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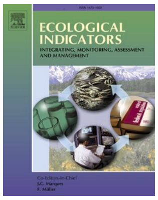

Original Articles

Mangrove dynamics and resilience in North Sulawesi, Indonesia, across the Holocene

Rachael Holmes [a,*], Ulrich Salzmann [b], Rignolda Djamaluddin [c], Emma P. Hocking [b], Mark Williams [a], Juan Carlos Berrio [a], Iskandar Siregar [d], B.Aiyen Tjoa [e], Marco Fusi [f,g], Karen Diele [g,h]

[a] *School of Geography, Geology and the Environment University of Leicester UK*
[b] *Department of Geography and Environmental Sciences Northumbria University UK*
[c] *Faculty of Fisheries and Marine Science Sam Ratulangi University Indonesia*
[d] *Department of Silviculuture IPB University (Institut Pertanian Bogor) Indonesia*
[e] *Faculty of Agriculture Tadulako University Indonesia*
[f] *Dove Marine Laboratory School of Natural and Environmental Sciences Newcastle University UK*
[g] *Center for Conservation and Restoration Science Edinburgh Napier University UK*
[h] *School of Applied Sciences Edinburgh Napier University UK*

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ABSTRACT

The mangroves of Sulawesi have been subject to widespread deforestation and degradation, which has intensified since the 1980s. Despite efforts by government and community initiatives to restore these intertidal forests, comprehensive, long-term assessments of restoration outcomes are lacking. This study aims to enhance understanding of mangrove responses to significant environmental and human disturbances over the long-term, informing future restoration and management in North Sulawesi. Sedimentary records from two study areas were analyzed using palynology, microcharcoal, diatoms, and exploratory cryptotephra, and chronologically controlled via ^{14}C and ^{210}Pb dating as indicators of mangrove forest dynamics and resilience. This study presents an ~8,000-year-old sediment record from a mangrove lagoon on Mantehage Island, Bunaken National Park, and two Late Holocene high-resolution sediment records, from two estuarine mangrove stands in Likupang. One site in Likupang was restored around 2003 CE following aquaculture pond establishment in the 1980s CE, while the other has no recent history of deforestation. Fossil pollen data shows mangroves dominated Mantehage lagoon for most of the last 8,000 years and Likupang since at least 1105 CE. Both areas experienced at least 18 disturbance events (volcanism, fire, storms, possible tsunamis, and human impacts), with mangroves showing varying resilience and full recovery of pollen abundance ranging from 14 to 903 years. Likupang's mangrove is still recovering 16 years after restoration but shows compositional similarity to its pre-deforestation state. Mantehage's mangrove is still recovering from a 14th-century seismic event which further reduced the ecosystem resilience to future natural and anthropogenic disturbances. Our findings indicate that both communities are on a trajectory towards the pre-disturbance state, based on pollen data, but may require management interventions to enhance resilience against future threats. This research provides a rare example of applying paleoecological methods to support restoration through long-term monitoring and offers a template for application in global mangrove conservation efforts.

1. Introduction

Indonesia hosts the most floristically diverse (Giesen et al., 2006) and largest extent of mangrove area in the world (2.86 million hectares (ha) in 2020) (Jia et al., 2023) but has lost around 1 million ha since the 1800s CE (Ilman et al., 2016). Archaeological evidence attests to the common use of mangroves in prehistory across Southeast Asia, indicated by settlement sites, shell middens near mangrove areas, and the expansion of specialist bone and shell tool technology for utilizing mangrove resources (e.g., O'Donnell et al., 2020; Boulanger et al., 2019;

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* Corresponding author at: School of Geography, Geology and the Environment, University of Leicester, University Road, Leicester LE1 7RH, UK.
E-mail address: rh419@leicester.ac.uk (R. Holmes).

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Rabett, 2005). For instance, Goa Topogaro caves in Central Sulawesi show mangrove exploitation within the Indonesian archipelago during the middle to late Holocene (Ono et al., 2020).

Though the global rate of mangrove loss slowed between 2000 and 2016 CE (Goldberg et al., 2020), Indonesia's mangrove reduction continues, resulting in deforested, fragmented, and degraded ecosystems. In the Wallacean biogeographical region with its exceptionally high yet imperilled biodiversity (Myers et al., 2000; Struebig et al., 2022), Sulawesi's mangroves have seen the second highest deforestation in Indonesia (39 % loss), intensified since the 1980s due to unsustainable shrimp aquaculture with excavated and embanked ponds typically left unused within 13 years due to shrimp diseases and accumulation of pollutants (Aslan et al., 2021; Ilman et al., 2016). Improving (sustainable) aquaculture productivity is crucial to halting mangrove loss (Ahmed et al., 2019), but restoration of converted, degraded areas could restore ecosystem function.

To meet international commitments like the UN Sustainable Development Goals and their National Determined Contribution Targets, Indonesia aims to restore 600,000 ha of mangrove by 2024 (Sasmito et al., 2023) and 3.49 million ha by 2045 (Regulation of the Coordinating Minister for Economic Affairs Number 4/2017 on Policy, Strategy, Program, and Performance Indicators of National Mangrove Ecosystem Management, n.d.). Successful restoration could enhance ecosystem services, such as habitat provision, carbon sequestration, coastal defense, and sustainable resource provision (Donato et al., 2011; Kristensen et al., 2008; Chang & Mori, 2021; Bimrah et al., 2022; Brander et al., 2012; Sofian et al., 2019).

Challenges remain for effective implementation of restoration policies (Arifanti et al., 2022), with low global success rates for mangrove projects (Friess et al., 2022; Lovelock et al., 2022). Restoration success, typically defined as $\geq$ 70 % survival of planted propagules (Ministerial Regulation Forestry No. P.70/Menhut-II/2008), does not necessarily ensure resilient, well-functioning mangroves (Su et al., 2021). Long-term site-specific data on mangrove dynamics and human interactions can support realistic target setting, alongside socioeconomic data and local stakeholder knowledge (Friess et al., 2022; Willis et al., 2010). To set realistic restoration targets, managers should consider a dynamic landscape model that incorporates the expectation of change into decision-making (Wingard and Wachnicka, 2017).

Historical and paleoecological data have supported ecological restoration and conservation across various ecosystems by providing reference states, disturbance frequency data, species status resolution, and enriching socio-cultural attachment to "place" through outreach and education (Gillson, 2015; Goodenough & Webb, 2022; Manzano et al., 2020; Pellatt et al., 2015; Riedinger-Whitmore, 2015; Cole et al., 2014, 2015; Hapsari et al., 2018; Lindbladh et al., 2013; Nogué et al., 2017; Castilla-Beltrán et al., 2020). Few studies have so far applied this to mangroves, focusing on climate adaptation, carbon sequestration, and recovery times (Rabett et al., 2023; Rull, 2023; Torrescano-Valle et al., 2012; Hapsari et al., 2020; González et al., 2010), and none within Wallacea.

In order to understand mangrove responses to long-term environmental change and disturbance to inform future restoration and management, we analyzed three paleosediment cores from protected and restored mangrove sites in North Sulawesi, Indonesia. We used palynology and diatom analyses, along with microscopic charcoal counts, sedimentology and radiometric dating, to reconstruct how mangroves responded over the last 8000 years to natural and anthropogenic disturbances. We also used our palynological results to quantify mangrove resilience and recovery rates, and to estimate their stage in the disturbance-recovery continuum. Finally, we discuss the implications of our research outcomes for future mangrove management.

2. Methods

2.1. Site description and core collection

Two mangrove areas in the North Minahasa regency, North Sulawesi, Indonesia, with differing anthropogenic impact histories, were selected to study long-term mangrove responses to disturbance (Fig. 1). Of the 48 true Indonesian mangroves (sensu Tomlinson, 2016; i.e., species which occur in mangrove forests only and not in other terrestrial communities), 31 species have been recorded in North Sulawesi (Djamaluddin, 2018a). Surface air temperatures in North Sulawesi, remain relatively constant year-round, fluctuating between ~24 to 28 °C from 1991 to 2021, with precipitation averaging 146–288 mm per month, predominantly during the wet season (November – April) (Station Manado, Climate-Data.org 2024).

The low intertidal estuarine mangrove at Likupang hosts at least 21 true mangrove species (Table 1; Djamaluddin et al., 2023). Approximately 55 % of Likupang's mangrove area was converted to shrimp aquaculture starting in 1985 CE, with abandoned ponds typically left unused within 13 years (Aslan et al., 2021). By 2003 CE, about 7 ha were restored via a community-led project that re-established natural hydrology and planted mixed mangrove species (e.g., *Rhizophora mucronata*, *R. apiculata*, and *Nypa fruticans*) to facilitate natural regeneration (Fig. 2a). A further 40 ha were restored using a monocultural approach (Djamaluddin et al., 2023). Despite legal protection under the North Minahasa Regency's Regional Regulation No. 1 of 2013, enforcement is lacking, and mangrove management is mostly community-based (Lumenta et al., 2017; Natalia et al., 2017).

The second mangrove area, Mantehage Island, is part of Bunaken National Park and contains approximately 1383 ha of mangrove forest (Sapsuha et al., 2018). Formed by two limestone reef islets creating a central lagoon (Fig. 2c) (Djamaluddin, 2004), Mantehage's mangrove flora includes at least 20 true mangrove species (Djamaluddin & Djabar, 2022) (Table 1). Though archaeological records are sparse, surveys indicate mangrove exploitation since ca. 1816 CE by the Bajo (Bajau) people (Djamaluddin, 2004). Dutch colonial small-scale timber harvesting began in the 1930s (Djamaluddin, 2004), with increasing exploitation for various resources over time. Conservation management has been stronger since 1995 CE under Bunaken National Park regulations (Newman & LeDrew, 2005).

Significant mangrove dieback events were reported in 1970 and 1982, linked to El Niño events and in 2012 CE, more likely due to anthropogenic changes in hydrology and sedimentology following road and bridge construction across a major inlet (Djamaluddin, 2004). Mantehage currently has four villages, Bango, Buhias, Tangkasi and Tinongko; and the nearest large city is Manado located on mainland Sulawesi. But between at least the 16th and 17th centuries CE the closer island of Manado Tua (then Manado) was the major political and trading centre in the region (Schefold, 1995; Wigboldus, 1987).

In July 2019, three sediment cores were collected using a D-Section peat corer. A 600 cm core was extracted from the edge of Mantehage lagoon (MH: 1°42′22.7988″ N 124°45′42.3″ E), and two cores, 300 cm and 193 cm long, from Likupang's multi-species restored (LK1: 1°40′24.93001″ N 125°2′29.97996″ E) and unlogged (LK2: 1°40′30.65999″ N 125°2′26.81988″ E) sites, respectively.

2.2. Chronology

In Likupang, aquaculture pond construction involved excavating sediment to about 70 cm below the contemporary surface, using it to build dikes (Fig. S1). We therefore sampled the core section below 100 cm and added a sample from the uppermost 2 cm of the core onlyto reconstruct the 16-years post-restoration pollen assemblage, We excluded samples between 2 – 100 cm from LK1.

13 dried sediment samples from the uppermost 30 cm oft LK2 were analysed for ^{210}Pb, ^{226}Ra, ^{137}Cs and ^{241}Am by direct gamma assay in the

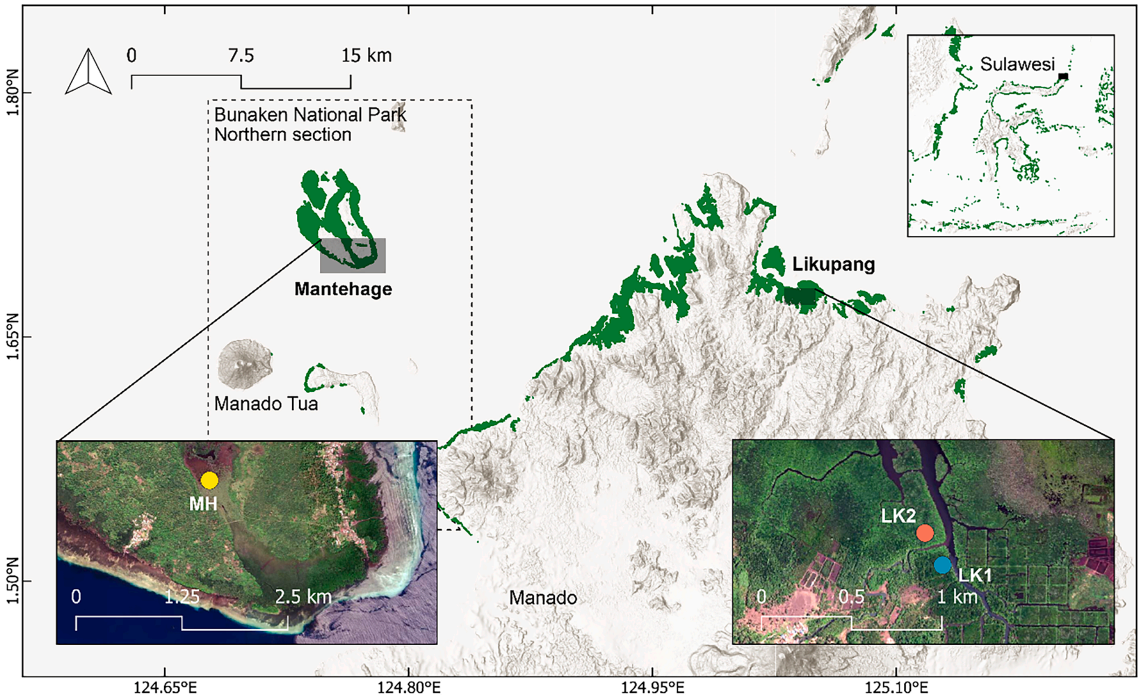

Fig. 1. Coring locations and contemporary mangrove extent (dark green) in North Sulawesi (MH, LK1, LK2). Basemaps: ESRI World Hillshade, Bing Maps Satellite Imagery.

environmental radiometric Facility at University College London (Table S3). Because of local mixing and high sedimentation rates, most likely caused by the pond excavation, a meaningful chronology for the top meter of LK1 could not be established. Accelerator mass Spectrometry (AMS) radiocarbon (^{14}C) analysis was conducted on bulk sediment organic matter from LK1 (n = 4), LK2 (n = 2), and MH (n = 15) (Table S2). Bayesian approaches were applied to build age-depth models which included the constant rate of supply (CRS) modelled ^{210}Pb dates (Appleby & Oldfield, 1978, 1983) for LK2. Measured ^{137}Cs was below the detection limit for LK2 and therefore could not be used as an independent tracer to validate the CRS model. We built age-depth models and estimated sediment accumulation rates using the IntCal20 calibrations for the Northern Hemisphere (Reimer et al., 2020) and Northern Hemisphere zone 3 (NHZ3) for post-bomb ^{14}C dates (Hua et al. 2022), with the package rbacon (Blaauw & Christen, 2011) in R version 4.2 (R Studio Team, 2020). We explored using a mixed (50:50) SHCal20 and IntCal20 curve suggested for pre-bomb dates when building our age-depth models to address the influence on radiocarbon dates due to mixing of air masses in monsoonal tropical regions (Hogg et al. 2020). However, this approach introduced much larger uncertainties in our modelled post-bomb dates and led to a poorer overall model fit, negatively impacting the recent past reconstructions that are critical for this study (e.g., the last 100 years).

2.3. Paleoecology

To reconstruct vegetation, all cores were processed for pollen and fern spores at ~10 cm resolution using a modified Faegri et al. (1989) method. This involved pre-treatment with either sodium pyrophosphate (for clays) or potassium hydroxide (for peats), sieving, acetolysis, and heavy liquid separation using a 2.0 s.g. bromoform solution. *Lycopodium* spore tablets were added as spikes to calculate pollen concentrations (Stockmarr 1971). Pollen counts were conducted using a Leica DM500 light microscope at 400x magnification, identified using literature and online databases (APSA Members, 2007; Mao et al., 2012; Poliakova and Behling, 2016; Tang et al., 2020). Ecological groups were informed by local vegetation surveys and published data (Djamaluddin, 2018b; Djamaluddin et al., 2023). For most samples, a minimum of 150 pollen and spores were counted and used to quantify their relative abundance. Where this was not possible, for example, due to low concentration, only samples with counts over 100 have been included. Pollen and spores which could not be allocated taxonomically were assigned to a 'type' number. The intersection of microcharcoal across 11 points of a 1 cm graticule in 45 fields of view were also counted on the pollen slides to quantify the fire frequency at each site, following the point count method of Clark (1982).

We additionally analysed diatoms at the lagoonal site of MH using standard procedures (Battarbee 1986; Battarbee et al., 2001) to further explore the impact of long-term Holocene changes in relative sea-level (RSL) on our mangrove vegetation record). Of 27 samples, only 10 showed good preservation. Diatom diagenesis is influenced by a range of factors, including high salinity and acidity (Flower, 1993; Flower & Ryves, 2009; Reed, 1998). High levels of sulphur in the MH core below 220 cm might have biased preservation in the MH record. Diatom taxonomy follows Guiry and Guiry (2023), with salinity preferences from regional literature wherever possible (Zong and Hassan 2004; Horton et al. 2007; Dam et al. 2001; van der Kaars et al. 2001; Risjani et al. 2021; Jaraula et al. 2014; Pham et al. 2011), or from global literature and databases (Guiry and Guiry, 2023; Atazadeh et al. 2014; Maltsev et al. 2021) in rare instances where local literature was not available.

The island of Mantehage is in close proximity to the volcano Manado Tua (Fig. 1). We therefore conducted additional exploratory qualitative scans for tephra after having detected a thin yellowish layer at ca. 63–60 cm in the MH sediment core, followed by an abrupt sedimentological change from dark organic-rich sediments to yellow–brown silty clay (Table S4) Sediment samples from the suspected tephra layer (n = 1) were analysed alongside sediments from a selection of depths (n = 4), following Blockley et al., (2005). Core sub-samples (n = 62) were processed for loss on ignition (LOI) by ALS Global.

2.4. Data analysis

All data analysis was conducted in R Studio version 4.2.1. (R Studio Team, 2020) unless explicitly stated.

Table 1
True mangrove taxa reported from North Sulawesi, Mantehage and Likupang, alongside presence (X) in pollen record (C = contemporary ecological surveys (Djamaluddin, 2018b; Djamaluddin et al., 2023; Djamaluddin & Djabar, 2022); P = pollen; * only possible to identify pollen to genus or morphotype i.e., Avicennia or Bruguiera/Ceriops type and may therefore indicate one or multiple species).

Family	Taxon	North Sulawesi	Mantehage		Likupang	
			C	**P**	**C**	**P**
Acanthaceae	*Acanthus ebracteatus* Vahl					
	Acanthus ilicifolius L.	X	X	X	X	
	Acanthus volubilis Wall.					
	Avicennia alba Blume	X			X	X*
	Avicennia marina (Forssk.) Vierh.	X	X	X*	X	X*
	Avicennia officinalis L.					
Arecaceae	*Nypa fruticans* Wurmb	X	X	X	X	X
Combretaceae	*Lumnitzera littorea* (Jack) Voigt	X		X		
	Lumnitzera racemosa Willd.	X	X	X		X
Euphorbiaceae	*Excoecaria agallocha* L.	X	X	X	X	X
Loranthaceae	*Amyema celebica* (Tiegh.) Danser					
	Amyema gravis Danser					
	Amyema mackayense (Blakely) Danser					
Lythraceae	*Pemphis acidula* J.R. Forst. & G. Forst.	X			X	
	Sonneratia alba Sm.	X	X	X	X	X
	Sonneratia caseolaris (L.) Engl.	X		X		X
	Sonneratia ovata Backer	X	X	X		X
Malvaceae	*Brownlowia argentata* Kurz					
	Brownlowia tersa (L.) Kosterm.					
	Camptostemon philippinensis (S. Vidal) Becc	X	X			
	Camptostemon schultzii Mast.					
	Heritiera globosa Kosterm.	X				
	Heritiera littoralis Aiton	X	X		X	
Meliaceae	*Xylocarpus granatum* J. Koenig	X	X	X*	X	X*
	Xylocarpus moluccensis (Lam.) M. Roem.	X			X	X*
	Xylocarpus rumphii (Kostel.) Mabb.					
Myrtaceae	*Osbornia octodonta* F. Muell.					
Orchidaceae	*Oberonia rhizophoreti* Schltr.					
Plumbaginaceae	*Aegialitis annulata* R. Br.					
Primulaceae	*Aegiceras corniculatum* (L.) Blanco	X	X	X*	X	X*
	Aegiceras floridum Roem. & Schult.	X				
Pteridaceae	*Acrostichum aureum* L.	X			X	X*
	Acrostichum speciosum Willd.	X	X	X*	X	X*
Rhizophoraceae	*Bruguiera* × *hainesii* C. G. Rogers					
	Bruguiera cylindrica (L.) Blume	X	X	X*		
	Bruguiera exaristata Ding Hou					
	Bruguiera gymnorhiza (L.) Lam.	X	X	X*	X	X*
	Bruguiera parviflora (Roxb.) Wight & Arn. ex-Griff.	X	X	X*	X	X*
	Bruguiera sexangula (Lour.) Poir.	X			X	X*
	Ceriops decandra (Griff.) W. Theob.					
	Ceriops tagal (Perr.) C. B. Rob.	X	X	X*	X	X*
	Ceriops zippeliana Blume	X				
	Kandelia candel (L.) Druce					
	Rhizophora apiculata Blume	X	X	X*	X	X*
	Rhizophora mucronata Poir.	X	X	X*	X	X*
	Rhizophora stylosa Griff.	X	X	X*	X	X*
Rubiaceae	*Scyphiphora hydrophylacea* C.F. Gaertn.	X	X	X	X	X

2.4.1. *Long term drivers*

Mangrove responses to long term trends in sea-level were qualitatively assessed. Comparative data on Holocene relative sea-level (RSL) was obtained from the SEAMIS database for ISEA (Mann et al., 2019). Data that have been rejected in the SEAMIS database due to a lack of sufficient information within the original sources (see Mann et al., 2019) have been excluded from this study. For comparison with the core paleoecological data, we interpolated regional RSL by building a Generalized Additive Mixed Model (GAMM) accounting for temporal autocorrelation using the mgcv package (Wood, 2023), which explained 78.6 % of the variation in the RSL data.

2.4.2. *Mangrove development and compositional change*

Stratigraphic diagrams and clustering based zonations were produced with the RiojaPlot package (Juggins, 2022, Juggins, 2023). Rarefied palynological richness, as a proxy for changes in plant alpha-diversity through time (Birks et al., 2016), was quantified using the Vegan package (Oksanen et al., 2022). Unconstrained principal components analysis (PCA) was performed on the total pollen (%) and mangrove pollen (%) to detect dominant drivers of vegetation change over time. To identify rapid periods of change in palynological compositional turnover, we produced principal response curves (PrC) (De'ath, 1999; Van den Brink and Braak, 1999) based on Hellinger transformed pollen counts using the the Analogue package (Simpson et al., 2021), and fitted generalized additive models (GAM) (Burge et al., 2023).

2.4.3. *Tracking mangrove resilience and recovery*

Ecosystem resilience can be conceptualized as engineering resilience, i.e., the time taken for an ecosystem to recover to its previous state following disturbance; and as ecological resilience, the ability of the system to withstand disturbance (Holling, 1973, 1996). Engineering resilience was quantified using pollen data after Cole et al., (2014) using several parameters: mangrove abundance pre-disturbance (M_{pre}), minimum mangrove abundance during disturbance (M_{min}), maximum mangrove abundance before stabilizing or decreasing following disturbance (M_{max}), mangrove decline (MD), mangrove recovered (MR); T_{pre}, T_{min}, T_{max}, are the timing (T) of M_{pre}, M_{min}, M_{max}, and T_{rec} is the time from M_{min} to M_{max}; and recovery rate (RR) is the rate of increase in mangrove pollen abundance per year relative to the degree of mangrove pollen decrease following a disturbance event (for definitions and

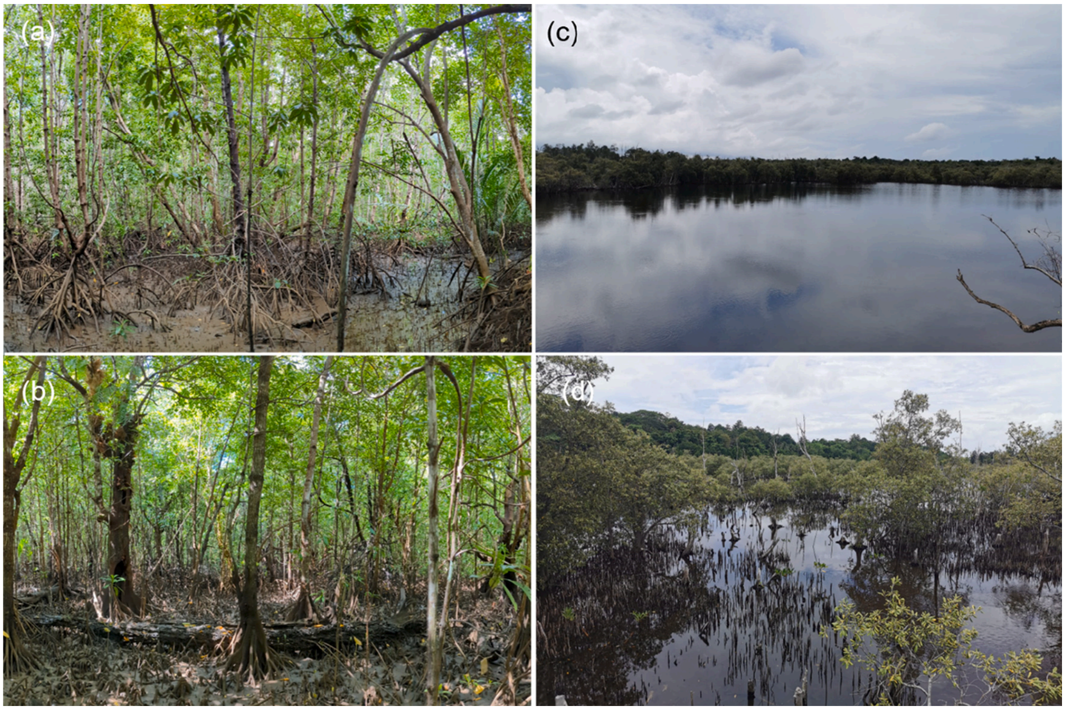

Fig. 2. Contemporary environmental setting at: a) Likupang multi-species restored site (LK1); b) Likupang unlogged site (LK2); c) Mantehage lagoon; d) mangrove surrounding Mantehage lagoon.

notation see Table S1). When the amount of mangrove pollen was on the rise after an initial disturbance-induced decline (but before restored mangrove abundance (MR) exceeded 50 %), and a second disturbance occurred, the baseline for the second disturbance was set to the pre-first disturbance mangrove level. This was done to prevent the baseline for recovery from being established in a disturbed state (Soga and Gaston, 2018). Additionally, to investigate recovery in terms of composition, we used non-metric multi-dimensional scaling (NMDS) to compare the Jaccard dissimilarity between the "recovered" mangroves with a baseline which incorporates the range of variability prior to the disturbance (Burge et al., 2023). We assessed ecological resilience semi-quantitatively by comparing our records of local and regional disturbance to our vegetation proxy data to identify if they do, or do not, illicit a response (Table 2).

Our quantification of resilience and recovery involves several caveats, particularly disentangling local from regional signals in proxy data and measuring disturbance intensity. While recovery has been assessed relative to the type of disturbance on mangrove pollen abundance (RR), the intensity of each disturbance (e.g., Class 1 vs. Class 6 storms) has not been directly measured. This limitation prevents us from distinguishing whether variations in recovery times are due to differences in resilience, disturbance intensity, or disturbance magnitude. Additionally, microscopic charcoal and pollen can travel long distances by wind or water, complicating the determination of whether proxies reflect local or regional fire and vegetation. This is particularly true for the LK sites which are located close to a small river, whereas allochthonous input of microscopic charcoal and pollen is less likely in the closed lagoonal and remote island setting of MH. Where these caveats could lead to alternative interpretations of the results, they have been highlighted.

Table 2
Mangrove response to disturbance: disturbance event (Dist.), recovery time (RT), mangrove decrease (MD), recovery rate (RR), percent of maximum mangrove recovered (MR). Disturbance events: fire (F), hydrological change (HC), deforestation/aquaculture (D/A), strong El Niño (EN), storm/possible tsunami (S/T), volcanic eruption/uplift (V/U). Question marks (?) indicate that the data are not obtainable and hyphens (–) indicate not applicable.

Event	Core	Year (CE/BCE)	Evidence	Dist.	RT (years)	MD (%)	RR (%)	MR (%)	Recovered
1	LK1	2019	Microchar.	F	?	?	?	?	?
2	MH	2012	Historic	HC	?	10.21	?	?	?
3a	LK1	1985	Historic	D/A	16	?	?	78.10	?
3b	LK2	1985	Historic	D/A	4	23.16	6.25	82.62	Partial
4/5	MH	1970/1982	Historic	EN	12	33.65	3.81	81.74	Partial
6	LK2	1944	Sand lens	S/T	–	Dec < 5 %	–	–	–
7	LK2	1930	Sand lens	S/T	18	33.65	4.27	92.23	Partial
8	LK2	1884	Microchar.	F	14	29.72	10.58	114.29	Full
9	LK2	1810	Sand lens	S/T	23	33.97	7.73	126.44	Full
10	LK2	1797	Sand lens	S/T	–	Dec = 0 %	–	–	–
11	MH	1641	Sand lens	S/T	–	Dec = 0 %	–	–	–
12	MH	1452	Microchar.	F	397	83.54	0.32	122.34	Full
13	MH	1397	Tephra, diatoms	V/U	55	89.41	0.14	17.65	Not
14	LK1	1274	Coral grav.	S/T	79	7.15	1.90	103.56	Full
15	LK1	1228	Coral grav.	S/T	–	Dec < 5 %	–	–	–
16	LK1	1211	Microchar.	F	–	Dec < 5 %	–	–	–
17	LK1	1105	Microchar.	F	14	8.27	0.72	92.56	Partial
18	MH	−3723	Coral grav.	S/T	903	8.80	0.11	99.92	Full

Our estimates of recovery times use the mean age of our age-depth model (Fig. 3). The uncertainty of these estimates is therefore related to the accuracy and precision of the radiometric age of each individual sample with uncertainties ranging from ± 2 to 39 years (SI Tables S2 and S3). While these uncertainties should be considered when interpreting absolute recovery rates, it is unlikely that they put a constant positive or negative bias on our estimates.

Analysis of mangrove vegetation recovery using fossil pollen is also limited by the difficulty of identifying ecologically key taxa to species level based on morphology alone. Modern vegetation surveys in Likupang (2019) identified species differences between LK1 and LK2 that are not evident in the pollen record, risking overstated similarity and stability through time.

3. Results and interpretation

3.1. Stratigraphy and chronology

Detailed stratigraphy and chronology, including calibrated and modelled 14C and 210Pb dates, are available in Appendix S1 (Tables S2, S3; Fig. S2). We use mean calibrated ages from the age-depth models (Fig. 3). Both Likupang cores consist mainly of very dark brown to black organic-rich silty clays with varying sand content and sand lenses (Table S3). Notably, the LK1 core contains layers of broken corals and mollusc shells at 200 cm and 252–255 cm (Fig. S3; Table S3), suggesting strong storm events or high-energy tsunami events (Yue et al., 2019). The 3 m LK1 core spans c. 845 to 72 calibrated years before present (cal. BP) (1105–1878 cal. CE), including a surface sample at −69 BP (2019 CE). The 2 m LK2 core's basal date is c. 173 cal. BP (1777 cal. CE), overlapping with LK1 by about 100 years (Table S2; Fig. 3).

The 6 m MH sediment core covers 7905 cal. BP (5955 cal. BCE) to −69 cal. BP (2019 CE) (Fig. 4; Table S1). Between 600–250 cm, the core transitions from dark brown clay to black organic-rich peaty silt (Table S2), with a high sediment accumulation rate (5 yr/cm), likely due to Middle Holocene mangrove expansion (Chua et al., 2021; Mann et al., 2016). An abrupt transition at 64–63 cm replaces organic-rich sediments with yellow–brown silty clay from 63-60 cm (Fig. 3). Above 60 cm, the stratigraphy alternates between organic-rich silty clay and sand (Table S3). The age-depth model indicates that the top 30 cm covers the last 60 years.

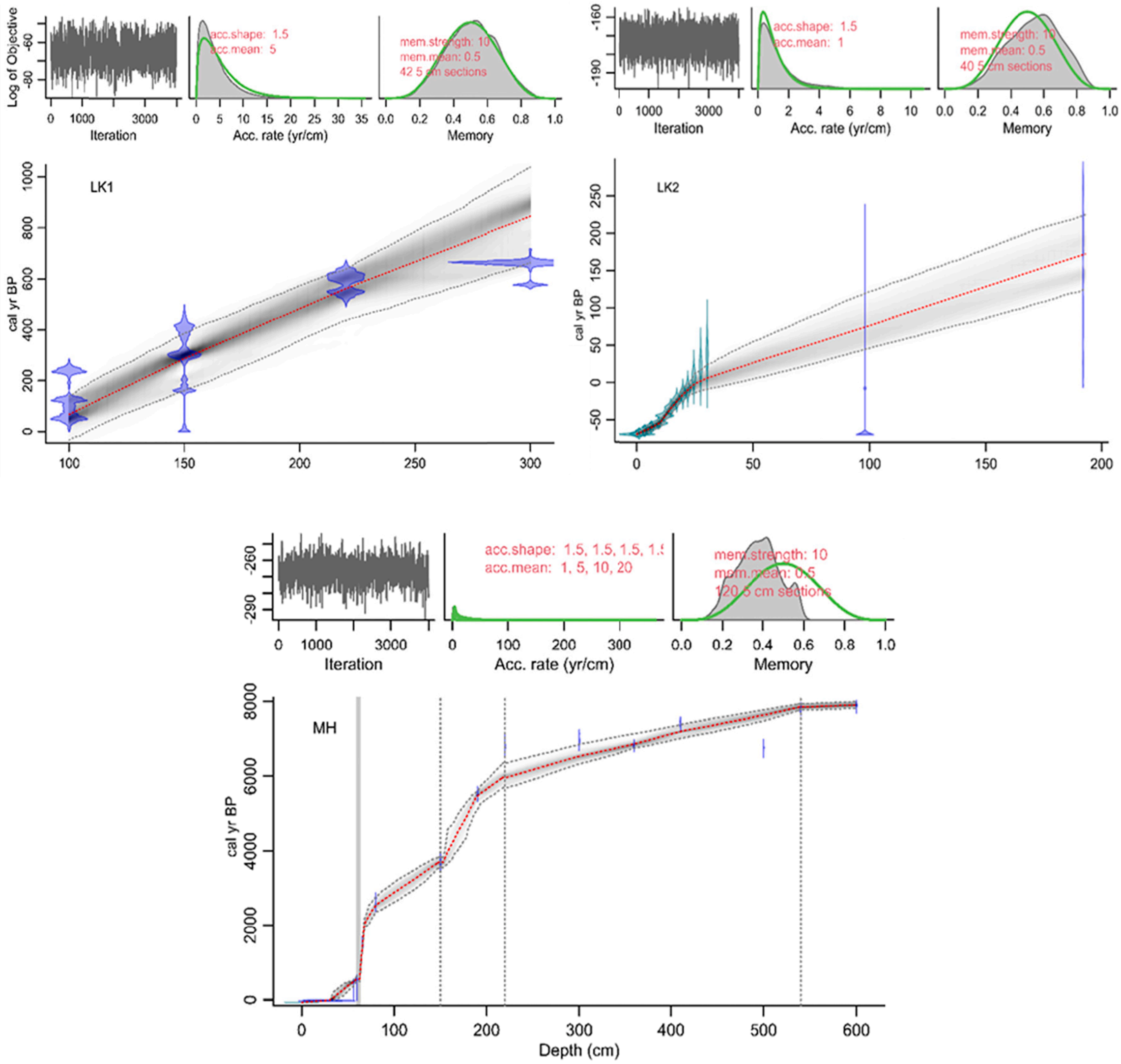

Fig. 3. Bayesian age-depth models for Likupang (LK1 and LK2) and Mantehage (MH). Blue polygons are calibrated ^{14}C dates; green polygons are CRS modelled ^{210}Pb dates; red dashed line is the mean age for the age-depth model surrounded by the 95 % confidence interval of the modelled age; dashed grey lines are boundaries input into the model to indicate changes in sediment accumulation rate between core sections; and the thick grey bar on the MH model indicates a rapid depositing of sediment.

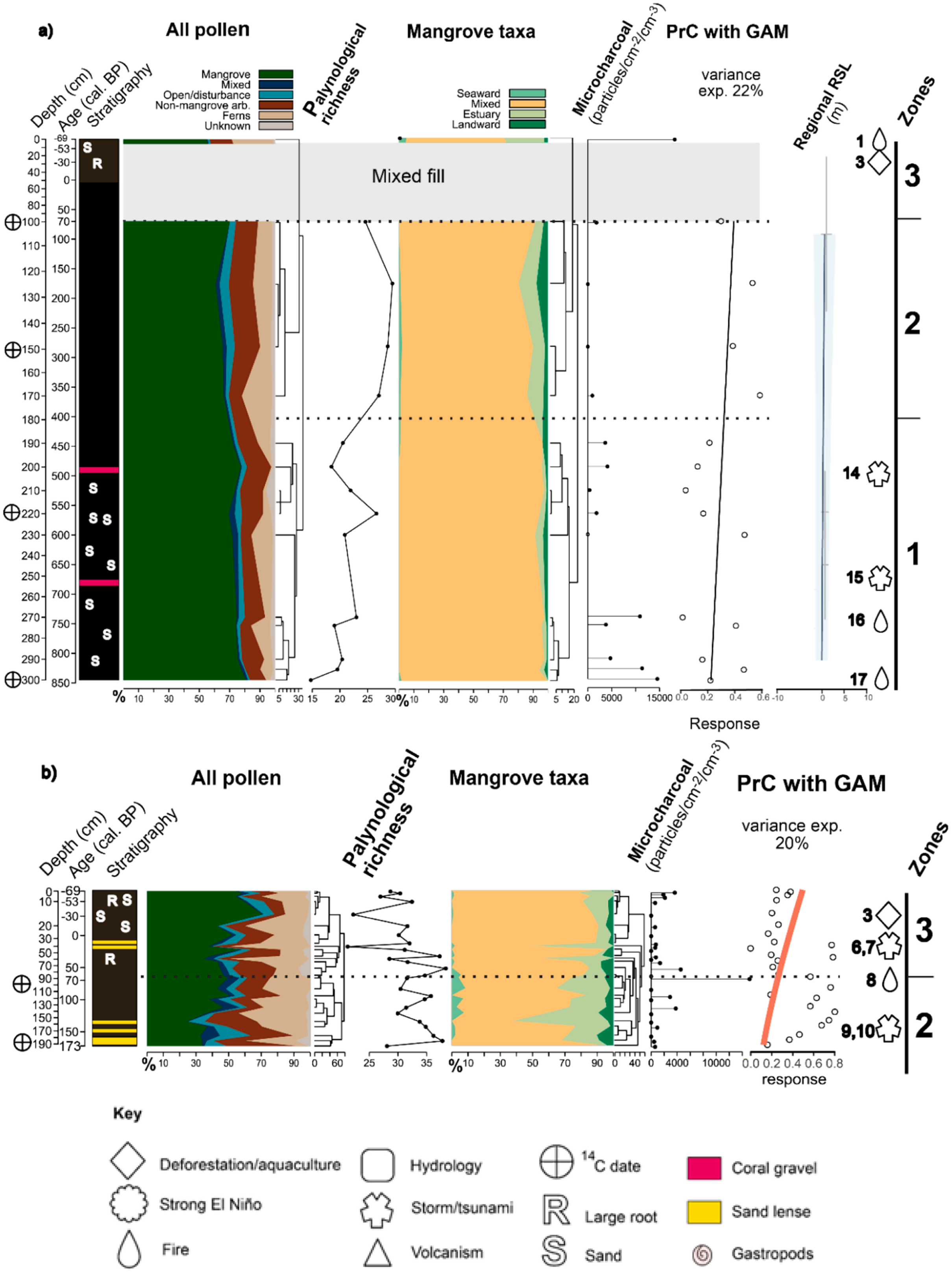

Fig. 4. Likupang paleoecology summary by calibrated age for a) LK1 as relative abundance of pollen by ecological group, rarefied palynological richness, relative abundance of mangrove pollen by mangrove ecological zonation, microcharcoal, principal response curve fitted with a GAMM to identify rapid periods of change (no rapid period found) (GAMM RES), pollen abundance zones marked by dotted black lines; b) LK2 paleoecology summary – as LK1, but GAMM identified rapid period of change as indicated by thick red bar. Key shared with Fig. 6. Disturbance number after Table 2.

3.2. *Environmental reconstruction*

Full palynological diagrams for all cores are presented in Appendix S1 (Figs. S5, S6, and S7). The pollen assemblages include 191 morphotypes with 45 types unidentified. LK2 has the highest average rarefied richness (31.69), and MH has the highest total mangrove pollen richness (Table 1). Pollen from 22 mangrove taxa were identified across all cores (Fig. S8). Mangroves were the dominant vegetation community at all sites throughout much of the Holocene (Figs. 4 and 6). *Rhizophora* is the most abundant taxon in all cores (mean = 46 %, 44 %, and 25 % at MH, LK1, and LK2, respectively). This dominance aligns with contemporary mangrove forests, where *Rhizophora* species often form monogeneric stands and are prolific pollen producers, thus frequently over-represented in sediments (Ramdzan et al., 2022).

3.2.1. *Likupang*

Significant assemblage zones identified through constrained hierarchical clustering for LK1 and LK2 were reduced to three zones to focus on significant changes in pollen composition and integrate both records (Fig. 4.4a and 4.4b). LK2 (147 taxa) exhibits higher palynological richness than LK1 (118 taxa). Of the 160 total taxa, 13 are unique to LK1 and 42 to LK2. Both cores contain pollen from 18 mangrove taxa (Table 1), with *Barringtonia* pollen unique to LK1 and *Sonneratia* cf. *ovata* pollen unique to LK2 (Fig. S8). Despite the close proximity of the two Likupang cores (~200 m), their past pollen assemblages differ, with LK1 being more *Rhizophora*-dominated and LK2 having higher proportions of estuarine mangroves such as *Nypa fruticans* and *Oncosperma* (Fig. 5a). Over time, they have become more similar, with the 16-years post-restoration pollen sample from LK1 clustering closer to LK2 subsamples than to older LK1 subsamples in the PCA (Fig. 5b).

At LK1, six discrete disturbance events since the 12th century CE were identified based on fossil (three microcharcoal peaks and two coral gravels) and historic records (deforestation and aquaculture) (Table 2). None of these disturbances led to rapid periods of change in the PrC for LK1 (Fig. 4a). Only small changes in the pollen record were observed, coincident with fire and storms (<10 %) (Table 2). A minor decline in mangrove pollen following fire (<5%) at LK1 may imply either resilience to local fire or non-local fire impact. In two cases where mangrove decline exceeded 5 %, recovery of ~93 % and 104 % was achieved in 14 and 79 years, respectively. The recovery rate associated with deforestation and aquaculture in 1985 CE and recent burning (~2019 CE) could not be fully assessed due to lack of data on minimum and maximum mangrove pollen abundance. We can, however, still comment on the percentage of mangrove recovered (MR) and compositional change in the post-restoration assemblage.

Mangroves constituted 60–80 % (mean = 72 ± 5) of the total pollen assemblage in the LK1 core before deforestation. The surface sample, reflecting the pollen assemblage 34 years after deforestation and 16 years post-restoration, shows mangrove pollen at 54 % of the total assemblage – 75 % of the average abundance for the 773-year period between 1105–1878 cal. CE. This falls short of the 95.5 % abundance benchmark for a "fully restored" ecosystem (Cole et al., 2014). However, NMDS analysis (Fig. 5b) suggests that post-restoration, LK1 remained compositionally similar to, but outside of, its historic baseline, indicating partial recovery. The remaining differences likely result from higher proportions of *N. fruticans* in the contemporary mangrove. Increased *N. fruticans* abundance could be due to changes in site hydrology, active planting, or both. An effect of burning on mangrove pollen recovery in the post-restoration sample could not be detected (Table 2).

At LK2, seven disturbances since the late 18th century CE were recorded which include five disturbances by storm as evidenced by sand lenses, a fire event as evidenced by one microcharcoal peak, and historic (observed) deforestation (Fig. 4b). Storm events in the LK2 record caused little change in mangrove pollen abundance (<5%). Compositional shifts occurred as *N. fruticans* and *Oncosperma* increased at the expense of *Rhizophora* and *Bruguiera* (Fig. S8b). Mangrove abundance recovered to >90 % of pre-storm levels within 25 years. A microcharcoal peak in the late 1800s was followed by a ~30 % reduction in mangrove pollen and the quickest recovery rate (~11 %) in this study (Table 2). This disturbance was associated with a compositional change, an assemblage zone boundary, and an increase in disturbance indicators and unknown non-mangrove arboreal species in Zone 3. The decline and recovery of mangrove pollen at 59 cm could not be linked to a specific disturbance type. Mangrove pollen decreased by 23 % after 1985 CE, coincident with nearby deforestation, and then increased quickly (RR = 6 %) reflecting recovery due to post-2003 CE restoration efforts, although it declined again in the surface sample (~2019 CE) (Table 2).

3.2.2. *Mantehage*

The MH record covers the last c. 8000 years and is split into two significant assemblage zones (Fig. 6), based on recovery of 158 pollen taxa (Fig. S7). Rarefied richness fluctuated between 10.5 and 35.2 (Fig. 6); and was lowest during the periods that mangroves where the dominant vegetation. Out of the 20 true mangrove species reported from ecological surveys on MH (Table 1), only *Camptostemon philippinensis* and *Heritiera littoralis* were absent in the fossil record, and pollen was also recovered from two true mangrove species, *Lumnitzera littorea* and *Sonneratia caseolaris,* which are unknown from the island today (Table 1, Fig. S9). In total, 39 diatom taxa were present in the MH sediment core. Three diatom species, *Diploneis papula*, *D. ovalis,* and *Halamphora coffeaeformis,* were the most abundant (24 %; 15 %; 13 %). These diatoms

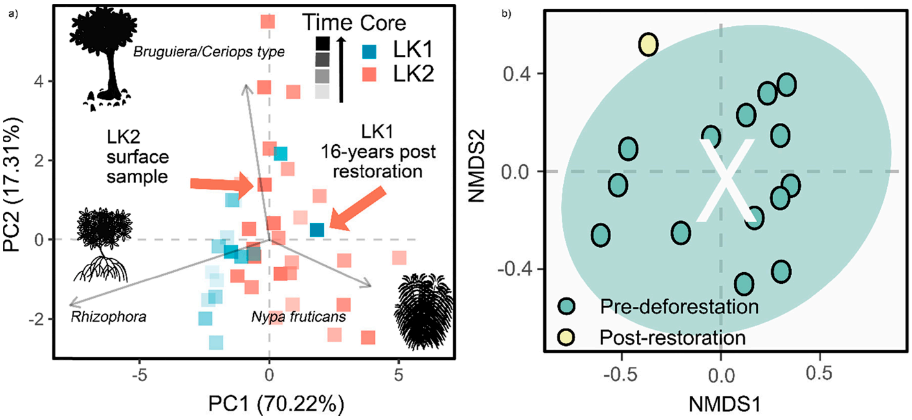

Fig. 5. Ordinations of LK pollen composition as a) PCA based on total pollen for LK1 and LK2, and B) compositional distance between the post-restoration (yellow) and the pre-deforestation compositional range of variability over the LK1 core (green ellipse) for mangrove taxa based on an NMDS of mangrove pollen Jaccard dissimilarity. In b), the post restoration assemblage remains close to but outside for the range of the historic baseline.

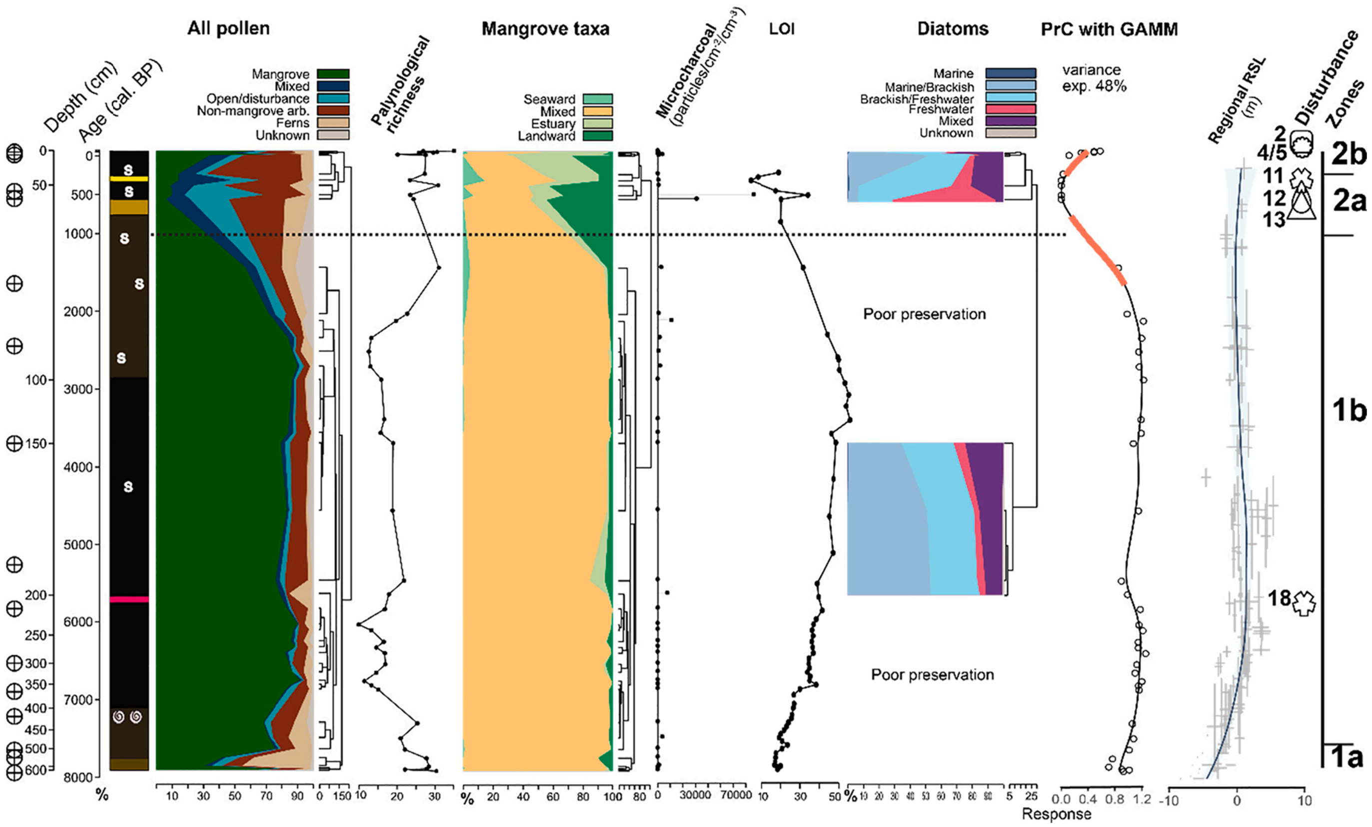

Fig. 6. Overview of environmental change for MH, including a summary pollen diagram by ecological groups, pollen influx, palynological richness derived through rarefaction, summary pollen diagram as a percentage of mangrove taxa by mangrove ecological zonation preference, microcharcoal concentration, and diatoms – where well-preserved – grouped by salinity tolerance. Dotted black line indicates assemblage zone based on pollen clustering. Symbology follows the key in Fig. 4 and disturbance numbers after Table 2.

occur globally and have also been previously reported from Indonesian mangroves (Horton et al. 2007). Tephra was absent in three out of five sub-samples but abundant at 61 cm and a few shards were present at 47 cm.

After a slight decline in mangrove pollen abundance and rise in fern spores at ca. 5800 ca. BP, potentially caused by a flooding event indicated by a layer of coral gravel (Fig. 6), the mid to late Holocene mangrove quickly recovered in line with the gradual rise in regional relative sea level (Fig. 6). Over most of the Holocene, mangrove pollen makes up c. 80 % of the total assemblage, indicating stability in the mangrove ecosystem. However, around 2000 cal. BP, mangrove abundance slowly declines, again in association with a period of sea-level regression (Fig. 6).

Mantehage experienced fewer disturbance events (n = 7) than Likupang sites (LK1 = 6, LK2 = 7) (Table 2), likely due to distinct depositional settings and lower anthropogenic pressure. The most significant disturbance occurred around 553 cal. BP (1397 CE) in the Mantehage core, marked by tephra abundance and sediment changes, resulting in an 89 % loss of mangrove abundance. Both the disturbed and recovering mangrove communities show rapid changes in the GAMM of the PrC (Fig. 6). Diatom records indicate a shift from Middle Holocene marine/brackish to freshwater conditions, associated with this 14th-

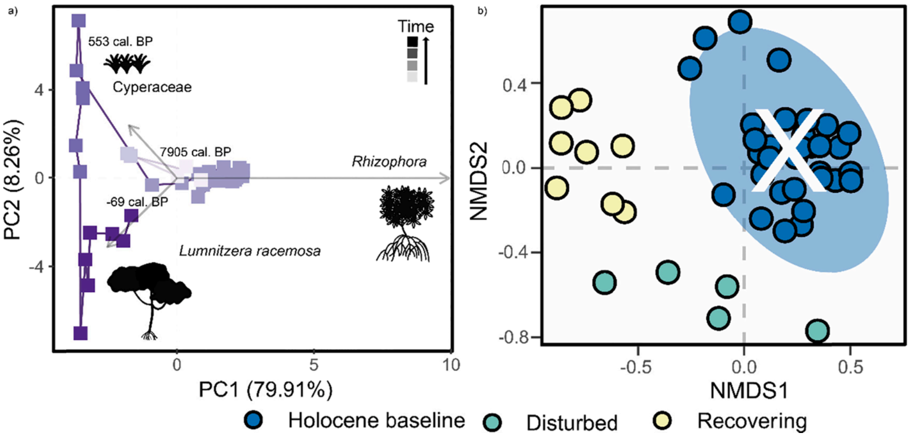

Fig. 7. Ordinations of MH pollen composition as a) PCA based on total pollen, and B) NMDS on Jaccard dissimilarity of mangrove pollen only. In b) the ellipse indicates the Holocene compositional range of variability.

century CE disturbance event. This abrupt shift converted the ecosystem from a *Rhizophora*-dominated mangrove to open freshwater vegetation dominated by *Cyperaceae*, *Arecaceae* (excluding *Nypa*), and *Rubiaceae* (Fig. 7a). Back mangrove taxa, typical of landward zones, were notably prevalent during this period compared to other Holocene epochs (Fig. S9). The opening of the canopy likely expanded the pollen catchment area.

Only about 18 % of mangrove abundance recovered before a second disturbance occurred, evidenced by two major peaks of microcharcoal around 498 cal. BP (1452 CE). Microcharcoal is otherwise largely absent in the MH record. This suggests that the two major peaks were caused by local natural or human induced fires that can be linked to a decline in mangroves and increase in more open herbaceous community on MH. A third disturbance, a storm event around 1641 CE, left no preserved record of mangrove loss and abundance continued to increase following the previous fire disturbances. *Lumnitzera*, tolerant of both freshwater and estuarine conditions, was among the first mangrove taxon to recover, driving initial pollen abundance increases (Fig. 7a). This was followed by more generalist taxa like *Bruguiera/Ceriops*, with *Rhizophora* recovering fully only after 1950 CE. It was not until the early 1970s that mangrove pollen abundance recovered to over 95.5 % of pre-1397 CE levels. However, the “recovered” mangrove pollen assemblage remains compositionally dissimilar to the Holocene range in variation based on the NMDS (Fig. 7b), though may be on a trajectory towards it when total pollen composition is considered (Fig. 7a). The MH record’s temporal resolution is insufficient to distinguish between reported historic El Niño-induced disturbances in 1970 and 1982, but it indicates partial recovery of mangrove pollen after these events until the onset of the most recent anthropogenically induced dieback due to road construction in 2012 (Table 2). Contemporary mangroves have yet to recover from this recent disturbance.

4. Discussion

Through this first assessment of mangrove paleoecology in North Sulawesi, we have identified highly variable responses of mangroves to discrete disturbances with regards to both the magnitude of mangrove pollen decline and recovery rate at Mantehage and Likupang over the last 8000 years. Over the Holocene and into the Anthropocene (c. 1950 CE; Waters et al., 2023), both mangrove areas have demonstrated ecological and engineering resilience, especially to more frequent natural disturbances such as storms. Average recovery times for mangrove pollen abundance (*c.* 95 %) at Mantehage and Likupang (104.5 years) are around half the reported global average for tropical forests and for mangroves specifically (>200 years), based on paleoecological data (Cole et al., 2014). However, this is considerably greater than modelled estimates for mangrove recovery of asymptotic biomass of 375 t/ha^{-1} (20 – 40 years) from similar disturbances (Mukherjee et al. 2014); and the “years to decades” reported in a review of mangrove recovery from large infrequent disturbances based on modern and historical ecological data (Alongi, 2021). These results demonstrate that mangrove sediment can provide valuable paleo-archives for identifying more realistic long-term trends in resilience, despite their known limitations with regards to species-level identification, dating, and bioturbation (Ellison, 2008; Sefton et al., 2021). Variable and potentially long periods of recovery (hundreds of years, see Table 2) indicate that further conversion of these mangroves, or significant changes to their hydrology, could result in economic and ecological costs that are unlikely to be recouped within timelines relevant for supporting national and international policy commitments. But this will ultimately depend on the type and frequency of future disturbances and any interventions taken to accelerate natural regeneration.

4.1. Long-term trends: Sea level and ENSO

For most of the Middle, and the early Late Holocene, changes in mangrove pollen abundance in the MH record were largely driven by marine transgression and regression with proxy evidence for only one disturbance over a period of *c.* 7000 years. As sea-level in the region during this time has been estimated to have increased to a high-stand of between 0.5 – 5 m above modern levels (Chua et al., 2021; Li et al., 2023; Mann et al., 2019), it is likely that mangroves at Mantehage will have the resilience to predicted regional increases in sea-level of 80 cm by 2100 (Indonesian National Development Planning Agency, 2009); and the global mean (range 0.69–1.05 m) predicted in a worst-case scenario of 5 °C warming (IPCC, 2023).

Resilience to total increases in RSL have similarly been reported for mangroves in Sumatra (Setyaningsih et al., 2019). The establishment of mangrove forest at MH around 8000 years ago coincides with the expansion of extensive mangrove forest worldwide, principally driven by a deceleration of high rates of relative sea level rise from 10,000 to 8000 years ago across tropical and subtropical latitudes (Saintilan et al., 2020). Using a compilation of Holocene proxy data, Saintilan et al. (2020) proposed a relative sea level rise threshold of 6.1 mm/year above which mangroves are unable to initiate sustained vertical sediment accretion. Under high-emission scenarios (RCP8.5), this threshold is expected to be exceeded between 2030 and 2050 in low-latitude mangrove regions, where rates of relative sea level rise are expected to be higher than global average (Church et al., 2013). Our results therefore highlight the importance of establishing mangrove restoration areas as protected restoration forests, in particular in the densely populated coastal regions of Sulawesi, such as Likupang. This would allow for the expansion of mangrove across coastal lowlands in response to future sea level rise.

The capacity for adaptation at Mantehage to changes in sea-level may have been further decreased following a reduction of resilience since the 14th Century CE. It may have additionally weakened due to an increased frequency and intensity of other disturbance phenomena associated with increasing global temperatures, such as fluctuations in the El Niño-Southern Oscillation (ENSO), which highly influence inter-annual variability in climate (Timmermann et al. 2018).

The modern ENSO modality (ca. 2–7 years) was established by the end of the Middle Holocene; though the magnitude of ENSO events increased from the Late Holocene (Gagan et al., 2004). In Sulawesi, El Niño events manifest in dry periods and can lead to extreme drought (Lestari et al., 2016; Setiawan et al., 2017). Particularly strong historic El Niño events in the region occurred in 1972–73 and 1982–83, CE (Gushchina et al., 2019; Setiawan et al., 2017), which both resulted in an observed drought-related mass mangrove dieback at Mantehage (Djamaluddin, 2004). However, we are limited in our interpretation of mangrove response to this disturbance as the paleorecord during this period did not have high enough resolution to disentangle the two El Niño events which occurred within ca. 10 years. The compounded palynological signal, indicates the loss of c. 33 % of mangrove pollen abundance to which only partial recovery was achieved before a subsequent disturbance. Given the resistance of these mangroves to past El Niño events, as indicated by little fluctuation in mangrove pollen over the record, we infer that the mangroves may now have less resilience to this type of disturbance. This weakening of resilience is likely exacerbated by the global intensification in ENSO variability since the pre-industrial era (Grothe et al., 2020). Re-establishing resilience to trends in ENSO should be a management priority at Mantehage as future El Niño events have been predicted to be more frequent and extreme (Cai et al., 2021). For example, this could involve interventions to facilitate faster recovery of mangroves in the current dieback area around the lagoon.

4.2. Earthquakes

The largest decline in mangroves at Mantehage occurred in the late 14th century CE. The disturbance driving the decline manifested geologically, as a distinct stratigraphic boundary and was associated with a contemporaneous replacement of diatoms that prefer brackish conditions with freshwater specialists, microcharcoal, and the presence of cryptotephra, which is indicative of volcanic activity. Changes indicated that tidal inundation was likely reduced at this time and though regional RSL was declining, the rapidity of the shift suggests that this could not be the sole driver of mangrove loss. We interpret this Late Holocene ecosystem change as driven by a short period of rapid localised tectonic uplift around the lagoon, out of the tidal range, due to a paleoseismic event such as an earthquake, potentially linked to volcanic activity. Sulawesi is one of the most tectonically active places in the world and has a long paleoearthquake record (Tournier et al. 2023). Within other tectonically active regions, several similar episodes of uplift driven disturbance have been reported, which have had immediate and long-lasting impacts on mangroves (e.g., Albert et al., 2017; Brown et al., 2015; Duke, 2008; Ramakrishnan et al., 2020; Rollon et al., 2015). A contemporary regional example is Simeulue Island, off the west coast of Sumatra. The 2004 earthquake in the Indian Ocean resulted in parts of Simeulue Island becoming submerged or uplifted by between 25–150 cm in different areas of the island (Briggs et al., 2006). Mangroves experienced die back in uplifted areas over a series of weeks and were replaced with landward species (Brown, 2007), similar to the vegetation change in the MH record with landward mangrove and non-mangrove pollen taxa more dominant than at any other time in the record.

The disturbance caused an ecosystem shift to a freshwater lagoon, indicated by a change in diatom composition and the presence of Cyperaceae (sedges), was followed after 150–200 years by a reversal to more saline conditions. We hypothesise that the reversal in salinity is the result of subsidence in the years following the earthquake, as would be expected by the Earthquake Deformation Cycle; in a process like that reported for Isla Santa María in Chile (Wesson et al., 2015), or the opposite process of coseismic subsidence in coastal Sumatra, Indonesia (Kelsey et al. 2015). The recovery of the Mantehage mangrove from this hydrological disturbance had the slowest rate in this study, and was further delayed by additional disturbance from fire, lagging restoration of saline conditions in the lagoon. This result highlights the dynamic capability of mangroves to recover from significant loss, but indicates that this process may be slow, even after hydrological conditions have been restored. We interpret the freshwater lagoon as a potential alternative stable state for this ecosystem and therefore management should seek to minimise any actions that may restrict tidal inundation or significantly increase freshwater input at this site.

4.3. Storms/Tsunami

Storm/tsunami events were the most frequent form of disturbance at Likupang. Mangroves at Likupang resisted many of these disturbances and when mangrove pollen abundance did decline, it rebounded relatively quickly. The Likupang mangroves have shown high levels of resilience to this relatively common form of natural disturbance – to which mangroves are typically well adapted (Alongi, 2021; Krauss and Osland, 2020). This is important, as extreme storm events are predicted to increase in the future under moderate and high emissions scenarios (Shared Socioeconomic Pathways; SSP2-8.5; O’Neill et al., 2016), and to a lesser degree if emissions are lower (SSP1-2.6) (Ridder et al., 2022). Given their ability to withstand and recover quickly, Likupang’s mangroves are well suited to act as protective buffers for coastal human communities. Coastal protection through resilience to storm/tsunami events is a valuable service (Barbier, 2016) that these mangroves provide, which needs to be incorporated into future estimates of the value of Likupang’s ecosystem services, as current estimates tend to focus only on provisioning services (Tamsir et al., 2022). However, it is again challenging to predict future mangrove resilience to storms and tsunamis of varying strengths at Likupang, given that the mangroves are yet to be fully restored following their conversion for aquaculture in the 1980s CE.

4.4. Anthropogenic and natural fire

As with evidence for paleostorms and tsunamis, fire is a very rare disturbance type at Mantehage and appears to be a facet only of the disturbed mangrove system at this site. The exceptionally high and singular peaks in the charcoal record, which show otherwise only very low or absent counts, support the interpretation of a local forest fire event at Mantehage. An increase in deadwood following the mass mangrove dieback and increased abundance of sedges in response to the shift in hydrological conditions are likely the cause of the rare fire event. Recovery from the single peak in microcharcoal was slow as this was a secondary disturbance, occurring when the mangrove was in a process of recovery from the most major disturbance at the site to have occurred during the Holocene, marked by tephra abundance around 553 cal. BP (1397 CE). At Likupang, evidence for fire was more common than at Mantehage, but peaks in microcharcoal remained infrequent. Limited neoecological studies have been published tracking the impact and recovery of mangroves from fires (e.g, Langner and Siegert, 2009; Smith et al., 2001; Smith et al., 2013), and even less research has been conducted on mangrove fire frequency over decadal to centennial timescales (e.g., Punwong et al., 2013a, 2013b). The relatively higher occurrence of fire at Likupang may also reflect greater anthropogenic pressure, for example due to agriculture and mining in the hinterland, and therefore be a feature of the different depositional environments of the two sites. While the Likupang record captures potential allochthonous influx of airborne charcoal from the hinterland or through rivers and coastal tides, the Mantehage record, from a small and isolated island, represents a much smaller catchment area. However, the observed differences may also reflect the higher anthropogenic pressure directly within, and adjacent to, Likupang’s mangroves. A targeted study of macrocharcoal would allow to better disentangle the regional vs local signal of these fires (Whitlock and Larsen, 2001). While human −induced fires are a major threat to some mangrove ecosystems, for example in the Sundarbans of South Asia (Islam and Bhuiyan, 2018), the rare occurrence of natural fires throughout the Holocene and mangrove responses suggest that natural fires are not a management priority at either mangrove site, provided the mangroves are not in a period of recovery when the fire occurs.

4.5. Anthropogenic impacts and implications for local mangrove restoration efforts

Our paleoecological data support the conclusions of O’Connell et al. (2022) on species network interactions, and Djamaluddin et al. (2023) on vegetation structure and diversity, that the community based mixed species restoration undertaken at Likupang has set the mangrove on a trajectory of recovery following its history of use for aquaculture. At only 16-years post restoration, c. 78 % of mangrove pollen abundance has recovered at LK1 and in 2019 the pollen assemblage closely resembled its historic compositional baseline which was based on variability in the Late Holocene. However, we also identified some compositional differences in the past between the LK1 and the LK2 cores from the adjacent non-deforested site which was used as a “space for time” reference by Djamaluddin et al. (2023) and O’Connell et al. (2022) to assess restoration success. Our analysis was conducted retroactively to restoration action at the site and therefore was not factored into decisions of mangrove species selection for planting. Despite this, the pollen record supports the selection of *Rhizophora* species, as this genus has been dominant at the site since at least 1105 CE. Future restoration of the remaining disused aquaculture ponds in the Likupang area may benefit from planting locally native species of *Bruguiera* and *Ceriops* (Table 1), which have also been important components of the historic mangrove diversity at the site during periods of warmer climate during the Middle Holocene. *Ceriops tagal* has a high salinity tolerance (Patel et al., 2010) and is therefore more capable to withstand high evaporation and drought that might occur more often in a warmer-than-present future climate. Mangrove species selection for restoration should also depends on other factors than the historic species pool, for example the perspectives and needs of local communities.

Decreases in mangrove pollen at Likupang following conversion for aquaculture were much lower than expected, given the significant area of mangroves that was cleared. This therefore indicates that even small declines in mangrove pollen abundance in our paleo-records from North Sulawesi may equate to large losses of mangrove forest area and structure. Future research of modern pollen rain–vegetation relationships within these mangroves, spanning natural ecological and human impact gradients, may help to quantify this relationship. Additionally, this would contribute towards defining historical ranges of variability with regards to the composition of mangrove vegetation, as has been employed for savannah ecosystems in Kruger National Park, South Africa (Gillson et al., 2007), therefore improving the direct utility of these data for guiding management objectives.

The 2012 mangrove dieback, following a major road construction at Mantehage resulted in a *c.* 10 % decrease in mangrove pollen abundance to which the mangroves are still recovering. The role of the road construction and bridge in changing the timing and duration of tidal inundation into the lagoon and surrounding area should be a focus of future research, as the construction of artificial barriers have been implicated in mass mangrove dieback and lower resilience to disturbance in other regions (Lagomasino et al., 2021; Wemple et al., 2018). One of the most prominent examples are the wetlands of the Ciénaga Grande de Santa Marta, Colombia, where road construction and subsequent modification of hydrological connectivity led to one of the largest mangrove diebacks on record (Jaramillo et al. 2018). If identified as the cause for mangrove dieback on Mantehage, then engineering adaptations such as increasing the number and size of box-culverts, which would support the re-establishment of natural hydrologic conditions (Rivera-Monroy et al., 2011), should be further investigated to avoid reaching a tipping point which shifts the ecosystem into the alternative state described above. Despite the presence of mangrove forests since at least the Middle Holocene on Mantehage, the 14th century seismic disturbance and subsequent historic disturbances mean that the modern mangrove vegetation community at this site is not representative of the final stage of ecological succession for a mangrove. Management of the mangrove forest here should therefore seek to facilitate recovery (passively or actively) to a less disturbed and more stable stage in the past, rather than considering the diversity and ecology of the last decades only as a natural baseline.

The anthropogenic disturbance of hydrological connectivity through new shrimp pond construction is an ongoing threat, and reality, for mangrove forests at Likupang. Re-establishing the natural hydrological conditions is therefore of uppermost priority to achieve restoration success (Djamaluddin et al., 2019). In addition, mangrove restoration efforts must be carried out with the aim of ensuring the continuity of the natural regeneration process. Restoration activities should not be limited to just planting certain mangrove species, but must be followed by efforts to facilitate the natural regeneration process and ability of certain species to survive.

One key aim of mangrove restoration, led by the communities of Likupang, was to restore their forest diversity, ecosystem functioning and provisioning services (Djamaluddin et al., 2023). Our study shows that mangroves vary largely in their recovery time following major disturbances, depending on the disturbance type (e.g., storm, drought etc), severity and frequency. However, in restoration/rehabilitation projects there is no standard as to what constitutes “recovery”, since this will depend upon the original drivers and goals of such projects. For example, if timber production for construction was the goal, restoration success would likely be reached faster than if bringing back biodiversity and complex ecological networks was the goal (Djamaluddin et al., 2023).

5. Conclusion

Our study reveals that mangroves in North Sulawesi have demonstrated ecological and engineering resilience over thousands of years to disturbance induced by changes in sea-level, drought, seismic uplift, storms, possible tsunamis, fire and human activity. However, the recovery times we observed, though shorter than global averages, are still substantial in some cases, underscoring the importance of conservation over restoration at these sites. Mangrove recovery time appears to vary depending on the type of disturbance. While recovery time from regular storm and flooding was short, with often full recovery, we identified a potential tectonic uplift along with hydrological changes as the most severe disturbance that required the longest recovery time. The contemporary mangroves at Mantehage and Likupang are currently on a trajectory towards recovery in terms of their pollen composition or mangrove abundance following historic and recent disturbances, but full recovery will be dependent upon on-going management and changes in the intensity and frequency of future disturbances due to a warming global climate. We have identified key factors for guiding local management and restoration efforts: 1) the potential existence of an alternative stable state at Mantehage lagoon; 2) the high priority of re-establishing resilience to ENSO-induced droughts; 3) the creation of a list of locally native mangrove species based on long-term ecological data, which will aid in selecting species for future restoration projects; and 4) our quantification of a local historic baseline which has been used to assess the success of mangrove recovery efforts to date. By applying paleoecological techniques for long-term monitoring, this study offers a distinctive framework that can be adapted for mangrove conservation worldwide.

CRediT authorship contribution statement

Rachael Holmes: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **Ulrich Salzmann:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Rignolda Djamaluddin:** Writing – review & editing, Investigation, Conceptualization. **Emma P. Hocking:** Writing – review & editing, Resources, Methodology, Investigation. **Mark Williams:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition. **Juan Carlos Berrio:** Writing – review & editing, Supervision, Resources, Methodology, Investigation. **Iskandar Siregar:** Writing – review & editing, Supervision. **B.Aiyen Tjoa:** Writing – review & editing, Resources. **Marco Fusi:** Writing – review & editing, Investigation. **Karen Diele:** Writing – review & editing, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.113231.

Data availability

Palaeoecological data and code used in the analysis and to make stratigraphic plots is accessible online via the papers GitHub repository at CoReNat-Palaeo/Palaeo_Mangrove_Supplementary.

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