of the record of bulk sediment phosphorus concentrations with the record of $n\mathrm{C}_{29}$ alkane δD values, macrocharcoal influx rates and Ba : Ti ratio from the Bulusan sedimentary sequence.

Methods S1 Physical and geochemical properties.

Methods S2 Magnetic susceptibility record.

Methods S3 Age-depth modelling.

Methods S4 Microcharcoal influx rates.

Methods S5 Phosphate oxygen isotope analysis.

Notes S1 Pollen accumulation rates as a proxy for past plant dynamics.

Notes S2 Potential drivers of changes in phosphorus availability at Bulusan.

Notes S3 Comparison of generalised additive models with Gamma and Quasi-Poisson distribution.

Notes S4 Identifying significant periods of change with generalised additive models.

Notes S5 Potential drivers of charcoal influx rates in the Bulusan record.

Table S1 AMS^{14}C dates of the Bulusan sedimentary sequence.

Table S2 Summary of results of the best-fitted generalised additive models with a Quasi-Poisson distribution for describing the effects of abiotic factors on plant taxa abundance at Bulusan.

Table S3 Description of the best-fitted generalised additive models of temporal dynamics of palaeo-records from Bulusan Lake with GCV-based smoothness selection.

Table S4 Description of the best-fitted generalised additive models of temporal dynamics of palaeo-records from Bulusan Lake with a continuous-time AR(1) process estimated using restricted maximum likelihood smoothness selection.

Table S5 Description of the best-fitted generalised additive models with a Gamma distribution for describing the effects of abiotic factors on plant taxa abundance and C_3/C_4 vegetation composition at Bulusan.

Table S6 Description of the best-fitted generalised additive models with a Quasi-Poisson distribution for describing the effects of abiotic factors on plant taxa abundance at Bulusan.

Please note: Wiley is not responsible for the content or functionality of any Supporting Information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.