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Insights for restoration: Reconstructing the drivers of long-term local fire events and vegetation turnover of a tropical peatland in Central Kalimantan

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ABSTRACT

Fire events in tropical peatlands often relate to dry peat conditions associated with climate variability (drought) and anthropogenic-driven ecosystem degradation. However, drought is not the only driver of long-term fire events and peatland ecosystem changes. This study used palaeoecological and geochemical proxies to investigate the long-term drivers of charcoal influx to identify local fires and examine the associated responses to the tropical peatland ecosystem in Central Kalimantan, Indonesia. The results showed local fire events increased after 756 cal. yr BP, and possible drivers of charcoal influx include changes in sea level, increased frequency of El Niño events, increased biomass, and anthropogenically-driven ecosystem degradation. However, the vegetation composition showed changes since ~2300 cal. yr BP from a mix of peat swamp forest (PSF) and open vegetation (OV) during the late Holocene (~2300 to 1129 cal. yr BP), to predominantly PSF from 1128 to 375 cal. yr BP, dry lowland mixed with swamp forest (LMS) and open vegetation (OV) from 374 to 135 cal. yr BP, and predominantly OV and freshwater swamp forest (FSF) from 134 to −62 cal. yr BP. The possible drivers of the vegetation turnover were hydrological conditions and the availability of peat nutrients, while the vegetation turnover affected the accumulation and decomposition of recalcitrant organic matter in peat. The thresholds of the peatland ecosystems over longer-term timeframes provided the following restoration insights: 1) PSF species (i.e. *Eurya* and *Ilex*) showed high fire tolerance and increased in abundance up to charcoal influx threshold of ~23 grains mm^{-2} cm^{-3} yr^{-1} while LMS and OV species increased up to a lower threshold of ~13 grains mm^{-2} cm^{-3} yr^{-1}before declining; 2) PSF species expanded during periods of wet conditions and high peat nutrients (i.e. TN - enriched); and 3) Future revegetation in the region can focus on tree taxa such as Euphorbiaceae, *Arenga, Ficus*, and *Trema* as they were historically able to thrive in fire events and dry hydrological conditions.

1. Introduction

The peat and vegetation in the tropical peatlands of Indonesia form a large carbon pool of 13.6 to 57.4 Gt and contribute to one-third of the total carbon stock in tropical peatlands (Page et al., 2011; Warren et al., 2017). In addition to acting as carbon stores, tropical peatlands contribute to maintaining water quality and availability (Price et al., 2016; Wösten et al., 2008), rich biodiversity (Morrogh-Bernard et al., 2003; Yule, 2010) and socio-economic benefits to locals (Harrison et al., 2019; Dewi et al., 2005). Tropical peatlands in Indonesia have been

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present since the late Pleistocene as a result of the increase in moisture availability from sea level rise over the Sunda Shelf associated with Melt Water Pulse 1a (Dommain et al., 2011; Anshari et al., 2001; Steinke et al., 2003) and the intensification of the Asian monsoon rainfall arising from higher sea surface temperatures (Wang et al., 2001; Partin et al., 2007). Together with the low altitude and topography of the inland tropical peatlands, peat deposits have accumulated over time, dominated by peat swamp forest (PSF) species (Rieley and Page, 2016; Shiodera et al., 2016; Page et al., 2004; Cameron et al., 1989; Ritzema et al., 2014).

Holocene climate variabilities such as the alterations of sea level and the increase in intensity and frequency of El Niño Southern Oscillation (ENSO) events have resulted in changes to flooding conditions (overbank flow) and moisture availability in tropical peatlands in Indonesia respectively, which have an impact on the peatland ecosystem (Griffiths et al., 2009; Geyh et al., 1979; Dommain et al., 2011; Rosenthal et al., 2003; Page et al., 2004; Susilo et al., 2013; Parish et al., 2002). In addition, initial human activities in the late Holocene such as the practice of small-scale swidden agriculture by the Dayak communities in peatland close to rivers could have altered the vegetation present (Hapsari et al., 2021; Alam et al., 2023; Wiesner and Dargusch, 2022; Jewitt et al., 2014). For recent anthropogenically-driven degradation, it is primarily due to land use changes associated with logging, conversion to industrial plantations, forest fires for land clearing and construction of drainage and irrigation canals (Posa, 2011; Osaki et al., 2016; Gao et al., 2016; Dohong et al., 2017). The recent anthropogenic degradation of peatland in Indonesia is estimated to result in carbon loss of at least 0.9 GtC year^{-1} (Warren et al., 2017; Dohong et al., 2017). Since 2016, the Indonesian government has focused on peatland restoration by establishing the National Peatland and Mangrove Restoration Agency (*Badan Restorasi Gambut dan Mangrove*), whose remit includes coordinating and facilitating rewetting, revegetation and revitalization efforts on degraded peatland (BRG, 2018; Widodo, 2020).

Drought conditions, driven by recent anthropogenic and climatic factors in tropical peatlands, have led to the lowering of groundwater levels and subsequent effects on peat decomposition, which threaten the survival of peat swamp forest (PSF) species (Susilo et al., 2013; Wösten et al., 2008; Gallego-Sala et al., 2016; Biagioni et al., 2015). However, drought is not the only factor affecting tropical peatland ecosystems in the long term. Fire events can affect the peat decomposition rates, peat nutrients, and vegetation diversity of the peatland (Hapsari et al., 2021; Yu et al., 2011; Page et al., 1999; Wösten et al., 2008). For example, shifts from PSF to OV (open vegetation) by fire events will alter the type of OM from woody (recalcitrant) to leaf litter (labile) entering the peat system which will result in higher degree of decomposition and lower carbon content of peat (Millard and Singh, 2009; Dom et al., 2021; Berg and Mcclaugherty, 2008). The combustion of these OM in fire will also result in the mineralisation of peat nutrients (e.g. nitrogen, phosphorus and potassium) making them available for plant growth (Davidson et al., 2007; Turner et al., 2007), but the low groundwater level of burnt peatland may hinder the growth of some PSF species such as *Campnosperma* (Osaki et al., 2021; Smith et al., 2022). Furthermore, the increase in OV (i.e. Poaceae) following fire events increases the fire susceptibility of the peatland due to reduced protection from the solar radiation by the forest canopy and the increase in the peat surface temperatures (Ludang et al., 2007; Wust et al., 2007).

Palaeoecological studies conducted in lakes and peatlands in Indonesia and Borneo have revealed that fire events did not result in significant changes in vegetation (i.e. dominant PSF species) prior to 500 yrs. BP but the transition to open vegetation (OV) species (e.g. Poaceae, *Ardisia, Stenochlaena*) occurred post- 500 yrs. BP due to anthropogenically-driven fire (Anshari et al., 2001; Yulianto et al., 2004; Cole et al., 2015; Cole et al., 2019). In these studies, the lack of changes in vegetation species following fire events before 500 yrs. BP was attributed to the peatland conditions such as stable groundwater levels and dense PSF. However, past fire events identified on the basis of the charcoal records in peat cores can be dependent on the biofuel composition (i.e. vegetation types present in peatlands) and charcoal redeposition during river flooding (e.g. overbank flow) by high relative sea level (Bradstock, 2010; Adeleye et al., 2020; Muller, 1963; Hanebuth et al., 2000; Dommain et al., 2011). Hence, it is important to determine the origin of the charcoal in peat (e.g. taphonomy and depositional setting) before investigating the responses of tropical peatland ecosystem to local fire events. Furthermore, these long-term responses of vegetation turnover, hydrology and peat conditions to fire events are essential knowledge to help improve peatland restoration efforts and management under recent climate change and increased anthropogenic pressures.

Hence, we examine palaeoecological and geochemical proxies from peat to investigate the drivers of charcoal influx trends to identify local fires and examine the responses of the vegetation turnover to fire and alterations in hydrology and peat conditions in a peatland (Sebangau National Park) in southern Borneo for the past ~2300 cal. yr BP. In doing so, we reconstruct the associated responses and thresholds of vegetation turnover to the changes in hydrology and peat conditions, and local fire events to inform future restoration efforts. In particular, we identify the thresholds of native vegetation species to localised fire events using charcoal influx, provide the thresholds of the expansion of PSF species to varying hydrology conditions, and suggest species for revegetation that can cope with current peatland conditions.

2. Study site

The peat core analysed in this study was obtained from the special research zone within the Sebangau National Park (SNP) (734,700 ha) (Fig. 1). The 2 m core was retrieved from 2°19′23.22"S, 113°54′14.02″E using a D-section auger and was approximately 2 km from the Sebangau River, where the present vegetation consisted of a relatively intact marginal riverine forest, peat swamp forest and low pole forest such as Dipterocarpaceae, Myrtaceae, Apocynaceae and Euphorbiaceae. (Fig. 1) (Page et al., 1999; Husson et al., 2018). While the peatland in the wider landscape are relatively intact, they have nevertheless experienced some degradation due to past logging and associated drainage since the 1970s, recent fire events in 2015 and 2019, and recovery from which is being aided by ongoing revegetation and rewetting efforts (Page et al., 2002; Page et al., 2004; Wösten et al., 2008; Dohong et al., 2017).

Daily weather records measured at special research zone in SNP show the study site experiences a humid tropical climate with an annual temperature range of 21.6 to 30.3 °C and total rainfall between 2187 and 4563 mm/year between 2004 and 2017 (BMKG, 2023). The total rainfall is influenced by the ENSO cycle, with lower dry season rainfall every 3 to 7 years coinciding with El Niño events and higher wet season rainfall associated with La Niña periods (Susilo et al., 2013) (Fig. 2). The peat in SNP is mainly ombrotrophic, derived from the accumulation of partially (hemic) and highly (sapric) decomposed organic matter (OM) over thousands of years in a flat floodplain under a wet tropical climate (Rieley and Page, 2016; Page et al., 2004; Cameron et al., 1989). Peat thickness assessed in SNP using satellite images and in situ measurements indicate depths ranging from 0.5 to 12.2 m with a carbon pool of approximately 2.30 Gt (Page et al., 1999; Page et al., 2004; Jaenicke et al., 2008). The current elevation of SNP is between 15 and 40 m above sea level (SRTM, 2000).

The peatland ecosystem of SNP supports high biodiversity and provides necessary socio-economic services to the local community such as flood and fire prevention to housing settlement in the proximity, timber and non-timber forest product provision, and livelihoods such as fishing (Husson et al., 2018; Harrison et al., 2019; Murdiyarso et al., 2019; Dewi et al., 2005; Thornton et al., 2020). In addition, restoration efforts have been increasingly carried out in SNP via rewetting by constructing dams in canals to raise the water level and revegetating highly degraded areas to decrease fire risk (Dohong et al., 2017).

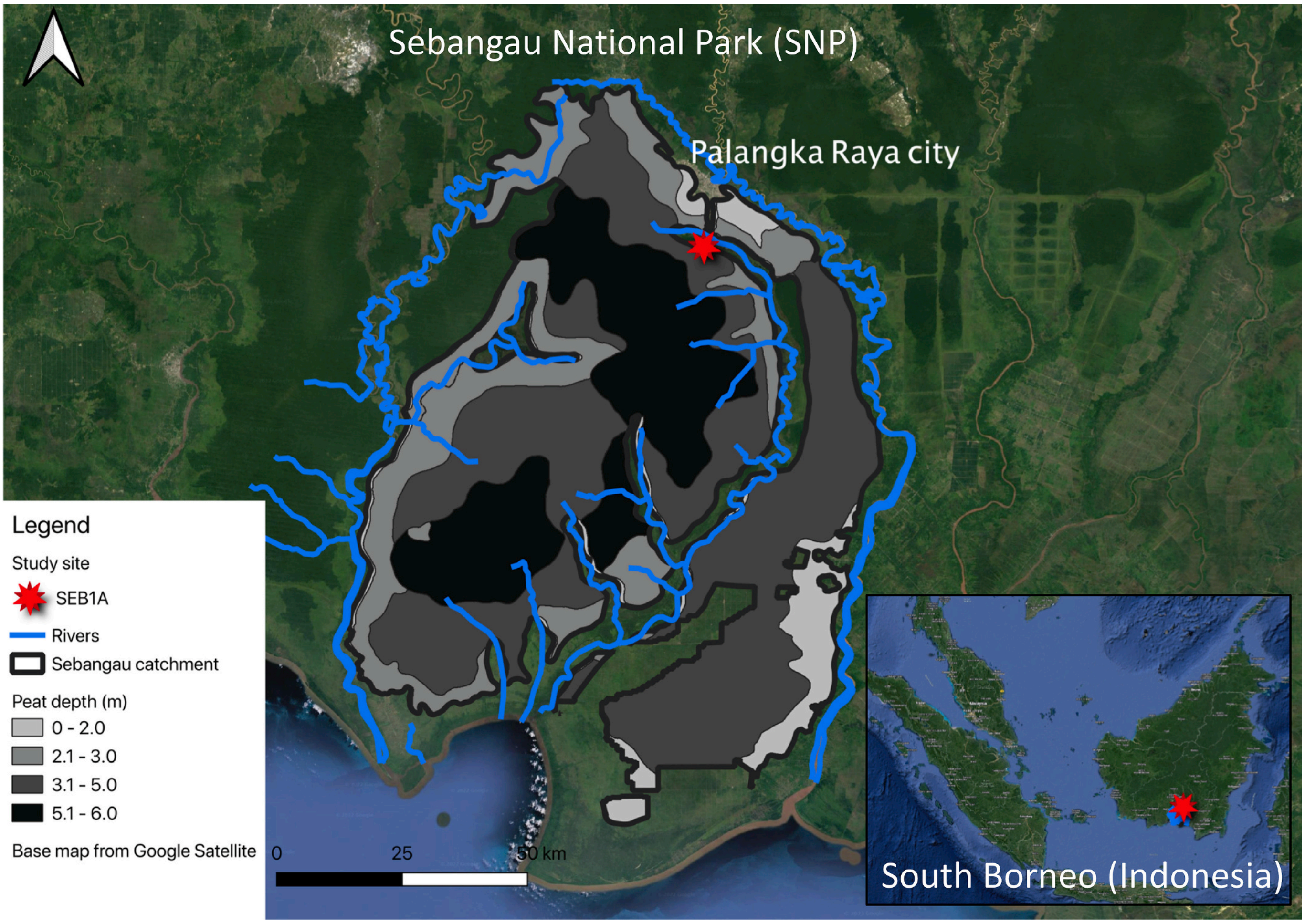

Fig. 1. Study site, core location (SEB1A), and peat depths in Sebangau catchment in Central Kalimantan, Indonesia. Peat depth data are based on satellite images in Jaenicke et al., 2008.

3. Methods

For this study, the peat core was sub-sampled at every 1 to 2 cm for palaeoecology and geochemical analysis. The top 77 cm of the peat core was focused on in this study due to the dominance of PSF species in the pollen record compared to the lower peat depths, and this will aid in our investigation to examine the responses of vegetation turnover for peat swamp forest in SNP.

3.1. Chronology

Six bulk (excluding roots) peat samples from the peat core were analysed for radiocarbon (^{14}C) dates in the Accelerator Mass Spectrophotometer (AMS) at the Scottish Universities Environment Research Centre (SUERC) and Australian Nuclear Science Technology and Organisation (ANSTO). The measured ^{14}C -specific activity was corrected for fractionation effects using the respective $\delta^{13}C$ values to estimate the appropriate atmospheric ^{14}C level for the sample (Hua et al., 2001). In addition, twelve bulk peat samples from the top 15.5 cm of the peat core were analysed for ^{210}Pb at the University of Exeter laboratories to date the younger material, i.e. the last ~100 years. The peat ages are estimated from the ^{210}Pb activity in the Constant Rate Supply (CRS) model (Appleby, 2008; Turetsky et al., 2004). The ages and uncertainties from ^{14}C (Table S1 in Supplementary data) and ^{210}Pb (Table S2 in Supplementary data) analyses were incorporated into a Bayesian statistics package in R ('BACON') to develop an age-depth model using a calibration curve for the pre-and post-bomb periods for the Southern Hemisphere (SHCal20 and SH1–2) and the year 2019 CE for the top of the peat core (Blaauw and Christen, 2011). The weighted median calibrated ages (cal. yr. BP) produced at every 1 cm of the peat core were used to represent the peat ages and accumulation rates for the top 77 cm for this study.

3.2. Palaeoecology proxies: palynology, testate amoeba and macro- and micro-charcoal

Palaeoecological analysis was conducted on subsamples at every 2 cm of the peat core. The peat samples for palynology and micro-charcoal analysis were prepared following the methods outlined in Moss (2013), while testate amoeba were extracted using the pre-treatment methods outlined in Booth et al. (2010). The pre-treatment includes using *Lycopodium clavatum* markers, chemical deflocculant to disperse larger aggregates, sieving to capture samples between 8 and 125 μm for pollen/spores and 15 and 300 μm for testate amoeba and staining using Safranine. For pollen and spores, additional steps were taken to remove organic and inorganic materials using Potassium hydroxide (10%), Sodium polytungstate and acetolysis treatment. For macro-charcoal analysis, samples were pre-treated using Hydrogen peroxide (4 to 6%) and sieved to capture charcoal pieces larger than 125 μm in size using the Stevenson and Haberle (2005) protocol.

All pre-treated samples were placed under the microscope at 100× magnification for palynology and micro-charcoal and 10× magnification for macro-charcoal for identification and counting. To obtain a strong representation of palaeoenvironmental signals, a sum of 250 to

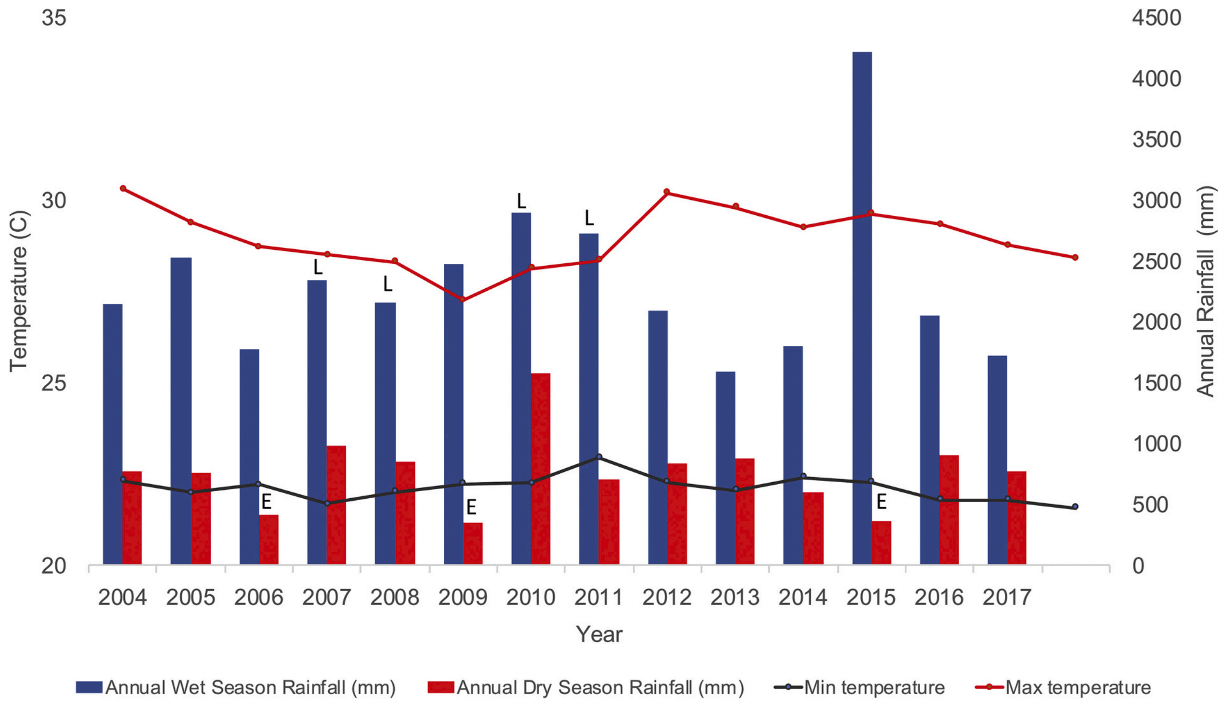

Fig. 2. Minimum (blue line) and maximum (red line) temperatures, and annual wet (mm, blue bar) and dry (mm, red bar) season rainfall from 2004 and 2017 based on daily measurements at special research zone in SNP (BMKG, 2023). El Niño (E) and La Niña (L) years are also shown in the plot. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

300 pollen/spores species, at least 100 micro and macro-charcoal particles, and 50 to 100 testate amoeba specimens were counted for each sample (Cole et al., 2015; Biagioni et al., 2015; Swindles et al., 2016). The concentration (grains mm^{-2} cm^{-3}) of pollen, testate amoeba and micro-charcoal per sample was calculated based on the grains counted, area of the microscope slide traversed and concentration and counts of marker spore *Lycopodium clavatum* (Moss, 2013), and identification was resolved at genus and species level where possible, based on the reference database and literature from Indonesia and the broader tropics (APSA, 2022; Cheng et al., 2020; Biagioni, 2015; Charman, 1999; Krashevska et al., 2020; Liu et al., 2019). For macro-charcoal, the concentration (grains mm^{-2} cm^{-3}) was calculated based on the grains counted per area of the petri-dish traversed and the volume of prepared material in water.

Pollen taxonomy was classified according to the following vegetation groups: coastal vegetation (CV), upland montane (UM), lowland montane (LM), freshwater swamp forest (FSF), lowland vegetation mixed with swamp forest (LMS), peat swamp forest (PSF), early succession pioneer swamp forest (early PSF), open vegetation (OV) (i.e. grass and agricultural species) and monolete spores (MS) (Ramdzan et al., 2022; Cole et al., 2015; Biagioni et al., 2015; Yulianto and Hirakawa, 2006). For testate amoeba, the taxon diversity in the core was low and the dominant taxa present were *Hyalosphenia subflava minor and H.s. major, Cryptodifflugia crenulate* and *Cyclopyxis eurystoma*. As the *Hyalosphenia subflava* group and *C. crenulate* are generally found to be indicators of dry and wet conditions respectively (Mitchell et al., 2008; Liu et al., 2019) and these taxa are negatively correlated, we used the variability (z-score) in *C. crenulate* as an index of peat wetness to represent local hydrology. Lastly, macro (>125 μm) and micro (<125 μm) charcoal concentrations represent localised and regional fires respectively as large charcoal are deposited in situ while small charcoal pieces can be deposited from surrounding peatland through wind and water (e.g. river overbank flow) (Gardner and Whitlock, 2001). Charcoal influx (grains mm^{-2} cm^{-3} yr^{-1}) was also calculated from the macro-charcoal concentration and peat accumulation rates in the 'paleofire' package in R to represent the amount of biomass consumed during fire events which could also indicate the severity of fire events (Arienzo et al., 2019).

All palaeoecology data were presented using Tilia (Grimm et al., 2013), with pollen/spore taxonomy, testate amoeba species and vegetation groups in percentages of its respective total concentration, peat wetness in z-score and charcoal counts in concentration and influx. Cluster analysis of the vegetation groups dataset using change point analysis (CPA) in the 'strucchange' package in R was conducted to identify the breakpoints that signify the significant environmental and vegetation changes occurring over time (Zeileis et al., 2002). Five vegetation zones (A to E) were identified based on the lowest residual sum of squares (RSS) obtained from the linear model with five breakpoint segments.

Vegetation turnover was calculated using the Square Chord Distances (SCD) pairwise dissimilarity metric (binning approach) in the 'analogue' package in R software to estimate the rate of vegetation compositional turnover through time (Adeleye et al., 2021; Simpson, 2007; Connor et al., 2019). The binning approach involves dividing the vegetation group percentages of each year into bin SCD scores and calculating the inter-sample SCD score between adjacent bins at a random selection of 50 times before averaging the bin-to-bin SCD score for each sample. The SCD cut-off at the 5th percentile, which is 0.16 for this study, was calculated using Monte Carlo simulations (1000 bootstrap cycles) to represent the empirical threshold of significant vegetation turnover (Fig. 3) (Simpson, 2007).

3.3. Geochemical proxies: particle size, bulk density, TC and TN concentration and peat humification

Geochemical analysis was conducted every 1 or 2 cm along the 77 cm peat core. A total of 38 peat samples were analysed for the median grain size (D50) using the Malvern Mastersizer 3000 (MM3000) to identify possible deposition of larger materials from the rivers. Bulk peat samples were dispersed in sodium hexametaphosphate and sieved through a 250 μm sieve to remove large-size organic material before being placed in the MM3000 (Loizeau et al., 1994).

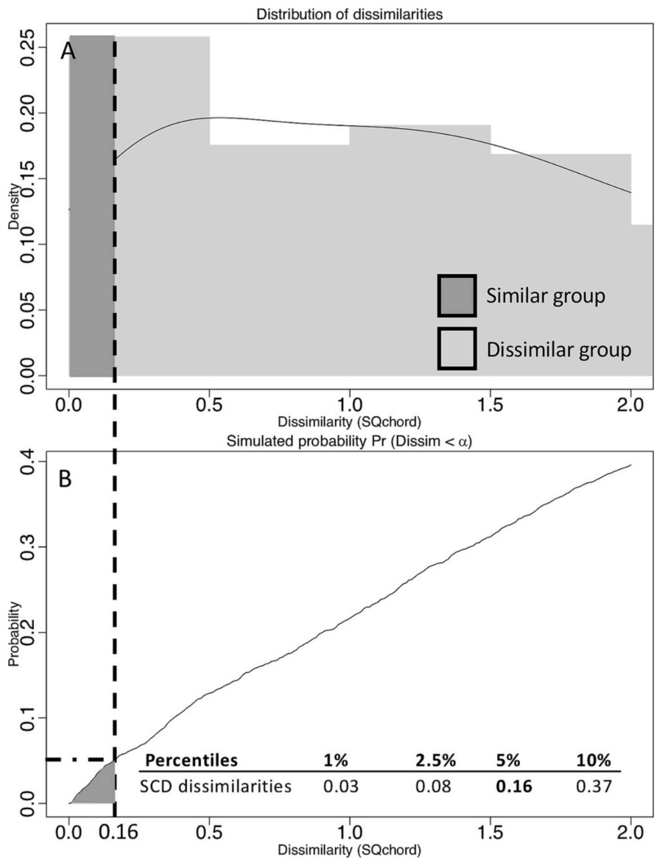

Fig. 3. A) Squared chord distances (SCD) of the pairwise dissimilarity between similar and dissimilar groups using vegetation group percentages derived from the peat core. B) The Monte Carlo analysis identified a SCD score of 0.16 (at the 5% percentile/0.05 probability) as the empirical turnover threshold. Generally, similar vegetation groups between samples have a SCD <0.16 while most dissimilar vegetation groups have a SCD > 0.16.

The dry bulk density of 77 peat samples was calculated based on the known peat volume and mass of dry peat sample (Kauffman and Donato, 2012). These dried peat samples were also analysed in Elemental Analyser to obtain the total Carbon (TC) and total Nitrogen (TN) content. High values of TC denote peat sequestration while high values of TN represent the mineralisation of N during fire events and microbial decomposition of OM (Kuhry and Vitt, 1996; Brinson, 1977; Limpens et al., 2008). In addition, the apparent carbon accumulation rates (aCAR) of each sample were calculated by multiplying the peat accumulation rate, dry bulk density and TC content to provide the present-day observations of peatlands carbon stores as peat in deeper depths had gone through decomposition with time (Page et al., 2004; Young et al., 2021). However, we do acknowledge the 'acrotelm effect' of near-surface samples can also result in large aCAR values due to recently added plant litter that has decomposed much less than older peat (Young et al., 2021).

The degree of peat humification of 38 peat samples was measured based on the percentage of light transmission in a spectrophotometer after pre-treatment using the methods outlined in Chambers et al. (2011). For this study, a peat humification index (PHI) was generated by inversing the light transmission values so that higher values represent high aerobic and anaerobic decay of OM (Blackford and Chamber, 1993; Payne and Blanckford, 2008). The PHI represents the degree of decay of OM into humic and fluvic acids (soluble) and humin (insoluble), and is typically dependent on moisture content, available oxygen and temperature (Burrows et al., 2014). However, peat humification can be affected by the types of OM in peat as recalcitrant OM from tree species (i.e. woody materials) and labile OM from grass/herbaceous species (i.e. carbohydrates) have low and high degradability respectively (Dom et al., 2021; Berg and Mcclaugherty, 2008; Rovira and Vallejo, 2002).

3.4. Statistical analysis

All palaeoecology and geochemical data generated in this study were interpolated for every year to aid in comparative analysis to the long-term records of the reconstructions of relative sea level based on the present day above sea level (asl) in Malacca straits (Geyh et al., 1979) and regional rainfall in Liang Luar Cave, Flores, Indonesia (Griffiths et al., 2009). The rainfall proxy data (based on oxygen isotope measurement) from Flores was used for comparison due to proximity to site and continuous records up to 2300 cal. yr BP (Griffiths et al., 2009), and the oxygen isotope data was inversed and z-scores were calculated so that high values represent wet conditions.

To identify the drivers of charcoal influx, a generalised linear model (GLM) with Gaussian distribution was produced using the following potential drivers: sea level, regional rainfall, vegetation turnover and peat wetness. Another GLM was constructed to predict the drivers of vegetation turnover using peat (TC, TN, and PHI), hydrological (peat wetness) and fire (charcoal influx) proxies. However, this research shows that the peat, hydrology and fire conditions could also be a response to the vegetation turnover and discuss them in the discussion section. To remove the effects of temporal autocorrelation of the GLM, each variable was resampled at a lower temporal resolution through analysing at 1000 bootstrapping cycles (Mellin et al., 2010). A final GLM using a stepwise variable selection procedure based on the Corrected Akaike's information criterion (AICc) and delta AICc (dAICc) was produced to rank the models to identify the main drivers of charcoal influx and vegetation turnover (Mazerolle, 2006). The percentage of deviance explained, t-value and adjusted r^2 (ar^2) were also computed for the GLM relationships (Mellin et al., 2010).

To obtain the threshold estimates of the drivers for vegetation turnover, the segmented relationship using the log-likelihood function of the GLM was applied to each parameter in each vegetation zone (Muggeo et al., 2014). A segmented relationship is defined by the breakpoints when linear relation changes between two parameters and only significant breakpoint relationships with a high confidence level ($<$ 0.1) are used in this study (Muggeo et al., 2014). The linear relationships between breakpoints are described based on the trends: negative-positive (N—P), positive-negative (P—N), negative-negative (N—N) and positive-positive (P—P). Furthermore, principal component analysis (PCA) between geochemical properties of peat (TC, TN, D50, PHI and aCAR), hydrology (peat wetness), vegetation (pollen taxa) and fire (charcoal influx) parameters were analysed to understand the co-variance relationships between vegetation species and peatland conditions (Ijmker et al., 2012; Husson et al., 2017). The percentages of explained variance of PCA dimensions and squared cosine ($cos^2 > 0.5$) of the eigenvectors were used to quantify the quality of the relationships between parameters (Husson et al., 2017). All analyses were done in R software using the 'stats' (Ishiguro et al., 1997), 'AICcmodavg' (Mazerolle, 2006), 'FactoMineR' (Husson et al., 2017), and 'segmented' (Muggeo et al., 2014) packages.

4. Results

4.1. Geochronology and peat accumulation rates

The age-depth model indicates median calibrated ages ranging from ~2300 to −62 cal. yr BP and a mean peat accumulation rate of 0.31 mm yr^{-1} for the top 77 cm of the peat core (Fig. 4). Although the model identified the radiocarbon age at 80.5 cm as an outlier, the possibility of hiatus or missing peat layer between 64.5 cm (known radiocarbon age of 1013 ± 36 yr BP) and 77 cm can be ruled out as the pollen records showed continuity in trends (Table S1 in Supplementary data). The

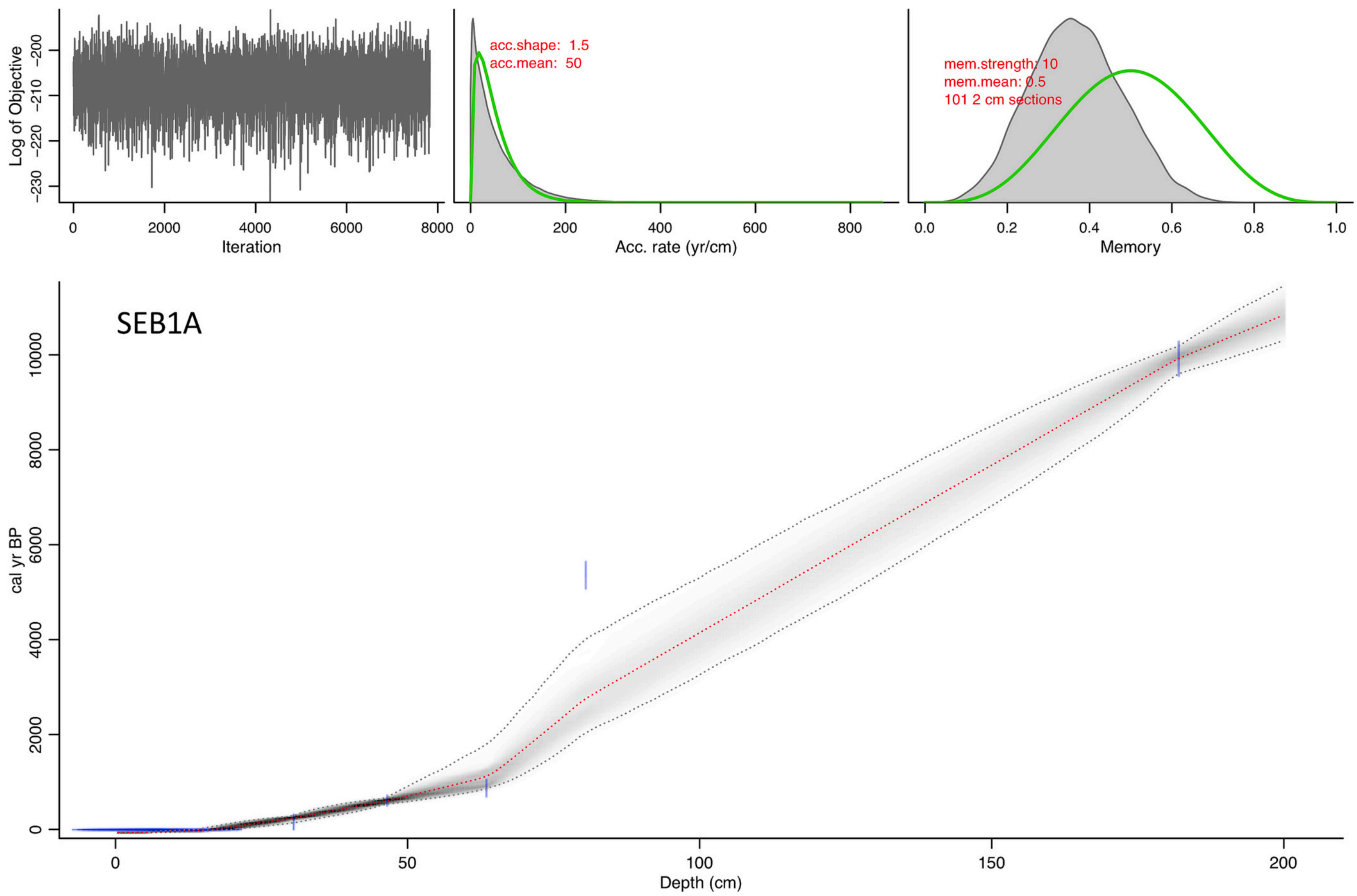

Fig. 4. Age–depth model generated using 'Bacon' model using a standard calibration curve for the pre and post-bomb periods for the Southern Hemisphere (SHCal20 and SH1–2). Prior information used in this model are the ages and uncertainties from ^{14}C (Table S1 in Supplementary data) and ^{210}Pb (Table S2 in Supplementary data) as presented by the blue line in the plot, gamma distribution shape of 1.5, a sedimentation rate of 50 years per cm, a memory strength of 10 and a memory mean of 0.5, and the year 2019 CE for peat surface. This study used the weighted median calibrated ages (cal. yr BP) produced at every 1 cm for the top 77 cm to represent the peat ages and accumulation rates. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

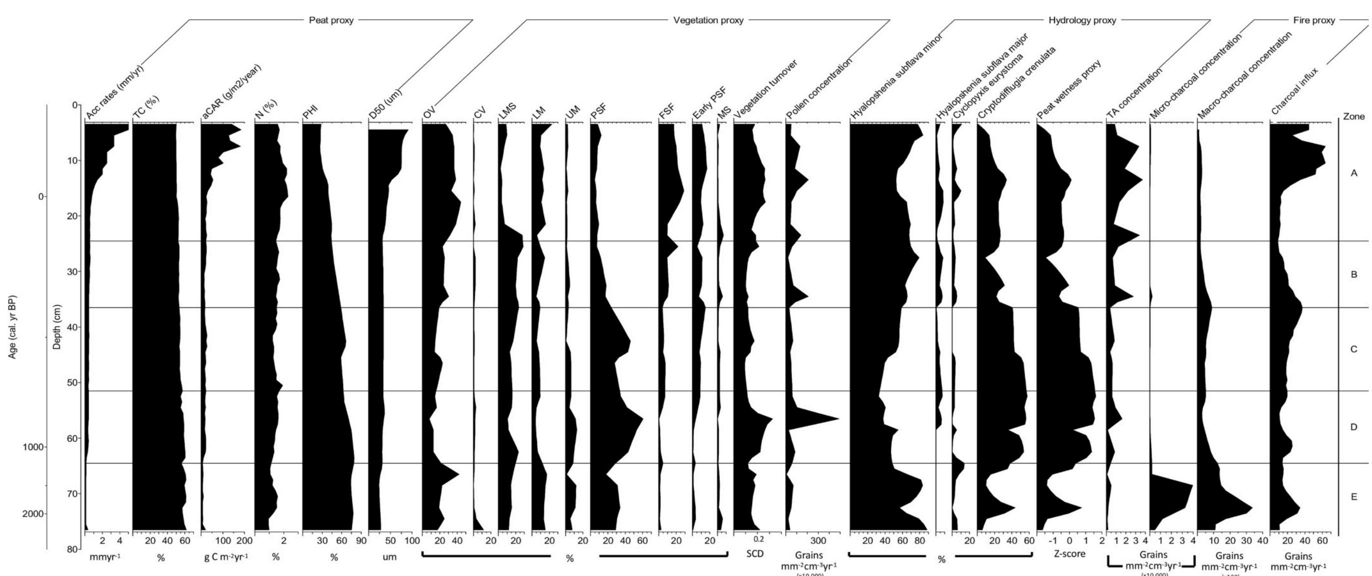

Fig. 5. Chronostratigraphy of the peat core showing variation in geochemical properties of peat conditions, vegetation groups, TA species concentration, peat wetness (wet hydrological conditions), and charcoal concentration and influx. The peat parameters include accumulation (acc) rates, total carbon (TC), apparent carbon accumulation rates (aCAR), total nitrogen (TN), peat humification index (PHI) and median peat grain size (D50). The vegetation groups are coastal vegetation (CV), upland montane (UM), lowland montane (LM), freshwater swamp forest (FSF), lowland vegetation mixed with swamp forest (LMS), peat swamp forest (PSF), early succession pioneer swamp forest (early PSF), open vegetation (OV) and monolete spores (MS).

continuity in vegetation species was also captured in the five vegetation zones using clustering analysis with the following ages: Zone A (134 to −62 cal. yr BP/ 24.5 to 0 cm), Zone B (374 to 135 cal. yr BP/ 36.5 to 24.5 cm), Zone C (756 to 375 cal. yr BP/ 51.5 to 36.5 cm), Zone D (1128 to 757 cal. yr BP/ 64.5 to 51.5 cm) and Zone E (~2300 to 1130 cal. yr BP/ 76.5 to 64.5 cm) (Fig. 4). The basal zone E has the slowest peat accumulation rate at 0.10 mm yr^{-1} and the finest peat materials with a mean grain size of 26.0 μm (Fig. 4 and Fig. 5). The accumulation rates increased rapidly to 0.35 mm yr^{-1} in zone D and remained relatively constant at 0.42 mm yr^{-1} and 0.51 mm yr^{-1} for zones C and B respectively (Fig. 4). The similar mean grain size between 32.4 and 33.4 μm in zone B, C and D also confirmed the steady peat accumulation rates during this period (Fig. 5). Transitioning to zone A, the sediment increased in mean grain size to 45.0 μm and had the fastest peat accumulation rates at 1.12 mm yr^{-1} (Fig. 4 and Fig. 5).

4.2. Palaeoecology and geochemical trends in each zone

4.2.1. Zone E (~2300 to 1130 cal. yr BP/ 76.5 to 64.5 cm)

The vegetation turnover (SCD) in this period ranges between 0.12 and 0.22. High vegetation turnover (SCD > 0.16) was due to a decrease in PSF species (33.9 to 17.8%) such as *Eurya, Ilex* and Euphorbiaceae, and an increase in OV species (17.4 to 42.3%) such as Poaceae, Asteraceae and palms from ~2300 to 2100 cal. yr BP and 1450 to 1200 cal. yr BP (Fig. 5 and Fig. 6). However, LM species (12.0 to 17.0%) such as *Agathis* and Arecaceae and LMS species (11.9 to 19.6%) such as Myrtaceae and *Casuarina* had constant presence in zone E (Fig. 6). The high vegetation turnover occurred primarily during the dry period (negative peat wetness z-scores) (Fig. 5 and Fig. 7- Panel IV and V). In contrast, the peak charcoal influx of 34.1 grains mm^{-2} cm^{-3} yr^{-1} occurred concurrently with the peak peat wetness z-score of 0.74, peak TN of 1.6% and peak PHI of 78.6% from 2000 to 1800 cal. yr BP (Fig. 5). For the majority of the period in zone E, the peatland was dry with mean peat wetness z-scores of −0.74, relatively high mean charcoal influx of 19.7 grains mm^{-2} cm^{-3} yr^{-1}, and peat conditions with the lowest mean TN of 1.2%, slowest mean aCAR (7.3 g C m^{-2} yr^{-1}), highest mean TC of 59.5% and highest mean PHI of 75.8% compared to the other zones (Fig. 5).

The GLM analysis to determine the drivers of charcoal influx ranked peat wetness as the main driver ($ar^2 = 0.50$, $p < 0.01$) with positive relationship which indicates that higher charcoal influx occurred during wet hydrological conditions (Table 1). Other drivers such as rainfall, vegetation turnover and sea level showed weak but significant GLM relationships to charcoal influx (Table 1). For the GLM analysis of vegetation turnover, peat wetness was also identified as the main driver ($ar^2 = 0.60$, $p < 0.01$), followed by PHI ($ar^2 = 0.45$, $p < 0.01$), both with negative relationships (Table 2). The log-likelihood function of GLM showed that high vegetation turnover corresponded to decreasing peat wetness z-score up to a threshold of −1.54 and increasing PHI up to a threshold of 75% (Table 2, Fig. S1 in Supplementary data). The other drivers (TC, charcoal influx and TN) had weak but statistically significant GLM relationships with vegetation turnover (Table 2).

4.2.2. Zone D (1128 to 757 cal. yr BP / 64.5 to 51.5 cm)

Vegetation turnover (SCD) in Zone D was the highest in our record with a mean of 0.21, and this was due to the large increase in PSF taxa (28.7 to 60.7%) such as *Campnosperma, Eurya, Ilex* and Euphorbiaceae, and LMS taxa (10.6 to 23.2%) such as Myrtaceae (Fig. 5 and Fig. 6). In contrast, the OV (7.7 to 21.2%) and LM (4.1 to 12.0%) groups decreased drastically compared with Zone E (Fig. 5). The PSF and LMS groups increased concurrently with high mean peat wetness z-scores of 1.14, high mean PHI of 73.6% and high mean TC of 58.3% (Fig. 5). There were also low variations of charcoal influx from 10.4 to 25.4 grains mm^{-2} cm^{-3} yr^{-1}, and a slight increase of aCAR from 7.2 to 21.6 g C m^{-2} yr^{-1} and TN from 1.1 to 1.6% (Fig. 5).

The GLM analysis to determine the drivers of charcoal influx ranked sea level as the primary cause ($ar^2 = 0.27$, $p < 0.01$) with a negative

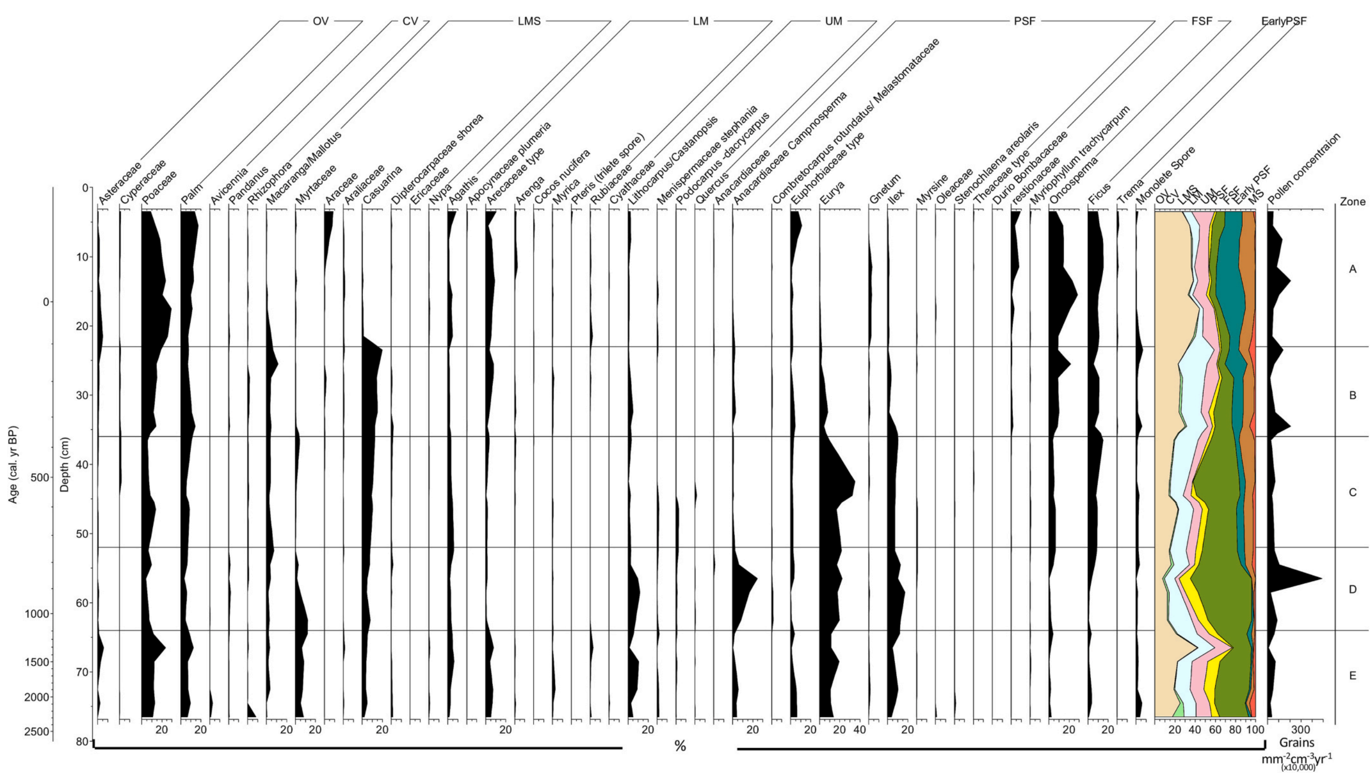

Fig. 6. Pollen taxonomy and their associated vegetation group changes through time, peat depth and vegetation zones. Vegetation species with at least 5% at any depth are shown here. Palm under the OV category includes Acaceae spp., *Elaeis guineensis* and undetermined palm species. The vegetation groups are coastal vegetation (CV), upland montane (UM), lowland montane (LM), freshwater swamp forest (FSF), lowland vegetation mixed with swamp forest (LMS), peat swamp forest (PSF), early succession pioneer swamp forest (early PSF), open vegetation (OV) and monolete spores (MS).

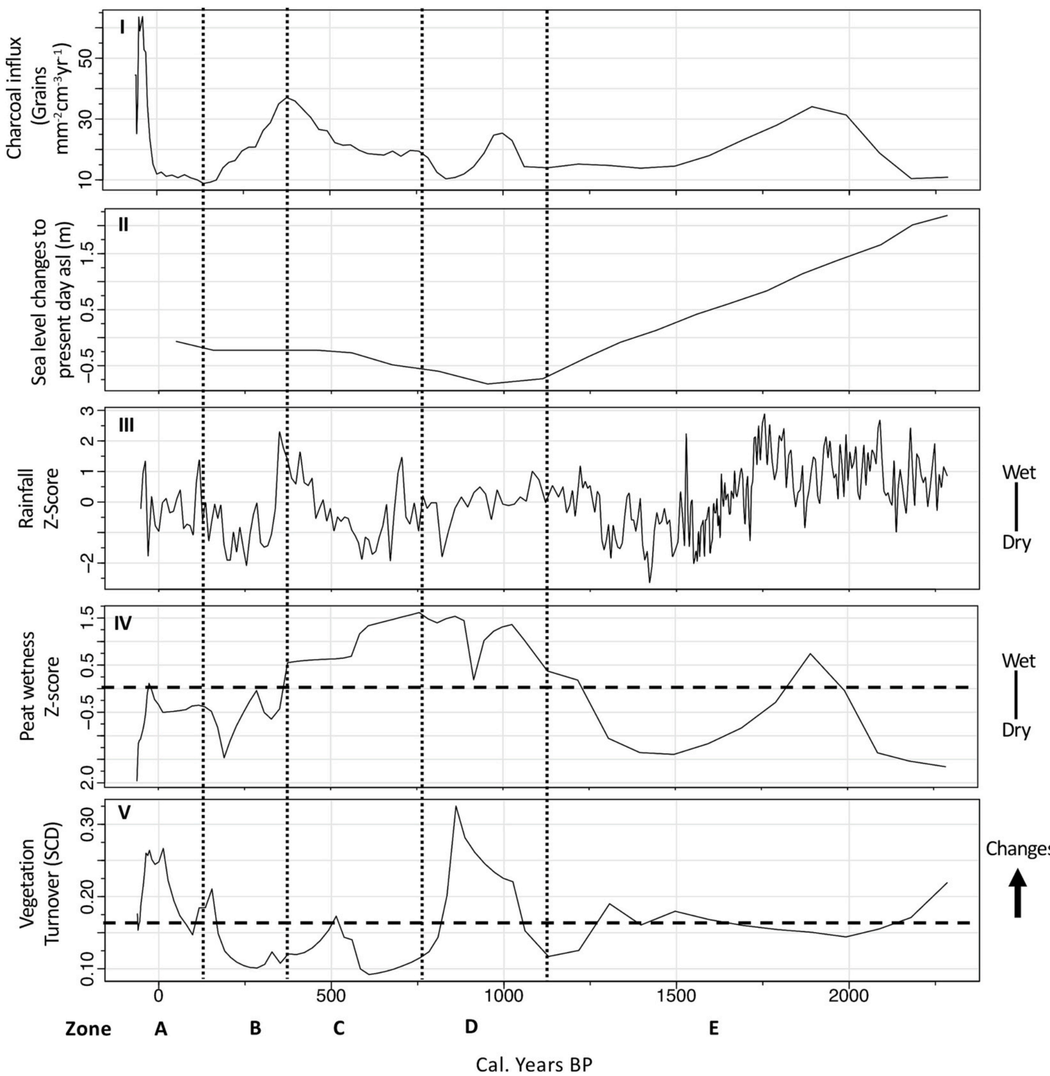

Fig. 7. Temporal variation of I) charcoal influx (this study), II) relative sea level based on present above sea level (asl) in Malacca straits (Geyh et al., 1979), III) regional rainfall in Liang Luar Cave, Flores, Indonesia (Griffiths et al., 2009), IV) local hydrological conditions (peat wetness) (this study) and V) vegetation turnover (this study).

relationship which indicates that decreasing sea level resulted in increased charcoal influx (Table 1). The negative relationship was also supported by the lowest sea level at −0.8 m asl corresponding to the peak in charcoal influx at 25.4 grains mm^{-2} cm^{-3} yr^{-1} at about ~1000 cal. yr BP (Fig. 7 - Panel I and II). Other drivers such as rainfall and peat wetness showed a weak but significant GLM relationship to charcoal influx (Table 1). In contrast, the GLM analysis to determine the drivers of vegetation turnover identified peat conditions such as TC ($ar^2 = 0.29$, p < 0.01) and TN ($ar^2 = 0.14$, $p < 0.01$) with positive relationships (Table 2). Furthermore, the log-likelihood function of GLM showed that increasing vegetation turnover corresponded to increasing TC and TN up to the thresholds of 59% and 1.36% respectively (Table 2, Fig. S2 in Supplementary data). Other drivers (PHI and peat wetness), except for charcoal influx, had weak but statistically significant GLM relationships with vegetation turnover (Table 2).

4.2.3. *Zone C (756 to 375 cal. yr BP / 51.5 to 36.5 cm)*

Vegetation turnover (SCD) was the lowest in Zone C across all zones, ranging from 0.09 to 0.17. This was due to the constant presence of PSF taxa (23.9 to 46.0%) such as *Eurya* and *Ilex*, and LMS (12.9 to 23.3%) taxa such as *Macaranga/Mallotus* and *Casuarina* (Fig. 6). The peak in vegetation turnover (0.17) occurred concurrently with the peak in PSF species (46.0%), decrease in charcoal influx (22.3 mm^2 cm^{-2} yr^{-1}), peak in PHI (66.5%) and slightly drier conditions (peat wetness z-scores of 0.63) at ~500 cal. yr BP (Fig. 5). Compared to zone D, any declining trends of PSF and LMS species were replaced by OV families such as grass and palm (13.9 to 23.1%) and early PSF succession taxa such as *Ficus* (7.8 to 14.9%) (Fig. 6). The changes in vegetation occurred concurrently with a lower mean peat wetness z-score of 1.0 and a higher charcoal influx range between 17.8 and 37.1 grains mm^{-2} cm^{-3} yr^{-1} (Fig. 6). This resulted in peat conditions with slightly lower mean TC of 54.5%, lower mean PHI of 62.0%, a large TN range from 1.2 to 1.9%, and an increase in aCAR from 16.4 to 26.4 g C m^{-2} yr^{-1} compared to zone D (Fig. 6).

The GLM analysis to determine the drivers of charcoal influx ranked peat wetness as the main driver ($ar^2 = 0.59$, $p < 0.01$) with a negative relationship which highlights drier conditions resulted in high charcoal influx (fire severity) (Table 1 and Fig. 7 - Panel I and IV). Other drivers such as sea level, rainfall and vegetation turnover showed a weaker but significant GLM relationship to charcoal influx (Table 1). In contrast, the GLM analysis to determine the drivers of vegetation turnover ranked PHI ($ar^2 = 0.69, p < 0.01$) first with a positive relationship, followed by peat wetness ($ar^2 = 0.60$, $p < 0.01$) with a negative relationship (Table 2). The log-likelihood function of this GLM showed that increasing

Table 1
Summary of GLMs of charcoal influx for the selection of significant drivers: sea level, regional rainfall, local hydrology (peat wetness) and vegetation turnover (VEG) for the sampling site in SNP. The GLMs are ranked based on the Corrected Akaike's information criterion (AICc) and delta AICc (dAICc). The GLM estimate, standard error, adjusted r^2 (ar^2) and t-value were also computed between the variables. The number of years (n = samples) used for the GLM analysis are stated for each zone except for *Charcoal influx ~ Sea level (*n* = 82)_and Charcoal influx ~Rainfall (*n* = 185) in zone A.

Zone	GLM (Charcoal influx ~ Variables)	Estimate	Standard error	ar^2	T-value	p(>|t|)	AICc	dAICc	GLM ranks
A	Sea level*	17.20	1.28	0.68	13.37	0.00	97	0	1
(*n* = 195)	Rainfall*	5.81	1.75	0.05	3.31	0.00	1553	1455	2
	Peat wetness	−22.51	3.66	0.16	−6.15	0.00	1621	1524	3
	VEG	119.64	28.35	0.08	4.22	0.00	1639	1542	4
	NULL						1654	1557	5
B	VEG	−167.54	14.69	0.35	−11.41	0.0	1606	0	1
(*n* = 238)	Rainfall	4.26	0.42	0.30	10.12	0.0	1625	19	2
	Peat wetness	11.61	1.17	0.29	9.87	0.0	1628	22	3
	Sea level	−564.1	89.0	0.14	−6.34	0.0	1673	67	4
	NULL						1708	103	5
C	Peat wetness	−11.26	0.47	0.59	−23.61	0.0	2111	0	1
(*n* = 380)	Sea level	36.95	1.80	0.52	20.49	0.0	2171	61	2
	Rainfall	4.61	0.26	0.44	17.41	0.0	2231	121	3
	VEG	101.73	12.82	0.14	7.94	0.0	2397	286	4
	NULL						2454	343	5
D	Sea level	−29.54	2.54	0.27	−11.65	0.0	2085	0	1
(*n* = 370)	Rainfall	1.74	0.46	0.03	3.76	0.0	2187	102	2
	Peat wetness	0.95	0.66	0.00	1.45	>0.1	2199	114	3
	NULL						2199	114	4
	VEG	−0.59	3.99	0.00	−0.15	>0.1	2201	116	5
E	Peat wetness	7.24	0.21	0.50	33.91	0.0	7069	0	1
(*n* = 1154)	Rainfall	3.01	0.18	0.20	17.01	0.0	7609	541	2
	VEG	−164.97	10.16	0.19	−16.23	0.0	7630	561	3
	Sea level	2.12	0.26	0.06	8.32	0.0	7801	732	4
	NULL						7866	797	5

vegetation turnover corresponded to increasing PHI threshold up to a threshold of 62%, increasing peat wetness z-score up to a threshold of 0.63 and increasing charcoal influx up to a threshold of 23 grains mm^{-2} cm^{-3} yr^{-1} (Table 2, Fig. S3 in Supplementary data). The other drivers (TN, charcoal influx and TC) had weak but statistically significant GLM relationships with vegetation turnover (Table 2).

4.2.4. Zone B (374 to 135 cal. yr BP / 36.5 to 24.5 cm)

The mean vegetation turnover (SCD) remained low in Zone B at 0.12 but a large range from 0.10 to 0.21 (Fig. 5). The dominant vegetation types were OV taxa (19.2 to 30.1%) such as Poaceae, and LMS taxa (19.8 to 28.6%) such as *Macaranga/Mallotus* and *Casuarina* (Fig. 6). The high vegetation turnover (SCD > 0.16) was the result of the large increase in LMS and FSF taxa (4.2 to 21.9%) such as *Oncosperma* during the low constant presence of PSF taxa (7.1%) such as *Eurya* and *Ilex* from 150 to 135 cal. yr BP (Fig. 6). The changes in vegetation coincided with drier conditions (peat wetness z-score ranged from −1.47 to 0.51) and large charcoal influx range from 8.8 to 37.0 grains mm^{-2} cm^{-3} yr^{-1} (Fig. 5). The peat conditions also showed a higher TN range from 1.4 to 1.7%, lower TC range from 52.2 to 53.6%, lower PHI range from 44.1 to 58.5%, and lower aCAR range from 12.8 to 24.4 g C m^{-2} yr^{-1} compared to zone C (Fig. 5).

The GLM analysis to determine the main drivers of charcoal influx ranked vegetation turnover as the main driver (ar^2 = 0.35, p < 0.01) with a negative relationship, which means changes in vegetation types resulted in high charcoal influx (Table 1 and Fig. 5). Other drivers such as rainfall, hydrology and sea level showed weak but significant GLM relationships with charcoal influx (Table 1). For the GLM analysis of vegetation turnover, PHI (ar^2 = 0.44, p < 0.01) was ranked first with a negative relationship, followed by charcoal influx with a negative relationship (ar^2 = 0.35, p < 0.01) (Table 2). The log-likelihood function of GLM showed that decreasing vegetation turnover corresponded to increasing PHI up to a threshold of 48% and increasing charcoal influx up to a threshold of 16 grains mm^{-2} cm^{-3} yr^{-1} (Table 2, Fig. S4 in Supplementary data). The other drivers (TC, peat wetness and TN) had weak but statistically significant GLM relationships with vegetation turnover (Table 2).

4.2.5. Zone A (134 to −62 cal. yr BP / 24.5 to 0 cm)

The vegetation turnover (SCD) during the last ~200 years is high with values ranging from 0.15 to 0.27 and a mean of 0.20 (Fig. 5). The dominant vegetation present were OV families (26.9 to 44.3%) such as Poaceae and palm, and FSF taxa (9.5 to 28.9%) such as Restionaceae and *Oncosperma* (Fig. 6). Compared to zone B, some LMS taxa such as *Casuarina* and *Macaranga/Mallotus* decreased markedly while early PSF and LM taxa such as Arecaceae, *Agathis,* Apocynaceae*, Arenga* and *Ficus* increased (Fig. 6). The changes in vegetation occurred concurrently with the driest conditions in the record (peat wetness z-scores range from −1.95 to 0.11) and the highest maximum charcoal influx (fire severity) from 8.9 to 63.7 grains mm^{-2} cm^{-3} yr^{-1} (Fig. 5). The autogenic effects resulting from fire events and incomplete decomposition of OM at surface peat could have produced the largest range of aCAR from 19.1 to 182.9 g C m^{-2} yr^{-1}, the lowest TC from 49.5 to 52.8%, the highest TN from 1.5 to 2.3% and the lowest PHI from 26.8 to 44.6% (Fig. 5).

The GLM analysis of the charcoal influx variability ranked peat wetness as the main driver with a negative relationship (ar^2 = 0.16, p < 0.01) (Table 1 and Fig. 7 - Panel I and IV). Other drivers such as rainfall, vegetation and sea level showed significant but weak GLM relationships to charcoal influx or had lower sample sizes (n-values) (Table 1). In contrast, the GLM analysis to determine the drivers of vegetation turnover ranked TN first (ar^2 = 0.65, p < 0.01) with a positive relationship, followed by TC with a negative relationship (ar^2 = 0.37, p < 0.01) (Table 2). The log-likelihood function of this GLM showed that increasing vegetation turnover corresponded with the increasing TN up to a threshold of 1.63%, increasing TC up to a threshold of 51% and increasing charcoal influx up to a threshold of 13.0 grains mm^{-2} cm^{-3} yr^{-1} (Table 2, Fig. S5 in Supplementary data). The other drivers (PHI, peat wetness and charcoal influx) had weak but statistically significant GLM relationships with vegetation turnover (Table 2).

Table 2
Summary GLMs of vegetation turnover (VEG) for the selection of significant drivers or responses of peatland ecosystem (TC, TN, local hydrology (peat wetness), PHI and charcoal influx) for the sampling site in SNP. The GLMs are ranked based on the Corrected Akaike's information criterion (AICc) and delta AICc (dAICc). Threshold values and linear regression trends between breakpoints that result in vegetation turnover were identified using the segmented relationship of the log-likelihood function in the GLM analysis. *The two linear relationships between breakpoints are described here as negative-positive (N—P), positive-negative (P—N), negative-negative (N—N) and positive-positive (P—P) (Supplementary data for details). The number of years (n = samples) used for the GLM analysis is stated for each zone.

Zone	GLM								Log-likelihood coefficient	
	Variable	GLM rank	AICc	dAICc	% Deviance	p(>|t|)	adjusted R-squared	T-value	Threshold values	Linear relationships*
A (n = 195)	VEG ~ TN	1	−925	0	35	0.01	0.65	19.11	1.63%	N-P
	VEG ~ TC	2	−809	116	63	0.01	0.37	−10.73	51%	P-N
	VEG ~ PHI	3	−741	184	89	0.01	0.11	−4.97	41%	P-N
	VEG ~ Peat wetness	4	−740	185	89	0.01	0.11	4.90	−0.37	P-P
	VEG ~ charcoal influx	5	−735	191	91.6	0.01	0.07	4.22	13 grains mm^{-2} cm^{-3} yr^{-1}	P-N
	NULL	6	−720	206						
B (n = 238)	VEG ~ PHI	1	−1135	0	56	0.01	0.44	−13.61	48%	N-P
	VEG ~ charcoal influx	2	−1102	33	65	0.01	0.35	−11.41	16 grains mm^{-2} cm^{-3} yr^{-1}	N-P
	VEG ~ TC	3	−1004	132	97	0.01	0.02	2.57	53%	N-P
	VEG ~ Peat wetness	4	−1001	134	98	0.05	0.01	−1.97	−0.46	P-N
	VEG ~ TN	5	−1001	134	98	0.05	0.01	−1.92	1.63%	P-N
	NULL	6	−999	136						
C (n = 380)	VEG ~ PHI	1	−2267	0	31	0.01	0.69	29.0	62%	P-P
	VEG ~ Peat wetness	2	−2176	91	39	0.01	0.60	−24.15	0.63	P-N
	VEG ~ TN	3	−1923	344	77	0.01	0.23	−10.80	1.33%	N-P
	VEG ~ charcoal influx	4	−1879	388	86	0.01	0.14	7.94	23 grains mm^{-2} cm^{-3} yr^{-1}	P-N
	VEG ~ TC	5	−1860	407	90	0.01	0.10	−6.41	55%	N-P
	NULL	6	−1823	444						
D (n = 370)	VEG ~ TC	1	−1154	0	71	0.01	0.29	12.27	59%	P-N
	VEG ~ TN	2	−1083	71	86	0.01	0.14	7.75	1.36%	P-N
	VEG ~ PHI	3	−1032	122	99	0.02	0.01	2.19	72%	P-N
	VEG ~ Peat wetness	4	−1030	124	99	0.08	0.01	1.72	1.53	P-N
	NULL	5	−1029	125						
	VEG ~ charcoal influx	6	−1027	127						
E (n = 1154)	VEG ~ Peat wetness	1	−6955	0	40	0.01	0.60	−42.03	−1.54	N-N
	VEG ~ PHI	2	−6580	375	55	0.01	0.45	−30.95	75%	P-N
	VEG ~ TC	3	−6556	399	56	0.01	0.44	30.23	60%	P-P
	VEG ~ charcoal influx	4	−6119	836	81	0.01	0.19	−16.23	14 grains mm^{-2} cm^{-3} yr^{-1}	N-N
	VEG ~ TN	5	−5920	1034	97	0.01	0.03	−6.28	1.04%	N-P
	NULL	6	−5883	1071						

4.3. Principal component analysis: factors controlling vegetation species

The principal component analysis (PCA) between pollen taxonomy and peatland conditions showed a cumulative explained variance of 40.9% in the PCA dimensions (Dim) (Fig. 8). For zone C, D and E, the PCA plot showed a clear boundary on the positive Dim1 with positive co-variance relationships to peatland conditions such as peat wetness, TC and PHI (Fig. 8). In the PCA plot, the pollen taxonomy for zone E consists of LM and LMS taxa such as Myrtaceae, *Macaranga/Mallotus*, *Agathis, Myrica*, and Rutaceae, and some PSF taxa such as *Eurya*, *Campnosperma*, and *Ilex,* which had positive co-variance relationships to PHI, TC and peat wetness (Fig. 8). For zone C and D, the PCA plot showed predominantly PSF taxa such as *Eurya*, *Campnosperma*, *Ilex*, and *Combretocarpus* and LMS taxa such as *Casuarina* and Dipterocarpaceae *(Shorea)* which had positive co-variance relationships to peat wetness (Fig. 8).

For zones A and B, the PCA plot showed an overlapped boundary on the negative Dim 1 with positive co-variance relationships to peatland conditions such as D50, aCAR, TN and charcoal influx (Fig. 8). The PCA plot for zone A and B showed a complete shift from PSF taxa except for Euphorbiaceae towards LM taxa such as *Plumeria* (Apocynaceae)*and Arenga*, FSF taxa such as *Myriophyllum*, Restionaceae and Theaceae type, early succession PSF taxa such as *Ficus and Trema,* and OV taxa such as Cyperaceae and palms (Fig. 8). All these vegetation species had positive co-variance relationships with D50, aCAR and charcoal influx (Fig. 8). The PCA plot of pollen taxonomy for zones A and B also had other vegetation species which had positive co-variance relationships to TN such as *Oncosperma* (FSF), *Gnetum* (PSF), Poaceae *and* Asteraceae *(OV),* Arecaceae (LM) and Rubiaceae (LM) (Fig. 8).

5. Discussion

5.1. Drivers of charcoal abundance in peat

Long-term reconstruction of fire events in tropical peatlands generally assigns high charcoal abundance in peat to be the result of reduced rainfall (drought associated with El Niño conditions) and human activities, in particular, peat drainage and fire use (Anshari et al., 2001; Hope et al., 2005; Dommain et al., 2011; Biagioni et al., 2015; Cole et al., 2015; Page et al., 2002). However, charcoal abundance, as presented as influx or concentrations, in peat is also dependent on the biofuel composition (vegetation types) in the peatland, which in turn influences the amount of biomass and moisture content (Bradstock, 2010; Adeleye et al., 2020). Additionally, sea level variability and fluvial transport mechanisms (e.g. river overflow) can lead to charcoal redeposition in peatland with high concentrations of charcoal in peat which may not be related to the contemporaneous fire regime (Muller, 1963; Hanebuth et al., 2000; Hanebuth and Stattegger, 2003; Dommain et al., 2011).

The GLM analysis revealed that the presence of high charcoal influx and its drivers differ across vegetation zones. During the late Holocene, the charcoal influx in zone E was positively related to peat wetness in

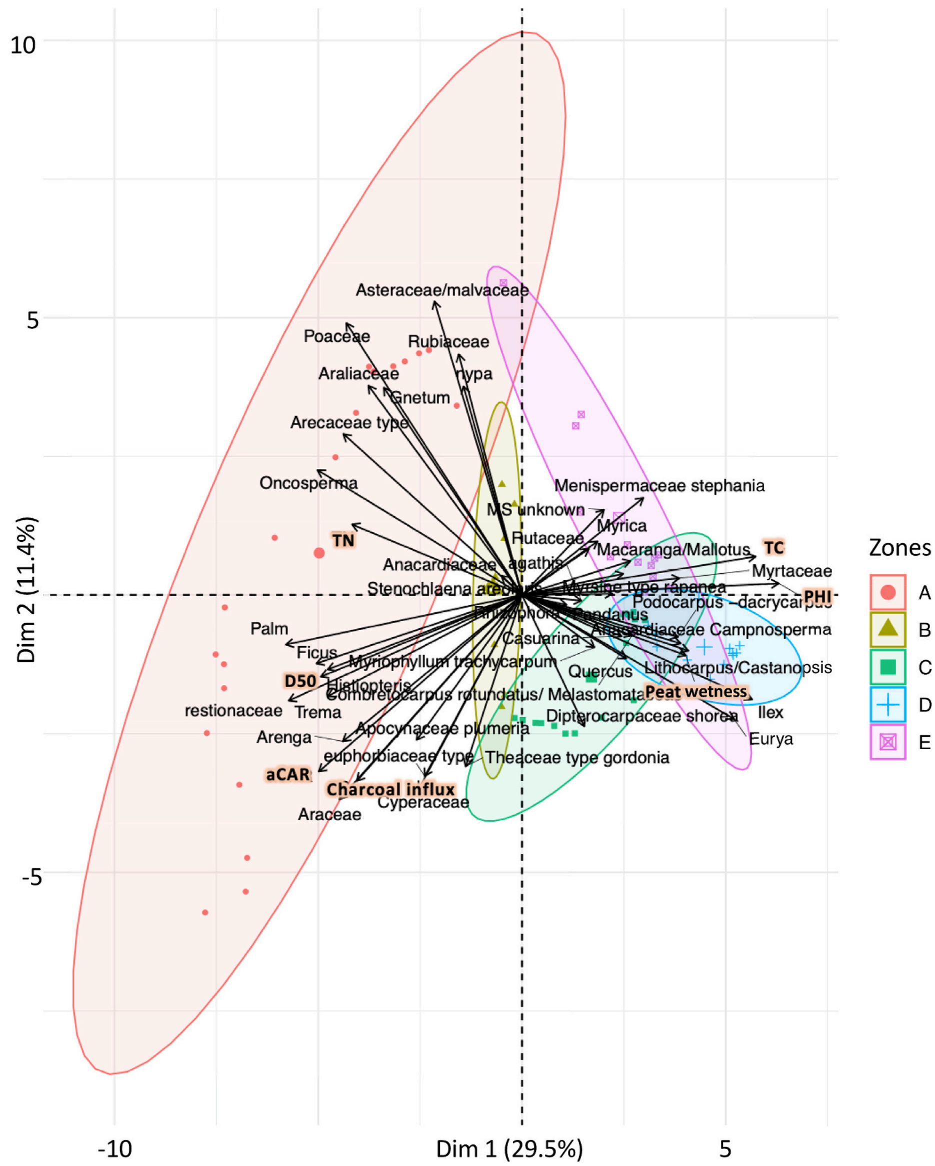

Fig. 8. PCA plot between pollen taxonomy and peatland conditions with explained variance of 29.5% and 11.4% in PCA Dim 1 and Dim 2 respectively. Only pollen taxa with high-quality representation ($\cos^2 > 0.5$) are presented here.

GLM and peaked at 34.1 grains mm^{-2} cm^{-3} yr^{-1} during a relatively wet period from 2000 to 1800 cal. yr BP (Fig. 7 - Panel I and IV; Table 1). These wetter peat conditions coincided with a regional increase in rainfall during the late Holocene (5000 to 1700 cal. yr BP) due to enhanced warm pool convection by increased Pacific zonal sea surface temperature (SST) (Fig. 7 - Panel I and III) (Partin et al., 2007; Griffiths et al., 2009). Notably, the dry periods in zone E did not result in higher charcoal influx and are associated with decreased regional rainfall during intense El Niño events between 1700 and 1200 cal. yr BP (Fig. 7 - Panel I and III) (Griffiths et al., 2009; Partin et al., 2007; Moy et al., 2002). These observations of high charcoal influx and micro-charcoal concentration during a relatively wet period point to the possibility of charcoal redeposition from surrounding peatland. The high sea level during this period at inland Kalimantan peatland may have elevated the local water table and reversed river flow leading to a decrease in hydraulic gradient in the landscape and possible deposition of organic material (e.g. charcoal) in locations adjacent to rivers (Fig. 9) (Glaser et al., 2004; Hanebuth et al., 2000; Dommain et al., 2011; Hapsari et al., 2017).

After 1129 cal. yr BP (zone D), the mean charcoal influx was the lowest (16.5 grains mm^{-2} cm^{-3} yr^{-1}) and sea level changes at the Malacca straits were the main driver of the charcoal influx in GLM with a negative relationship (Fig. 7 - Panel I and II and Table 1). The lowest sea level which coincided with a slight peak in charcoal influx was also observed across the Sunda Shelf between 1050 and 950 cal. yr BP (Fig. 7 - Panel I and II) (Geyh et al., 1979; Sathiamurthy and Voris, 2006). During this low sea level, rainfall trends were high in the Borneo and Sumatra region, resulting in saturated peat conditions with the highest mean peat wetness z-score (Fig. 7 - Panel IV) (Griffiths et al., 2009; Dommain et al., 2011). The wet conditions during this period could have acted as a fire suppression barrier for the peatland (Hapsari et al., 2017; Wösten et al., 2008). Hence, the peak in charcoal influx between 1050 and 950 cal. yr BP was possibly due to the deposition of charcoal when the sea level subsided (Hope et al., 2005; Hanebuth et al., 2000). Furthermore, the insignificant GLM relationship between charcoal influx and vegetation turnover supported the possibility of minimal fire events in this period, i.e. there is no evidence of direct impacts of fires on the vegetation (Table 1) (Hirano et al., 2012).

Subsequently, sea level conditions stabilised for the following ~400 years (zone C) but charcoal influx showed increasing trends with values

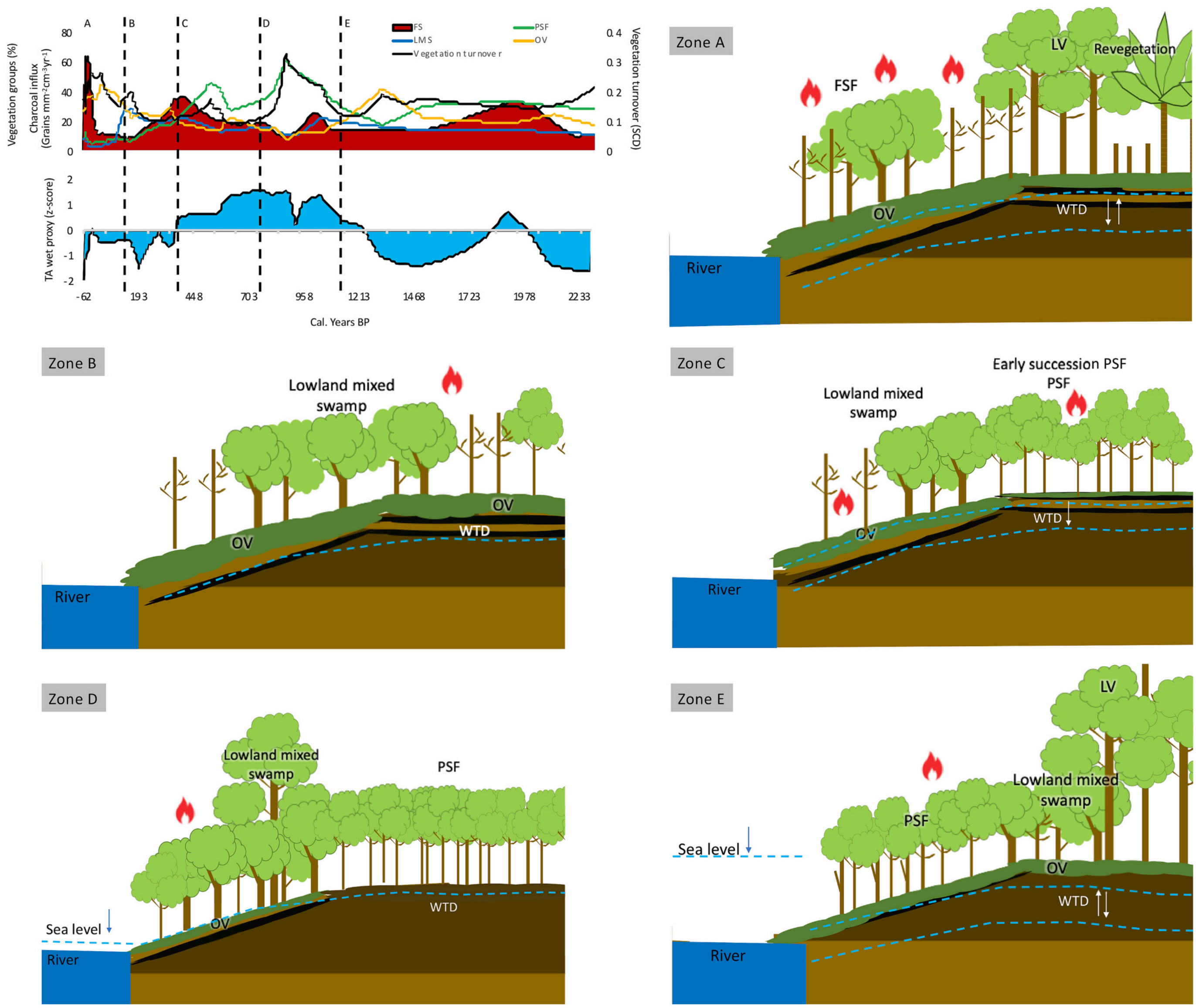

Fig. 9. Illustration of the changes in the peatland ecosystem from zone A, B, C and D. Variations of charcoal influx, hydrological condition and vegetation turnover are included in the top-left image to provide an understanding of the changes in vegetation groups over the ~2300 cal. yr BP. The acronyms used in the illustration are water table depth (WTD), lowland vegetation (LV), freshwater swamp forest (FSF), peat swamp forest (PSF), early pioneer swamp forest (early succession PSF), and open vegetation (OV).

of up to 37.1 grains mm^{-2} cm^{-3} yr^{-1} from 756 to 375 cal. yr BP (Fig. 7 - Panel I). The GLM identified peat wetness as the primary driver of charcoal influx with a negative relationship (Table 1, Fig. 7 - Panel I and IV). The slightly drier peat wetness, lower rainfall conditions and stable sea level during this period could have lowered the groundwater levels which enabled more fire events in the peatland (Fig. 9) (Dommain et al., 2011; Hirano et al., 2012). Other palaeoecology studies of the inland peatlands of Jambi and Lake Kalimpaa in Sulawesi also observed peaks in charcoal concentration between 675 and 654 cal. yr BP and 500 and 300 cal. yr BP, respectively, which coincided with ENSO warm events and the failure of the monsoon in the Indo-Pacific region (D'arrigo et al., 2006; Hapsari et al., 2021; Wündsch et al., 2014; Biagioni et al., 2015).

With the shift towards dry peat conditions and decreasing rainfall, the mean charcoal influx remained high at 20.6 grains mm^{-2} cm^{-3} yr^{-1} but showed decreasing trends from 374 to 135 cal. yr BP (zone B, Fig. 7 - Panel I, III and IV). The GLM analysis identified vegetation turnover as the primary driver of charcoal influx with a negative relationship; i.e. a shift from PSF to OV and LMS vegetation species in this zone is associated with decreasing charcoal influx (Table 2, Fig. 9). Since PSF vegetation has a higher biofuel composition (i.e. biomass) than OV, this likely contributed to higher charcoal influx at the beginning of this period at Sebangau site (Hapsari et al., 2017; Bradstock, 2010; Adeleye et al., 2020). The dry conditions during this period could have also provided optimal conditions for the combustion of OM from PSF and OV (Page and Hooijer, 2016).

Transitioning to zone A (134 to 62 cal. yr BP), the charcoal influx varied from 8.9 to 63.7 grains mm^{-2} cm^{-3} yr^{-1} (Fig. 7 - Panel I). The GLM identified peat wetness as the main driver for charcoal influx with higher charcoal influx occurring during drier conditions (Table 1 and Fig. 7 - Panel I and IV). The highest charcoal influx and driest conditions during this period could be due to extreme El Niño events in the Indo-Pacific region in recent years (BOM, 2021; Susilo et al., 2013) and anthropogenic activities (Dohong et al., 2017). Historical archives documented land use changes in Central Kalimantan after colonialization by the Dutch during the 1850s to 1950s AD (Chao et al., 2013). Furthermore, peatland drainage caused by logging and canal construction from the 1970s around the study site could have increased the fire susceptibility of PSF (Page et al., 2009; Jaenicke et al., 2010; Ritzema et al., 2014). Other contemporary causes of fires include accidental ignitions and intentional burning relating to land conflicts (Cattau et al., 2016; Gaveau et al., 2014; Dohong et al., 2017).

5.2. Drivers of vegetation turnover from ~2300 cal. yr BP to present

5.2.1. From ~2300 to 1129 cal. yr BP (Zone E): Mixed peat swamp forest (PSF) and open vegetation (OV)

The changes to the peatland ecosystem in Sebangau in the late Holocene are likely to have triggered the transitions of vegetation types and influenced the proportion of PSF species present (Wösten et al., 2008; Page et al., 1999; Hicks et al., 2003; Lampela et al., 2014). Between ~2300 and 1129 cal. yr BP, multiple vegetation types were present but PSF species were dominant in SNP (Fig. 8 and Fig. 9). However, a transition to primarily OV species from 1450 to 1200 cal. yr BP coincided with the intense El Niño drought conditions documented in several palaeoclimate records from 1700 to 1200 cal. yr BP (Fig. 7 – Panel III) (Moy et al., 2002; Griffiths et al., 2009; Conroy et al., 2008). The GLM of vegetation turnover also identified peat wetness as the main driver with a negative relationship (Table 2). Furthermore, the decreasing trends of PHI from 1450 to 1200 cal. yr BP could be due to the decrease in recalcitrant OM (i.e. a shift from PSF to OV species) available for aerobic decomposition (Fig. 5) (Ponette-González et al., 2016; Berg and Mcclaugherty, 2008; Dom et al., 2021).

In contrast, the relative dry peat conditions and the constant presence of dominant PSF from ~2300 to 1450 cal. yr BP could have contributed to a high amount of recalcitrant OM and prolonged aerobic decomposition processes which generated high PHI (Fig. 5) (Yule and Gomez, 2009; Dom et al., 2021; Dommain et al., 2011). The GLM of vegetation turnover also identified PHI as a possible response with a negative relationship (Table 2). Aerobic peat decomposition can result in low peat accumulation and aCAR which was observed for this vegetation zone (Lampela et al., 2014; Dommain et al., 2011). Similar trends of low carbon accumulation rates and high peat decomposition (high stable N isotopes) were also recorded in the Sungai Buluh peatland in Sumatra during this period (Hapsari et al., 2021).

5.2.2. From 1128 to 375 cal. yr BP (Zone C and D): predominantly peat swamp forest (PSF)

The expansion of PSF species (i.e. *Campnosperma, Eurya, Ilex* and Euphorbiaceae) from 1128 to 375 cal. yr BP occurred when the sea level decreased to the present levels and peat conditions were wet (Fig. 7 - Panel II and Fig. 9) (Sathiamurthy and Voris, 2006). Other palaeoecology studies in Kutai and Sungai Buluh peatlands also showed a similar transition from mixed riverine vegetation to PSF from 1200 cal. yr BP (Morley, 1981; Hope et al., 2005; Hapsari et al., 2017). The decrease in mixed-riverine vegetation during this period in these studies was possibly due to the reduction in overbank flow, nutrient deposition from rivers and fluvial seed dispersal (Hughes and Rood, 2003). In contrast, the increase in PSF could be due to minimal inundation at the time of low sea level that allowed the cambial growth of roots of swamp species such as *Combretocarpus rotundas* (Osaki et al., 2021; Kozlowski, 2002). The expansion of PSF under the wet conditions (positive peat wetness z-scores) also contributed to the increase in recalcitrant OM deposited in the peat which increased the mean peat accumulation rates and aCAR (Fig. 5) (Yule et al., 2016).

Despite the similarities in the dominant vegetation, the GLM identified the drivers of vegetation turnover to be TC and TN respectively with positive relationships for zone D, and PHI and peat wetness with positive and negative relationships respectively for zone C (Table 2). The differences in drivers of vegetation turnover suggest that the nutrients (high TN) deposited from the rivers when sea level subsided in Zone D may have contributed to the expansion of PSF species such as *Campnosperma, Eurya, and Ilex* (Hope et al., 2005; Hanebuth et al., 2000). Furthermore, the deposition of OM from these PSF species in zone D could have produced the outcome of higher TC in peat (Fig. 5 and Fig. 6) (Ponette-González et al., 2016; Berg and Mcclaugherty, 2008). In contrast, the transition to slightly drier conditions in zone C allowed some PSF species (i.e. *Eurya* and *Ilex*) to increase but resulted in the OM undergoing aerobic decomposition (high PHI) (Fig. 5 and Fig. 6) (Burrows et al., 2014). However, PSF species such as *Campnosperma* decreased significantly as it needs a high water table to survive compared to *Eurya* and *Ilex* which can cope with periodic flooding (Saw, 2010; Smith et al., 2022).

After 520 cal. yr BP in zone C, the increasing charcoal influx (fire severity) and slightly drier conditions eventually led to the decline of all PSF species and lower PHI possibly due to the burning of recalcitrant OM (Fig. 6 and Fig. 9) (Berg and Mcclaugherty, 2008; Dom et al., 2021). The mean TN also increased in zone C probably due to fire events that aided in the mineralisation and availability of N and other elements (i.e. P, K, Mg, S and Ca) in peat (Wang et al., 2014; Certini, 2005, Turner et al., 2007). Other peatland studies in Sumatra also observed a PSF decline from 1050 to 600 cal. yr BP but attributed it to anthropogenic activities during the occupation of the region by the Malayu empire (Biagioni et al., 2015; Hapsari et al., 2017). However, there is no recorded evidence of anthropogenic influence at our study site.

5.2.3. From 374 to 135 cal. yr BP (Zone B): transition to open vegetation (OV) and lowland mix swamp (LMS)

From 374 cal. yr BP, PSF species such as *Eurya and Ilex* species decreased, and the dominant vegetation was replaced by LMS (i.e. *Macaranga/Mallotus* and *Casuarina*) and OV (i.e. Poaceae) in high charcoal influx (fire severity) and very dry conditions (Fig. 6 and Fig. 9) (Saw, 2010; Smith et al., 2022). Similar transitions from PSF to OV also occurred in Sungai Buluh and Air-Hitam peatlands in Sumatra in this period due to dry conditions associated with El Niño events and high fire frequency related to anthropogenic activities (Hapsari et al., 2017; Biagioni et al., 2015). Furthermore, the mean TN was higher than in the previous period, probably due to the release of N during aerobic decomposition or mineralisation of N during high fire events (Fig. 5) (Turner et al., 2007; Tata et al., 2018; Hapsari et al., 2017). The aerobic peat conditions and predominant OV species may have contributed to the decrease in mean aCAR compared to zone C (Page et al., 1999; Berg and Mcclaugherty, 2008).

Despite the dry conditions, the GLM identified PHI and charcoal influx as primary responses of vegetation turnover with negative relationships (Table 2). Therefore, the lower PHI and charcoal influx during high vegetation turnover might be the outcome of lower recalcitrant OM available for decomposition and burning due to the transition from PSF to OV and LMS (Fig. 5 and Fig. 9) (Berg and Mcclaugherty, 2008; Dom et al., 2021). In addition, the vegetation turnover could be due to anthropogenic activities as there were historical archives on the practice of small-scale swidden agriculture on alluvial soils (that used to be covered by peat) by the Dayak community in Central Kalimantan during this period (Chao et al., 2013; Jewitt et al., 2014; Wiesner and Dargusch, 2022).

5.2.4. From 134 to −62 cal. yr BP (Zone A): mixed OV, LM, fresh swamp forest (FSF) and early succession PSF

Vegetation turnover during the last ~200 years was the highest in the record, mainly due to large variations in the dominant OV (i.e. Poaceae and Palm), FSF (i.e. *Oncosperma* and Restionaceae), LM (i.e. *Agathis, Arenga* and Arecaceae) and early PSF (i.e. *Ficus*) during very high charcoal influx (fire severity) (Fig. 6 and Fig. 9). The transition to predominantly OV following large-scale fire events in peatland was also observed in palaeoecological studies elsewhere in Indonesia during this period, and this was due to a combination of ENSO intensification and human disturbances (Yulianto et al., 2004; Biagioni et al., 2015; Hapsari et al., 2021; Cole et al., 2015; Cole et al., 2019). However, the GLM of vegetation turnover ranked charcoal influx last, which suggests this relationship could be obscured by anthropogenic activities. The expansion of OV could be the result of deforestation for logging of pulpwood and timber around the site from the 1970s to the 1990s (Smith et al., 2003), and the construction of a canal network by illegal loggers from 1997 to assist in the removal of logs from the forest (Page et al., 2009; Jaenicke et al., 2010; Ritzema et al., 2014).

Instead, TN and TC were identified as possible responses of vegetation turnover in GLM with positive and negative relationships respectively (Table 2). The highest TN in this period could be the outcome of the release of N during the aerobic decay of surface leaf litter in dry conditions (Wasis et al., 2019; Tata et al., 2018; Turner et al., 2007). Furthermore, the high maximum charcoal influx in this period could have raised the pH of the peatland surface (Tata et al., 2018), although this may have been a transitory effect (Page et al., 2022; Saharjo and Nurhayati, 2005). Less acidic conditions can promote the absorption of phenolic compounds (i.e. high elemental concentrations) by residual charcoal in peat which acts as a nitrification-inhibitor (NI) (Wang et al., 2014; Turner et al., 2007). The high TN and other elemental concentrations (i.e. P, K, Mg, S and Ca) were also observed in peat surface in regional peatland sites which could be attributed to bioaccumulation of fresh OM and NI phenomenon (Turner et al., 2007; Weiss et al., 2002; Hapsari et al., 2017). The transition to OV species and high fire severity events as observed from high charcoal influx could reduce the amount of recalcitrant OM in the peat, which decreased the PHI and TC content of peat (Fig. 5) (Berg and Mcclaugherty, 2008; Dom et al., 2021). However, the peat accumulation rates and aCAR were the highest due to the incomplete decomposition of recently deposited OM (i.e. high bulk density) in surface peat (Fig. 5) (Young et al., 2021).

5.3. Insights for restoration: thresholds of vegetation turnover to peatland ecosystem changes

This study identified sea level changes as possible drivers of high charcoal influx during ~2300 to 757 cal. yr BP (Zones D and E) while fire, hydrology and vegetation changes caused by local climate and anthropogenic factors were responsible for high charcoal influx between 756 to −62 cal. yr BP (Zones A, B and C). For climate and anthropogenic-driven fire events, PSF species such as *Eurya* and *Ilex* in zone C were able to cope with fire events and increased together with charcoal influx up to the threshold of 23 grains mm^{-2} cm^{-3} yr^{-1} before declining (Table 2, Fig. S3 in Supplementary data). In contrast, LMS and OV species in zone A increased abundance at lower charcoal influx threshold of 13 grains mm^{-2} cm^{-3} yr^{-1} before declining slightly at higher charcoal influx (Table 2, Fig. S5 in Supplementary data). Furthermore, the PCA identified tree taxa such as Euphorbiaceae (PSF), *Arenga (LM), Ficus (*early PSF), and *Trema (*early PSF) to be tolerant to high fire severity based on charcoal influx in the long term (Fig. 8). This information provides a gauge of different vegetation species' fire intensity tolerances, which could prove useful when deciding which species to use in restoration (i.e. revegetation efforts) (Froyd and Willis, 2008; Wingard et al., 2017; Bunting and Whitehouse, 2008).

Peat wetness also determined PSF species persistence, with *Eurya* and *Ilex* thriving under wet conditions (z-score threshold of 0.63) in zone C (Table 2) (Saw, 2010; Smith et al., 2022). In contrast, the drier peat conditions with a z-score threshold of −1.54 caused a shift from PSF to OV in zone E (Table 2). This implies that wet peat conditions provided the hydrological conditions needed for the growth of PSF species (Couwenberg et al., 2010; Limpens et al., 2008). This information is relevant to consider in the context of developing peatland rewetting strategies; i.e., different groundwater levels will better support different vegetation species (Graham et al., 2017; Dommain et al., 2016; Smith et al., 2022). Similarly, our data reiterates the importance of considering the groundwater level of the environment when choosing target species for peatland revegetation efforts (Graham et al., 2017).

The peatland in the last 200 years experienced frequent shifts between vegetation species, wet and dry peat conditions, and between very high and low charcoal influx (Fig. 9), reflecting the higher ecosystem's sensitivity to climate change and anthropogenic activities compared to the period before this (Susilo et al., 2013; Parish et al., 2002). Furthermore, the peat conditions of the disturbed peatland during this period may have resulted in less acidic conditions and higher minerals in peat (Tata et al., 2018; Wang et al., 2014). This baseline information suggests that revegetation in degraded peatland should consider using vegetation species whose populations were fire and drought-resilient over longer-term timeframes, such as Euphorbiaceae, *Arenga, Ficus*, and *Trema.*

6. Conclusion

This study uses palaeoecological and geochemical proxies to identify the drivers of fire events and vegetation changes in the Sebangau peatland. During the late Holocene (~2300 to 1129 cal. yr BP), the main driver of high charcoal influx was charcoal redeposition from the flooding conditions caused by high relative sea level. For the following ~400 years (1128 to 757 cal. yr BP), it was the sea level regression to the present level that drove the slight increase in charcoal influx. Next, dry conditions caused by frequent ENSO events were responsible for high charcoal influx during the period 756 to 375 cal. yr BP, and the high biofuel availability most likely drove charcoal influx for the next ~200 years until 135 cal. yr BP. Finally, frequent ENSO events and anthropogenically-driven fires have increased charcoal influx in the last ~200 years. Local fire events as presented by charcoal influx coupled with changes in peat and hydrology conditions have resulted in vegetation turnover from mixed swamp and OV types in the late Holocene period to PSF during the following ~800 years, and followed by mix LMS, FSF and OV in the last ~400 years. Peat conditions, primarily TN and PHI, and local hydrological conditions were drivers for vegetation changes from ~2300 cal. yr BP to present.

The drivers of charcoal abundance (fire severity) and vegetation turnover provide important insights for peatland restoration as it suggests that PSF species populations, especially *Eurya* and *Ilex*, were tolerant to high fire severity up to charcoal influx threshold of 23 grains mm^{-2} cm^{-3} yr^{-1} and thrived in wet peat conditions. In contrast, LMS and OV species increased in abundance at lower fire severity up to charcoal influx threshold of 13 grains mm^{-2} cm^{-3} yr^{-1} before declining in species abundance and could thrive in periodic wet and very dry conditions. These findings suggest that restoration efforts on degraded tropical peatland should consider the baseline groundwater level of the target peatland before deciding on the rewetting interventions and use suitable native and fire-tolerant vegetation species for revegetation. Furthermore, our long-term data suggest that future revegetation interventions may benefit from focusing on vegetation taxa such as Euphorbiaceae, *Arenga, Ficus*, and *Trema* that can withstand the current baseline conditions and may be more able to persist in the long term.

Author contributions

KNMR, PTM, GJ, AGS, DC, MEH, SP, SM, DAW, A, AJ, NY and DN conceived the project, and provided input towards the manuscript. KNMR conducted most of the lab and statistical analysis, and wrote the paper. AGS, DC and SP conducted field sampling, and provided data for radiocarbon, Pb-210 and TC and TN. SM, DAW, A and AJ also conducted field sampling and shared study site information. GJ assisted with radiocarbon analysis. DN, NY and MEH provided local peatland information and climatic data. All authors read and approved the manuscript.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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