A 16,000-year record of climate, vegetation and fire from Wallacean lowland tropical forests

Hamilton, R.^a, Stevenson, J.^b, Li, B.^c, Satria Bijaksana^d

^aCorresponding author. Rebecca Hamilton. School of Culture, History and Language, The Australian National University, Canberra, ACT 2610, Australia. <https://orcid.org/0000-0002-5443-8353>

rebecca.hamilton@anu.edu.au

T: +61 2 61250308

^b Janelle Stevenson. School of Culture, History and Language, The Australian National University, Acton, ACT 2610, Australia. <https://orcid.org/0000-0001-9640-7275>

janelle.stevenson@anu.edu.au

^c Brian Li. School of Culture, History and Language, The Australian National University, Canberra, ACT 2610, Australia.

brian.li@anu.edu.au

^d Satria Bijaksana. Faculty of Mining and Petroleum Engineering, Institut Teknologi Bandung, Bandung 40132, Indonesia. <https://orcid.org/0000-0001-6374-4128>

satria@fi.itb.ac.id

Abstract

The tropical forests of Sulawesi represent some of the most diverse, biogeographically significant ecosystems globally. However, long-term ecological data for the region are scarce, making it difficult to predict vegetation response to future climatic and anthropogenic drivers of change. This is problematic as gauging the acclimation thresholds of forests within tropical Asia has been identified as an IPCC policy imperative. This study uses palynological and geochemical analysis of sediments from a tectonic basin – Lake Lantoa – to reconstruct the hydroclimatic, fire, and tropical rainforest dynamics of south Sulawesi over 16,000 years, and reveal the response of lowland ultramafic forest to large-scale environmental change. Our results show that the Late Pleistocene was characterised by a drier, more seasonal climate and persistent fire in the landscape. These conditions supported a slightly open, *Gymnostoma*-rich, semi-seasonal forest, and constrained the available habitat range for hydrophilic tropical conifers. Increased effective moisture in the Holocene, interpreted from the onset of periodic lake stratification under deeper conditions, appears to have precluded forest burning, and facilitated the expansion of a lowland ultramafic rainforest and upland tropical coniferous forest. An increase in garden/secondary forest taxa and ground ferns from ~2 cal. kyrs BP implies increased human management of the landscape. While these data highlight the compositional dynamism of lowland forest in Wallacea to seasonality, fire, and reduced precipitation, they demonstrate biome-scale resilience to glacial-scale environmental change. This contrasts with interpretations of forest sensitivity to climatic change drawn from analysis of leaf wax isotopes from adjacent lake basins, highlighting the value of adopting multi-proxy, taxonomically high-resolution techniques for reconstructing floristic histories.

Keywords

Pleistocene; Holocene; Climate dynamics; Southeastern Asia; Sedimentology, lakes, lagoons & swamps; Vegetation dynamics; Tropical palynology; Geochemistry; Charcoal; Lake level

26 1 Introduction

27 The Wallacean tropics in maritime south-east Asia are significant not only for their exceptional
28 biodiversity (Myers et al., 2000; Olson and Dinerstein, 1998) and important biogeographic setting
29 (Wallace, 2010 (1869)), but also for the role that associated ecosystems play in regulating global
30 carbon and water cycles (Brandon, 2014). Despite this, very little is known about how tropical systems
31 in Asia, particularly lowland forests, will respond to future climate change (IPCC, 2014) which proves
32 problematic for conservation planning for the region. One major reason for the lack of data on long-
33 term forest dynamics in this region is not only a lack of palaeoecological data on vegetation change,
34 but also that, until recently, there has been a deficiency of information on drivers of change within
35 these systems – most notably a changing climate, anthropogenic disturbance, and altered fire regimes.

36 The work that has progressed our understanding of the palaeoclimate of the region indicates that
37 hydrological shifts in the Indo-Pacific Warm Pool (IPWP) – the primary climate driver in Wallacea –
38 have been significant at a glacial scale. Most notably, there appears to have been a dramatic rise in
39 regional humidity between ~16-14 cal. kyrs BP and ~11.7 cal. kyrs BP – the period spanning the Last
40 Glacial Maximum (LGM) to Holocene transition (Costa et al., 2015; Dam et al., 2001; Russell et al.,
41 2014; Vogel et al., 2015).

42 Superimposed on this overarching glacial-scale transition into the Holocene, are lower-magnitude
43 events such as the Bølling-Allerød warming (BA ~14.7-12.9 cal. kyrs BP), the Younger Dryas cooling (YD
44 ~12.9 to 11.7 cal. kyrs BP) and the Early- to Mid- Holocene Climate Optimum (HO). Within island south-
45 east Asia, the scale, magnitude and timing of these events are mediated by the complex interaction
46 of shifts in the Intertropical Convergence Zone (ITCZ), the Austral-Asian monsoon, and later, the El
47 Niño–Southern Oscillation (ENSO) (Chen et al., 2016; Partin et al., 2015; Wurtzel et al., 2018). This has
48 resulted in their having a heterogenous impact across the region, highlighting the need for higher
49 spatio-temporal palaeoenvironmental records for the area.

50 The BA and YD events in Sulawesi appear muted (Russell et al., 2014; Tierney et al., 2012) contrasting
51 with regional $\delta^{18}\text{O}$ speleothem records produced from Flores, Java and Sumatra (Ayliffe et al., 2013;
52 Mohtadi et al., 2011; Wurtzel et al., 2018). However, $\delta^{13}\text{C}_{\text{wax}}$ is the primary proxy used to reconstruct
53 the palaeoclimate of Sulawesi – a tool that relies on biome-scale vegetation change (i.e. forest to
54 grassland) to interpret the hydroclimate (Russell et al., 2014; Tierney et al., 2012; Wicaksono et al.,
55 2015; Wicaksono et al., 2017). This interpretation is potentially problematic given that it assumes a
56 linear forest to non-forest response to drying (and *vice versa*) which contrasts with work
57 demonstrating the non-linear threshold dynamics of forest and grassland systems to hydroclimatic

forcing (Hirota et al., 2011). Consequently, $\delta^{13}\text{C}_{\text{wax}}$ is likely insensitive to climatic shifts that are of an insufficient magnitude to trigger a stable state shift between forest and grassland. This demonstrates the need for additional multi-proxy data from the region that decouples climate drivers from biome-scale vegetation response (or lack thereof) particularly for analysis of lower magnitude climatic events.

The scale of Holocene climatic shifts within Wallacea is also uncertain. Notably, there is a large buffer in the interpreted timing of Holocene precipitation maxima in Sulawesi from lake proxies. This may relate to the different sensitivity thresholds of the proxies being assessed and/or the high geographic (and associated climatic) variability across the island. For instance, Titanium data presented in Russell et al. (2014) suggest heightened runoff (and thus high precipitation between ~10 and 8 cal. kyrs BP), and decreased runoff between ~8 and 4 cal. kyrs BP, whereas Dam et al. (2001) interpret a lake high stand (and hence humid conditions) from sediment and diatom proxies between ~11 and 4 cal. kyrs BP.

While work refining the nature and timing of lower magnitude climate events in Wallacea between the LGM and the present day is clearly needed, the emergence of palaeoclimatic records for the region, particularly those spanning the LGM - Holocene transition, presents an opportunity for gauging the response of the tropical landscape to large-scale climatic change.

Research on the response of forest to the Pleistocene-Holocene transition in Sulawesi suggests a shift from fire-influenced, open vegetation with a submontane element, to dense, more diverse, humid rainforest (Dam et al., 2001; Hope, 2001; Russell et al., 2014; van der Kaars et al., 2000; Wicaksono et al., 2015; Wicaksono et al., 2017). Interpreting more ecologically meaningful, compositionally specific vegetation response to both this major climate shift as well as any other lower scale climatic change between the Late Pleistocene and the present, however, proves problematic for several reasons. Firstly, there is lack of taxonomic resolution in the $\delta^{13}\text{C}_{\text{wax}}$ records (Russell et al., 2014; Tierney et al., 2012; Wicaksono et al., 2015; Wicaksono et al., 2017). This makes it impossible to interpret changes in forest composition, and introduces the potential for signal mixing between catchment and highly localised lake-edge wetland assemblage, the latter of which can expand during low lake stands and be comprised of C3 and C4 grasses and sedges (Bruhl and Wilson, 2007). The overprinting of a swampland (and anthropogenic) signal has, indeed, been shown to complicate interpretation of climate-driven shifts reconstructed from the sediments of Lake Tondano in north-east Sulawesi (Dam et al., 2001). Secondly, better taxonomically resolved pollen records from Sulawesi have major temporal gaps that are coincident with some key climate events picked up in the regional records, and, in some instances, unclear chronologies. For instance, the Wanda Swamp record presented in Hope (2001), which has a tenuous chronological model in the first place, appears to be missing the critical glacial termination period between ~17 and 5.5 kyrs. Similarly, the LGM portion of the Lake Tondano record (~33 to 13

ka) is compressed and likely incomplete (Dam et al., 2001). Other contiguous records only span the Late Holocene (Biagioni et al., 2015a; Biagioni et al., 2015b; Kirleis et al., 2010; Wündsche et al., 2014), or are sampled at a low temporal resolution over MIS 1 and MIS 2 (van der Kaars et al., 2000). Finally, the spatial resolution of the palaeorecords encompassing Late Pleistocene and Holocene vegetation transitions across the region, particularly in lowland communities, is very low (Dam et al., 2001; Hope, 2001; Russell et al., 2014; van der Kaars et al., 2000; Wicaksono et al., 2015; Wicaksono et al., 2017).

The aim of this study is therefore to review the role of climate and fire in contributing to the long-term dynamics of Wallacean lowland tropical forest from the Late Pleistocene to the present. This is done through a new, 16,000 year-long, multiproxy record of climate, fire and vegetation change from the lowland ultramafic rainforests of Sulawesi. The record sheds light on the nature of tropical forest response to long-term climate change over the Pleistocene-Holocene transition in south-east Asia, and contributes to informing future conservation planning for this climatically and socioecologically significant region.

2 Regional Setting

Lake Lantoa (Wawantoa) is a small (approx. 150 ha), shallow (~4 m at deepest location), north-east to south-west striking water body situated in the administrative district of East Luwu Regency, South Sulawesi (Fig. 1). It is located towards the eastern margin of the Malilli Lakes catchment, and forms one of two smaller, satellite lakes connected to three much larger water bodies (Matano, Mahalona and Towuti) by rivers. The Malili lakes formed from approximately 1.5 Ma in transtensional basins, driven by tectonic activity associated with the Matano strike slip-fault (Russell et al., 2016). Regionally, the catchment sits within the East Sulawesi Ophiolite which is comprised of ultramafic gabbros, basalts and peridotites (Kadarusman et al., 2004). The lake catchment geology is mapped as Lherzolite (Costa et al., 2015).

Figure 1: Regional and local elevation map of Lake Lantoo in South Sulawesi, including the coring location of LL2. Regional map shows location of key Wallacean sites referred to in this paper. A) Lake Towuti (Konecky et al., 2016; Russell et al., 2014; Vogel et al., 2015); B) Wanda Swamp (Hope, 2001); C) Lake Tondano (Dam et al., 2001); D) Lake Matano (Wicaksono et al., 2015); E) Mandar Bay (Makassar Strait) (Wicaksono et al., 2017); F) Banda Sea (van der Kaars et al., 2000).

Geomorphically, the lake sits at approximately 600 m ASL, and within the immediate vicinity of the lake basin, is surrounded by peaks of up to 800 m ASL to the south-east and north-east. Streams originating from the eastern margin of the Malili lakes catchment (approximately 4 km from the site), feed the lake. Ephemeral outflow from Lake Lantoo is west to Lake Towuti – the largest of the Malili Lakes (Fig.1). Outflow can only occur when lake levels are raised enough to breach the sill extending along the western margin of the lake, which is located approximately 5 m above present lake levels.

Sulawesi is located centrally within the Indo-Pacific Warm Pool – a key driver of global atmospheric convection – and is influenced by the interplay of the Austral-Australian Summer Monsoon, the shifting position of the ITCZ, and ENSO (De Deckker, 2016). Though situated in the humid tropics, the mountainous topography of Sulawesi results in heterogenous temperature and precipitation gradients across the island (Whitten et al., 1987). The local climate of Lake Lantoo (estimated for the period between 1901 and 2016 from Harris et al. (2014)) is characterised by a mean annual temperature of 24.8°C, and a mean annual precipitation of 2675 mm/year. Seasonality at the site is mild, with only two months (September and October) experiencing rainfall of less than 100 mm/month.

The interaction of the climatic and geological setting of the lake results in the catchment flora comprising lowland ultramafic rainforest – though much of the immediate forest has been disturbed via logging, agricultural and mining activity. The forests supported by ultramafic terrains in Sulawesi (mapped in Galey et al., 2017) are important both in terms of their spatial extent (ultramafic outcrops occur across 8.8% of the island), and the specialised traits that constituent plants require to facilitate establishment on nutrient poor, heavy metal rich substrates (van der Ent et al. 2013). While there is no comprehensive survey data for the forest immediately surrounding the site, there is data from ultramafic communities proximal to the site including Lake Matano and Sorako. Compositionally, key lowland trees comprise species from the Anacardiaceae, Aquifoliaceae (*Ilex*), Araucariaceae (*Agathis*), Burseraceae (*Canarium*, *Dacryoides*), Calophyllaceae (*Calophyllum*), Casuarinaceae (*Gymnostoma sumatrana*), Combretaceae (*Terminalia*), Dipterocarpaceae (*Hopea celebica* and *Vatica*), Elaeocarpaceae (*Elaeocarpus*), Lauraceae, Melastomaceae (*Memecylon*), Myrtaceae, Rosaceae (*Prunus*), Sapotaceae (*Planchonella*), and Thymeleaceae (*Wikstroemia*) families (Balgooy and Tantra, 1986; Brooks, 1987; Whitten et al., 1987; Wicaksono et al., 2017).

At higher elevations (approximately 700 m ASL), species from the Myrtaceae (*Metrosideros* and *Syzygium*), Burseraceae (*Santiria*) and Fagaceae (*Lithocarpus*) families remain dominant alongside Moraceae (*Ficus*) (Whitten et al., 1988). Disturbed forest on ultramafic soils tends to comprise Rhamnaceae (*Alphitonia*), Euphorbiaceae (*Macaranga* and *Homolanthus*), Verbenaceae (*Callipcarpa*), Cannabaceae (*Trema*) and Myrtaceae (*Baekia frutescens*) tree species with a grassy and/or fern rich understorey (Whitten et al., 1988).

Ultramafic lake fringing vegetation, best recorded Lake Matano (Fig. 1), tends to be overwhelmingly dominated by the Myrtaceae (*Metrosideros petiola*, *Xanthostemon confertiflorum*, *Kjellbergiodendron*, and *Syzygium*), and to a lesser extent, Rubiaceae (*Timonius*, *Canthium*, *Gardenia*, *Mussaendopsis* and *Psychotria*) families (Balgooy and Tantra, 1986). The lake margin – which has a stepped slope – is fringed by Cyperaceae, *Pandanus*, Poaceae and Myrtaceae species.

While evidence for human occupation of Sulawesi extends back to 40 cal. kyrs BP (van den Bergh et al., 2016), the archaeological record in the vicinity of the Malili lakes is sparse, with most sites post-dating 2.5 cal. kyrs BP (synthesised in Bulbeck, 2018). Hope (2001) summarises human use of the local landscape, and indicates that, prior to the development of nickel mining in 1970, landuse was largely restricted to gardening as ultramafic terrains are generally unsuitable for rice cropping or agriculture.

3 Materials and methods

3.1 Core recovery

Sediment cores were collected from the southern end of the lake in a water depth of approximately 3 m using a Geocorer (Fig. 1). The coring location was selected on the basis of there being a suitable shoreline area for vehicular access. Cores were recovered as one metre long drives in six sections. The recovered vs penetration depth was measured and recorded for each section, and core loss placed at the end of each respective drive. Assessment of whether core shortening was due to compaction vs. exclusionary sediment loss was made during development of the chronological model for the core.

Once retrieved, the five basal core sections were capped and sealed, and then transported to the Australian National University for sedimentological and palynological analysis. The uppermost core section (0 to 100 cm) was unconsolidated, and thus extruded and bagged at 1 cm intervals on site.

3.2 Chronology:

Sixteen samples (10 bulk sediment, and 6 isolated humic acid fraction duplicates) from 10 depth intervals were used for ^{14}C dating at the Australian National University Radiocarbon Dating (Fallon et al., 2010) and Direct AMS (Zoppi et al., 2007) Laboratories in 2014 and 2015 (laboratories indicated in Table 1). Dating of humic acid fractions isolated from the bulk samples was conducted in order to test for contamination with modern organic material. Prior to analysis, all samples were pre-treated using standard acid-base-acid washes. The laboratory ID and depth of all dated samples are outlined in Table 1.

Table 1: Laboratory ID, sample type, depth, conventional ^{14}C (1σ) and calibrated (2σ) ages of LL2 samples analysed for radiocarbon dating

Lab ID	Depth (cm)	Material	^{14}C date BP ($\pm 1\sigma$)	Cal. yrs BP (2σ)
ANU 45723	16	Bulk sediment	1138 ± 21	940-1058
ANU 45716	16	Humic	1169 ± 22	967-1062
ANU 45724	48	Bulk sediment	2960 ± 22	2966-3158
ANU 45717	48	Humic	3097 ± 22	3179-3354
DAMS008500	70	Bulk sediment	3858 ± 29	4299-4400
ANU 45725	132	Bulk sediment	4478 ± 24	5327-5584
ANU 45718	132	Humic	4921 ± 24	5492-5659

Lab ID	Depth (cm)	Material	14C date BP (+/-1σ)	Cal. yrs BP (2σ)
ANU 45726	232	Bulk sediment	7627 ± 28	8345-8428
ANU 45719	232	Humic	7819 ± 28	8452-8625
ANU 45727	332	Bulk sediment	10346 ± 32	11841-12383
ANU 45720	332	Humic	10573 ± 36	12563-12637
ANU 45729	432	Bulk sediment	12098 ± 37	13766-14045
ANU 45721	432	Humic	12131 ± 42	13778-14089
ANU 45730	532	Bulk sediment	12734 ± 40	14896-15286
ANU 45731	580	Bulk sediment	13471 ± 42	15969-16329
DAMS008501	600	Bulk sediment	13779 ± 54	16860

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187 The AMS ages returned from the samples were calibrated using the Southern Hemisphere calibration
188 curve (Reimer et al., 2013) using the program *clam* 2.2 (Blaauw, 2010) in R (R Core Team, 2013). A
189 Bayesian statistics-based age-depth model was developed for core LL2 using Bacon 2.2 (Blaauw and
190 Christen, 2011) in R (R Core Team, 2013). The model included the ages returned for the 10 bulk
191 sediment samples, and was run in 121 sections using a sediment accumulation rate (acc.mean) of 20
192 years per cm – estimated from linear interpolation between adjacent date samples. An assumed age
193 of -64 cal. yrs BP (2014 C.E.) was set for the core top (0 cm). The median age-depth model age output
194 was used to estimate ages for the core sediments at 1 cm intervals.

195 3.3 Core sedimentology

196 3.3.1 Loss-on-ignition analysis

197 The organic carbon content and water content of thirty, 1 cm thick sediment subsamples taken at
198 approximately 10 to 30 cm intervals was estimated via loss-on-ignition analysis following standard
199 methods (Heiri et al., 2001). Organic carbon content estimations were made via ignition at 550°C for
200 four hours (noting that mass lost may also capture inorganic iron carbonates such as siderite – a
201 mineral present in adjacent, albeit deeper, Malili Lake basins (Kuntz et al., 2015; Vogel et al., 2015).

3.3.2 XFR core scanning

3.3.2.1 *Data acquisition:*

The surfaces of the five intact core sections (100 cm to 600 cm) were scanned for XRF elemental analysis using an Avaatech core-scanner at the Australian National University Research School of Earth Sciences (20s count time 10kV voltage). Measurements were made at 5 mm intervals, and data recovered as peak areas for the elements Si to Ni.

3.3.2.2 *Data processing and normalisation*

XRF measurements coincident with sediment defects and core ends were deleted from the raw dataset. These were identified by comparison with significant drops in total counts per second data (cps) obtained for the sediments during the scanning process. Elements were removed from the dataset if the mean of all down core measurements was negative.

Following cleaning of the dataset, cps data (standardised using a z-score) were correlated with standardised loss-on-ignition and water content values obtained from the core sediments. The results of this correlation showed a strong negative relationship between cps data and both LOI ($r=-0.96$, $p<0.05$) and water content ($r=-0.78$; $p<0.05$). This demonstrates a significant relationship between these variables. A multiplier serving to flat-line the cps data (i.e. cps/ mean cps) was thus used to correct each elemental variable for the dilution effects of water and organic content in the core sediments.

Following normalisation, a 5pt (Ca, Mn, Fe, Ni, Cr) and 20pt (Al, Si, P, S, Ti) running mean (centralised) was applied to the variables depending on their detectability and resultant noisiness of the dataset. These data were then standardised using a z-score.

Elemental ratios useful for interpreting redox cycling in shallow, mafic lake sediments – notably Mn/Ti and Fe/Ti (Hamilton et al., 2019a; Rothwell and Croudace, 2015) were plotted in order to elucidate any relevant information on lake level fluctuations. Ti was used as a denominator for these ratios given that it is diagenetically inert, likely represents a detrital signal, and has reasonable detectability. Mn/Fe ratios were also calculated as an alternative means of calculating the oxic status of lake bottom sediments (Naeher et al., 2013). This is particularly useful when non-detrital Fe and Mn (i.e. Mn/Ti and Mn/Fe) do not covary due to Mn being more sensitive than Fe to changes in oxic state.

3.4 Palynological analysis

3.4.1 Plant microfossil analysis

3.4.1.1 Sampling and enumeration

Thirty-one samples were extracted from the core sediments for plant microfossil analysis. Samples were prepared in two batches. Batch one samples (n=18) were prepared using standard methods (Faegri and Iversen, 1989). As HF appeared to cause the batch 1 samples to clump, the second batch of samples (n=13) were prepared using density separation (Lithium-sodium-polytungstate specific gravity 2.0) (Caffrey and Horn, 2013). All subsamples processed for palynological analysis were 2.5 cm³ (field moisture), and were selected from 1 cm – (n=30) to 2 cm – (n=1 - core top) thick sediment slices spaced at approximately 20cm intervals down core. One *Lycopodium clavatum* tablet was added to each sample as an exotic spike to facilitate estimation of pollen and microcharcoal influx. Plant microfossils were enumerated under a Zeiss Axiolmager M.1 light microscope fitted with an AxioCam MRc5 camera under x400 magnification. A minimum count target of 200 pollen and spores (with a minimum of 100 arboreal taxa) was set for the analysis. Fragments of *Botryococcus* (>20 µm) were simultaneously counted during pollen and spore analysis. A qualitative estimation (absent, rare, common, abundant) of *Pediastrum*, and, from batch 2 samples (non-HF treated), diatoms and sponge spicules was conducted in order to provide an indication of past lake productivity.

Pollen grains were identified through comparison with published literature (Hamilton et al., 2019b; Huang, 1972; Wang, 1995) and reference pollen taxa held in the Australasian Pollen and Spore Atlas (APSA) at the Australian National University. The APSA has been updated for the purpose of this, and other ongoing research in Wallacea, to include an additional 327 reference samples from Sulawesi that were collected by JS and RH from vouchered reference housed at the Naturalis Biodiversity Center in Leiden, The Netherlands in 2016 and 2017.

3.4.1.2 Analysis

Stratigraphic plots of the relative abundance of pollen and spore data (percentage of both the total pollen count and the arboreal pollen count) were made in the program C2 (Juggins, 2014a). Data were decomposed using a PCA (in C2) and stratigraphically constrained cluster analyses (using the package rioja (Juggins, 2014b) in R (R Core Team, 2013)) to elucidate changes in the microfossil assemblage with depth. A PCA of the broad pollen functional types, grouped using relative abundances and standardised using a z-score, was conducted to look at broad scale shifts in vegetation through time. A second cluster analysis and PCA was run on arboreal-only (tree and shrub) pollen taxa converted into percentages of the whole tree/shrub assemblage. This analysis was used to examine changes in

the intra-forest assemblage through time. Microfossils making up greater than 0.5% of the total tree and shrub count were included in this analysis.

Classification of the pollen taxa into functional groups and habitat types was undertaken by comparison with a digitised herbarium list of 28,000 specimens collected from Sulawesi and compiled by the Naturalis Biodiversity Center in Leiden, The Netherlands. All relevant species that matched the arboreal pollen taxa (generally classified at a genera or family level) were extracted from the list, and their predominant habitat preference determined by assessment of the specimen notes in the herbarium list as well as published data (Whitten et al, 1988; Keßler et al., 2002; IUCN 2019). Where a dominant habitat preference could not be established (e.g. where one pollen type represented either multiple species with diverse habitat preferences, or a species with the capacity to grow in a range of settings), they were placed into a “generalist category”.

3.4.2 Charcoal analysis

Microcharcoal fragments retained in the slides prepared for pollen and spore analysis were counted alongside the plant microfossils. Macrocharcoal was sampled contiguously across all core sections in 2 cm intervals from 1 to 10 cm and in 1 cm intervals below that (n= 494). Charcoal was extracted from 2.5 cm³ samples via wet sieving through a 125 µm mesh following methods outlined in Stevenson and Haberle (2005). Charcoal fragments were enumerated under a Zeiss Stemi Stereo microscope at 20x magnification.

Following counting, micro- and macro- charcoal counts were converted to concentrations (fragments/dry cm³) and influx rates (fragments/dry cm²/yr) using water content data and the sediment accumulation. Stratigraphic plots were produced in C2 (Juggins, 2014a).

4 Results and Discussion

4.1 Chronology and sedimentation

The termination depth of core LL2 was 600 cm. Recovery of the first five drives ranged from 85% to and 95%. A “no core” gap was included within the total core sequence at the base of drives with less than 100% recovery. These gaps are shown stratigraphically in Fig. 2B.

Figure 2: Core LL2 (A) chronological model; (B) stratigraphic core gaps, water content (%), LOI 550 (%), algal (fragments per cm^2) and diatom (qualitative estimation) content.

The ^{14}C and calibrated ages (yrs BP) of core LL2 are presented in table 1. The dates show increasing age with depth. There is generally strong concordance between the bulk sediment and humic fraction ages returned from the same sample depths, indicating little contamination from modern organic carbon (table 1).

The age-depth model produced from the core is presented on Fig. 2A, with the oldest (median) modelled age for the sequence estimated to be 16.6 ka. There is no evidence from this model that the sediment loss reported for each of the extracted core sections is a product of compaction via frictional build up during coring. These gaps are therefore interpreted to represent loss of sediment during the coring process, presumably out of the base of the core tube. The modelled ages for the LL2 sequence suggest that these gaps encompass 14.8 to 14.5 cal. kyrs BP, 13.2 to 12.9 cal. kyrs BP, 10.8 to 9.6 cal. kyrs BP, 7.5 to 6.6 cal. kyrs BP, and 4.8 to 4.4 cal. kyrs BP. Age-depth modelling indicates three periods of changing sedimentation rate. The Pleistocene portion of the record between 600 cm to 323 cm – modelled at 16.6 to 11.65 cal. kyrs BP – shows relatively fast sedimentation, averaging 17.8 years/cm. Up core of 323 cm, the sedimentation rate decreases in a stepwise manner to 29.6 years/cm to 73 years/cm (modelled at 4.2 cal. kyrs BP), and then 59 years/cm between 73 cm and the core top sediments.

4.2 Loss-on-ignition and non-pollen microfossil indicators of lake productivity

Loss-on-ignition analysis indicates that the organic matter content of the core is relatively low (mean 12.1 %) between the basal core sediments and 340 cm (~12.1 cal. kyrs BP), before rising to an average of 15.4% percent between 320 cm and the core top sediments (i.e. the modelled Holocene portion of

the record). The upper three samples, modelled at 2.6 cal. kyrs BP to present, have the highest measured LOI values (in excess of 16.7%). This trend is inverse to the modelled sedimentation rate for the core sediments, suggesting the accumulation of organic material is not the primary driver of sedimentation within the basin.

The only diatoms encountered in the lake sediments comprise pennate, benthic–habitat type morphologies. These occurred in the analysed non-HF treated sequence twice - rarely at 564 cm (~15.8 cal. kyrs BP), and abundantly at 448 cm (~14.1 cal. kyrs BP) (Fig. 2B). Abundant sponge spicules are hosted within the same layers, as well as in non-HF treated samples extracted from the deepest part of the sedimentary sequence (548.5 cm to 580.5 cm – ~15.6 to 16.2 cal. kyrs BP) (Fig. 2a). *Botryococcus* cf. *braunii* is a consistent part of the sedimentary sequence from the basal sediments up to 232 cm (~8.4 cal. kyrs BP), after which it disappears before re-emerging within the two core top samples (18 cm to 0 cm – ~1.1 cal. kyrs BP to present). Large spikes in *Botryococcus* concentration occur in sediments extracted from 500 cm depth (~14.8 cal. kyrs BP), and between 448 cm and 432 cm depth (~14.1 to 13.9 cal. kyrs BP). *Pedastum simplex* (cf. *var. simplex*) (Jankovská and Komárek, 2000) occurs in a single sample at 316 cm depth – the first analysed Holocene sample (~11.4 cal. kyrs BP). There is no clear relationship between the presence and abundance of sponge spicules and diatoms, and the estimation of total organic carbon from LOI analysis.

4.3 Geochemistry and lake sediment input

The relationship between the thirteen analysed elemental variables (including the Fe/Ti, Mn/Ti and Mn/Fe ratios) is shown on the PCA plot on Fig. 3. Two groupings are evident on the plot: 1) those positively loaded along PC1 – interpreted as indicators of endogenic redox cycling, and 2) those positively loaded on PC2 – interpreted to represent terrestrially-sourced mineral material. Justification for this interpretation and variability in these groupings through time is discussed below.

Figure 3: Stratigraphic and PCA plot of geochemical data for LL2 as determined from μ XRF core scan.

PC2: terrestrial erosional influx

Cr, Al, Si, Fe and Ti correlate ($r > 0.5$ for all elements with the exception of Ti and Si ($r = 0.25$)), and are positively loaded on PC2 (19.4% variance), which is interpreted to represent a signal of terrestrially-sourced, mineral input to the lake (Fig. 2). Of these, the two elements that make up the highest proportion of the count data are Fe and Cr. While these elements are unstable under different oxic states and hence not typically used as a terrestrial erosional signal, their abundance and correlation with conservative elements more characteristic of terrigenous input (e.g. Ti and Al (Rothwell and Croudace, 2015)) can be explained by the ultramafic catchment geology of the site. Iron-bearing minerals are abundant within ultramafic settings and are resistant to chemical weathering, resulting in concentration in the regolith. As elaborated on below, redox-sensitive, endogenic Fe precipitation (represented by Fe/Ti), appears inconsequential in the core sediments, and the bulk of Fe in the core is thus taken to represent terrigenous influx to the basin. Cr is also concentrated in soils derived from ultramafic rocks (Kabata-Pendias and Pendias, 2001) particularly Lherzolites which form the catchment geology of Lake Lantao (Whitten et al., 1988). The strong correlation between Cr and stable detrital elements (e.g. Ti and Al — $r = 0.8$) indicates that it likely represents a predominantly erosional signal in the Lantao sedimentary sequence.

There is an overall reduction in detrital input (negative PC2 shift) to the lake at a depth coinciding with the gap in the sedimentary record from 300 to 264 cm (~10.8 to 9.5 cal. kyr BP) (Fig. 3). This generally corresponds with the stepwise reduction in sedimentation rate to the system estimated from the age-depth model (noting that there is no elemental data for the upper portion of the core (~4.8 cal. kyr BP to present)). Superimposed upon this trend are large-scale fluctuations in PC2 in the Late

Pleistocene, with peaks between 593 to 581 cm (~16.4 to 16.2 cal. kyrs BP) and 508.5 and <501 cm (~14.9 to 14.8 cal. kyrs BP), and troughs between 570.5 and 564 cm (~16 to 15.8 cal. kyrs BP), and 463.5 cm and 454 cm (~14.3 to 14.2 k cal. yrs BP). Troughs in PC2 in the Holocene occur at 306.5 cm to 305 cm (~11 cal. kyrs BP), 257.5 and 254.5 cm (~9.3 cal. kyrs BP), 235 and 227.5 cm (~8.5 and 8.3 cal. kyrs BP). Values between 170.5 and 100 cm (~6.5 and 4.8 cal. kyrs BP) are generally low.

PC1: redox cycling

Mn, Mn/Ti, and Mn/Fe relate, and are positively loaded on PC1 (25.4% loading) (Fig. 3). The close relationship between these variables in concert with their lack of correlation with Fe/Ti ($r = 0.06$, $r = 0.03$, $r = -0.05$, respectively), indicates that the majority of Mn in the sediments likely derives from redox cycling vs. terrigenous input. It is speculated that the lack of covariance between non-detrital Mn and Fe (Mn/Ti and Fe/Ti; $r = 0.03$) is due to the higher solubility under reducing conditions of Mn vs. Fe under anoxic conditions and suboxic conditions respectively. This could be facilitated by the substitution of Mn for Fe in siderite – a redox sensitive mineral that can form when lake bottom waters are oxygenated (LacCore, 2011). Consequently, co-fluctuations in Mn, Mn/Ti and Mn/Fe with depth (i.e. the stratigraphic plot of PC1 on Fig. 3), are interpreted to reflect changing levels of oxygenation at the sediment-water interface through time, with peaks (possibly related to siderite occurrence), associated with lake mixing events.

The PC1 values are relatively high and noisy in the Pleistocene portion of the record, but drop into a smoother, low frequency, high amplitude trend just prior to the Pleistocene-Holocene boundary at 330 cm depth (~12.0 cal. kyrs BP). It is therefore inferred that, prior to this time, either the lake was permanently mixed, or that fluctuations between sub/oxic and anoxic conditions occurred at the water/sediment interface with high frequency. There is a lack of correlation between the detrital elemental suite (PC2) and PC1 in the Pleistocene portion of the record ($r = 0.2$) – variables that should relate if Mn solely accumulates in basal sediments without anoxic reduction (i.e. if the lake was permanently mixed). Rapid state shifts between sub/oxic and anoxic conditions at the lake-sediment interface, causing Mn to periodically reduce and accumulate in the water column, is thus speculated to be a more viable interpretation. Under this scenario, the lake appears to have been shallow, but close to a critical threshold whereby fluctuating water levels and/or productivity could instigate a redox state shift at the sediment-water interface (and vice versa). High frequency lake level fluctuations are likely caused by short-term shifts in the evaporation: transpiration balance, potentially driven by a more seasonal climate.

Subsequent to 12.0 cal. kyrs BP, PC1 values overall drop, but variability increases, including an abrupt decline in PC1 values to 309 cm depth (~11.1 cal. kyrs BP) (Fig. 3). This is interpreted to represent an

overall state shift to a deeper lake with anoxic basal waters that are less frequently subject to sub/oxidation. A lower frequency of ingress of sub/oxic water to the surficial lake sediments means increased time for dissolved Mn 2+ to accumulate in the water column under anoxic conditions, resulting in higher quantities of Mn 3+ available for deposition at the water/sediment interface during basal water sub/oxygenation.

4.4 Fire activity

A total of 494 macro- and 30 micro- charcoal samples were analysed from the core sediment samples. The resultant counts, converted into influx values (fragments/cm²/year), are presented alongside summary pollen data on Fig. 4A, and provide an indication of local and regional fire activity at the site through time.

Figure 4: Broad changes in the Lake Lantaa charcoal record and pollen assemblage through time. A) down core changes in local (macrocharcoal) and regional (microcharcoal) fire activity; B) changes in the pollen from major plant functional types; C) & E) principle component plots of the functional pollen data, split into five zones – Z1 to Z5 – based on results of cluster analysis (D).

The macrocharcoal data indicate that local fire activity was high during the Late Pleistocene (595 to 331 cm, ~16.5 to 11.9 cal. kyrs BP), particularly between 534 to 511 cm (~15.2 to 14.9 cal. kyrs BP), and 454 to 437 cm (~14.2 to 13.9 cal. kyrs BP), and low during the Early Holocene (330 to 234 cm, ~11.9 to 8.5 cal. kyrs BP). Subsequent to this time, fire is virtually absent from the system, except for small peaks between 121.5 and 100 cm (~5.3-4.8 cal. kyrs BP), and at 31 cm (~1.9 cal. kyrs BP). A similar pattern is apparent in the microcharcoal record – a proxy for more regional fire activity in the landscape – despite the lower resolution of these data, with high (albeit variable) fire activity during the Pleistocene (580 to 332.5 cm, ~16.2 to 12 cal. kyrs BP). Two large peaks occur at 532.5 cm (~15.2

cal. kyrs BP) and 448.5 cm (~14.1 cal. kyrs BP). As with the local record, burning is low in the Holocene, and absent after 232.5 cm (~ 8.5 cal. kyrs BP).

4.5 Pollen and spore assemblage

An average of 302 pollen grains were counted from each of the 31 samples analysed for plant microfossil analysis (min count = 196 (564.5 cm); max count = 513 (416.5 cm)). These comprised 150 morphologies including 79 families and 26 unknown types. The sum of the unknown types makes up 2.7% (min. 0% (316.5 cm); max. 5.9% (148.5 cm)) of the total pollen count.

A summary of the changes in the major plant functional types through time is presented on Fig. 4B. Cluster analysis of broad plant functional groupings splits the data stratigraphically at four points: 1) 500 and 464.5 cm; 14836 and 14348 cal. yrs BP (dissimilarity distance = 1950); 2) 364 and 332.5 cm; 12606 and 11984 cal. yrs BP (dissimilarity distance = 900); 3) 264 and 232.5 cm; 9530 and 8415 cal. yrs BP (dissimilarity distance = 3550); 4) 134 and 116.5 cm; 5583 and 5182 cal. yrs BP (dissimilarity distance = 1550). These divisions are used to divide the dataset into five cluster zones – Z1 to Z5 (Fig. 4D) – that are overlain on the PCA curves (Fig. 4C) and plot (Fig. 4E) of the same functional type microfossil data. Herbaceous taxa are positively loaded on principle component 1 (PC1; 46% data variance), while trees and pteridophytes are negatively loaded on the same axis (Fig. 4E). Variably along PC2 (26% data variance) is driven by the expansion of pteridophytes and palms/*Pandanus* on the negative axis, and trees and dry herbs on the positive axis (Fig. 4E).

In spite of the clear shifts in functional types through time, arboreal taxa dominate throughout the record (Fig 4B), suggesting the persistence of forest at the site over the past 16 cal. kyrs BP. Changes in the arboreal component of the vegetation assemblage are summarised stratigraphically on Fig. 5. These data are plotted alongside both cluster analysis of the arboreal data, and the zones defined by cluster analysis of the whole pollen assemblage (Z1 to Z5). The PCA plot of the arboreal pollen data, which shows majors compositional shifts in the woody assemblage is presented on Fig. 6 (again, classified according to the divisions defined by cluster analysis of the whole pollen assemblage).

Low humidity, fire tolerant arboreal taxa are positively loaded on the arboreal PC1 (58% data variance) – predominantly controlled by Casuarinaceae abundance (Fig. 6). The Casuarinaceae pollen likely derives from *Gymnostoma sumatrana* (Jungh. ex de Vriese) L.A.S.Johnson, given the current distribution of Casuarinaceae in Sulawesi, the affinity of this species for ultramafic soils, and the capacity of this genera to regenerate in relatively dry conditions post burning (Proctor, 2003; Whitten et al., 1988). It is important to note that, being wind pollinated, Casuarinaceae tend to be overrepresented in the pollen record. However, the concentration data for *Gymnostoma* (shown on

Fig. 5) track the abundance data, indicating an overall increase in this type in the record in accordance with PC1.

The arboreal PC2 (13% data variance) is overwhelmingly driven by variability in abundance of *Dacrydium* pollen (positive loading) and *Phyllocladus* pollen (negative loading) (Fig. 6). There are three *Dacrydium* species listed in Sulawesi – *D. nidulum* de Laub, *D. novoguineense* (Gibbs) A.V.Bobrov & Melikyan and *D. xanthandrum* (Naturalis Biodiversity Center, 2016). These species have a broad elevation range (lowland to 2,700m ASL) and habitat tolerance (open, disturbed forest to primary rainforest). However, as *D. nidulum* is the only of these species recorded in vicinity of the Malili lakes (Naturalis Biodiversity Center, 2016), and proliferates as a lake-edge tree within rainforest (0 to 1,200m ASL) (de Laubenfels, 1988), this pollen type is interpreted as an indicator of a lowland/ lower montane, humid rainforest setting. Conversely, the only *Phyllocladus* species record in the Sulawesi herbarium list is *Phyllocladus hypophyllus* Hook.f. (Naturalis Biodiversity Center, 2016) – a mid- to upper- montane conifer, proliferating at elevations up to 4,000m ASL (Farjon, 2013), indicating a humid upland setting. Based on these assumptions, a shift from positive to negative loading on PC2 is interpreted to represent an expansion of higher elevation taxa.

Figure 5: Stratigraphic plot of dominant arboreal pollen taxa. The black clustering shows major changes in the arboreal assemblage, while the grey cluster zones (Z1 to Z5) represent major functional type boundaries for the whole assemblage (defined in Fig. 4).

Figure 6: PCA diagrams showing major changes in arboreal component of the pollen assemblage through time. Plot data are overlain with the major functional type cluster boundaries defined in Fig. 4.

Major down core changes in the pollen and spore abundance are discussed below in accordance with the zones defined by clustering of the whole microfossil assemblage (shown on Fig. 4).

4.5.1 Zone 1: 580 cm to 500 cm (~16.2 to 14.8 cal. kyrs BP)

Broadly, the pollen assemblage of this zone (sample $n = 6$) comprises relatively high levels of dry herbs (predominantly Poaceae) (negative loading on the whole assemblage PC1), and a corresponding lower abundance of woody taxa (negative loading on whole assemblage PC2) (Fig. 4).

The dominant arboreal component of the assemblage is Casuarinaceae (*Gymnostoma sumatrana*) with a low abundance of either lowland, ultramafic forest types or the dominant tropical confiners in the record (Fig. 6). There is a moderate contribution from forest generalists (i.e. pollen taxa that can occur in several, diverse forest types or elevation ranges due to the adaptability of a particular species/group of species, or low taxonomic resolution of the pollen identification) – notably Urticaceae/ Moraceae types and *Lithocarpus/Castanopsis* types. Pollen taxa commonly associated with secondary or seasonal forest including *Acalypha* and grouped *Macaranga/Mallotus* (Euphorbiaceae) and *Aphananthe* (Cannabaceae) are relatively abundant within this zone (Fig. 5).

4.5.2 Zone 2: 464.5 to 364 cm (~14.4 to 12.6 cal. kyrs BP)

The delimitation of Zone 2 (sample $n = 7$) from earlier samples is largely due to the dissimilarity of the plant microfossil assemblage at 14.4 cal kyrs BP (464.5 cm) from that of adjacent samples (dated at 14.8 and 14.1 cal. kyrs BP) with respect to both the relative abundance of plant functional types and the forest composition. This sample shows a marked decrease in all herbs, and resultant proportional

increase in arboreal taxa and Pteridophytes (negative loading on PC1 of the whole assemblage PCA – Fig. 4E). The tree and shrub taxa show a decrease in *Gymnostoma* and secondary/seasonal forest types, and increase in pollen from lowland/ lower montane types, including *Dacrydium*, *Lithocarpus/Castanopsis*, and *Hopea/Shorea/Anisoptera* (Dipterocarpaceae – other) pollen (Fig. 5). This 14.4 cal. kyrs BP shift suggests a temporary expansion of humid, lowland types in the record.

Zone 2 sediments between 14.1 to 12.6 cal. yrs BP largely revert to an assemblage similar to that described for Zone 1. It is however, notable to point out that Gymnosperm pollen, particularly *Dacrydium*, and to a lesser extent, *Aqathis*, make up a higher proportion of the forest taxa after 13.6 cal. kyrs BP (Fig. 5), suggesting a measured increase in humidity at the site (Stevenson, 2018).

4.5.3 Zones 3: 332.5 to 264.5 cm (~12.0 to 9.5 cal. kyrs BP)

The plant microfossil shift assemblage of Zone 3 (sample n = 4), shows a slight increase in palms/*Pandanus* and arboreal taxa, and associated decline in herbs (negative loading on the whole assemblage PC2 and PC1 (Fig. 4)). This suggests expansion of *Pandanus* fringe at the lake edge, and closing of the forest canopy at an extra-local to regional scale. The arboreal component of the assemblage shows a decline in *Gymnostoma* and *Aphananthe* taxa, and increase in pollen from *Lithocarpus/Castanopsis* and lowland ultramafic forest angiosperms, including *Garcinia* (likely *Garcinia celebica*) and, from 10.9 cal kyrs BP *Stemonurus* (likely *Stemonurus celebicus*) (Fig. 5). This is shown by the positive PC1 shift transition of the arboreal pollen assemblage along the negative arboreal PC1 axis on Fig. 6, and is interpreted to represent the establishment of an older-growth, non-seasonal, fire excluding lowland forest.

4.5.4 Zone 4: 232.5 cm to 134.5 cm (~8.4 to 5.6 cal. kyrs BP)

Zone 4 taxa (sample n = 6) show a further increase in arboreal taxa at the expense of Pteridophytes and palms/*Pandanus*, suggesting further closure of the forest canopy. A change in the forest taxa coincides within this functional type shift, which is characterised initially by the expansion of *Lithocarpus/ Castanopsis* at the expense of the *Dacrydium*, and, from ~8ka, a marked increase in *Phyllocladus* taxa (negative loading on the arboreal PC2 – Fig. 6). This shift is interpreted to represent an expansion of a mid-montane habitat range – possibly driven by increased cloud cover associated with increased humidity (Stevenson, 2018). This interpretation of high humidity after ~8 cal. kyrs BP is supported by the further decline of secondary forest types (Cannabaceae and Euphorbiaceae taxa), and increase in lowland ultramafic rainforest types.

4.5.5 Zone 5: 116.5 to 0 cm (~ 5.2 cal. kyrs BP to 2012 C.E.)

The Mid- to Late- Holocene portion of the record (sample n = 8) is characterised by a rise in *Gymnostoma* pollen, and decline in *Phyllocladus* and *Stemonurus* taxa (Fig. 5). This may indicate

decreased humidity (mid-montane habitat contraction) and/or increased human disturbance at the site. The expansion of seasonal/secondary forest taxa (*Macaranga*/ *Mallotus* and *Trema*), the edible mangosteen (*Garcinia celebica*), and Pteridophyte spores in the record from ~2 cal. kyrs BP points to an increase in human management of the Late Holocene landscape.

4.6 Climate-forest-fire dynamics at the site & relationship to pre-existing records

4.6.1 Local landscape dynamics

4.6.1.1 *The Late Pleistocene*

The climate of the site during the Late Pleistocene appears to be characterised by relatively low effective moisture, resulting in lower-than-present water levels in Lake Lantoa. This interpretation is supported by lake level induced cycling of redox sensitive elements – indicative of frequent lake mixing – and the presence of *Botryococcus cf. brauni* and, occasionally, pennate (benthic) diatoms, which favour shallow, mesotrophic to eutrophic conditions (Wolin and Stone, 2010) (Fig. 7). The abrupt shift in redox elements at ~12 ka, suggesting onset of anoxic conditions, appears to represent a stable state shift following either abrupt or gradual deepening of the lake that accompanied by a rise in productivity. This implies increased effective moisture at the site.

Figure 7: Comparison of Lake Lantoa redox cycling, charcoal and synthesised vegetation data (base) with key global and regional climatic and vegetation records referred to in this study. I) North Greenland Ice Core Project Oxygen Isotope Data (NGRIP 2004); II) insolation data (Berger and Loutre, 1991); III) Borneo speleothem data (Partin et al., 2007). Note: 1) Changes in the regional and local palaeoclimate records denoted by grey shading are relative to the individual records (i.e. they represent internal, site-specific changes); 2) all line curves have been plotted such that conditions indicating/ associated with drier conditions point downwards.

The pre-12.0 cal. kyrs BP, Late Pleistocene pollen and charcoal data suggest persistent fire activity in the landscape, and presence of a forest with a seasonal/ secondary element in the lowlands. Based on the low abundance of gymnosperms during this part of the record, it is expected that the local uplands were vegetated with generalist angiosperms (Fig. 7). The presence of fire in the local and regional landscape suggests a drier, seasonal climate supporting rapidly regenerating and/or fire-tolerant taxa in the lowlands (*Gymnostoma*, Euphorbiaceae and Cannabaceae taxa) (Proctor, 2003). At higher elevations, burning and low humidity (and hence cloud cover) may have played a role in limiting the distribution of fire-sensitive, hydrophilic gymnosperms – a hypothesis posed for the offshore Banda Sea record by van der Kaars et al. (2000). This, in turn, may permit an expanded upslope habitat range for *Gymnostoma*, which has a broad elevation range within ultramafic settings (Proctor, 2003).

The representation of Poaceae in this portion of the record suggests that a slightly open forest canopy may have permitted the establishment of some grass in the understorey. The interpreted dryland vs. wetland source for grass is favoured due to the low and high levels of wetland herbs (including Cyperaceae) and *Pandanus* pollen in the record, respectively, suggesting that any lake fringing grass/sedge wetland would be limited in extent.

The shift to a closed, ultramafic rainforest lowland assemblage with higher representation of Fagaceae (lowland or montane forest) and tropical conifers implies temporary onset of more humid conditions at the site at 14.4 cal. kyrs BP (Fig. 7). This vegetation shift may suggest the influence of the Bølling-Allerød warming/wetting within Wallacea, though higher temporal resolution palynological work across this time period is necessary to validate this interpretation. There is, however, limited evidence of a significant increase in effective moisture at the site from the elemental data. The compositional shift in the vegetation assemblage occurring between 14.1 and 12.0 cal. kyrs BP (gradual expansion of Pteridophytes, lowland ultramafic forest angiosperms and lowland tropical conifers and decline in grass), alongside the reduction in fire activity, suggests onset of increasingly humid, conditions at the site.

4.6.1.2 The Holocene

The record of redox cycling for Lake Lantoa indicates that the lake state between ~12.0 and after 4.8 cal. kyrs BP was characterised by periodic mixing, indicating a transition to an overall deeper lake levels

(Fig. 7). The apparent increase in redox state fluctuations between ~7.5 and 6.6 cal. kyrs BP suggests an increased frequency of shallowing events in the mid-Holocene (Fig. 7). However, the timing of increased redox cycling overlaps with a decline in *Botryococcus cf. braunii* from the record (post-7.5 to pre-1.1 cal. kyrs BP) suggesting a decline in lake productivity over the same period (Fig. 7). Reduced uptake of oxygen by algae can result in higher oxygenation at the sediment-water interface, and hence a higher susceptibility to precipitation of oxyhydroxides within this zone (Holmer and Storkholm, 2001). Consequently, linking heightened redox cycling in the Holocene to the hydroclimate requires additional climatic data to clarify.

The plant microfossil assemblage from Lantoa shows an expansion in trees, Pteridophytes, and lowland ultramafic rainforest taxa between the Late Pleistocene-Holocene boundary and ~8 cal. kyrs BP. This indicates the continuing replacement of slightly open, (semi-)seasonal lowland forest with closed, ultramafic rainforest. The shift in vegetation between ~8 and 5 cal. kyrs BP, including peak abundance of lowland forest types and arboreal taxa (Fig. 7) in concert with expansion of higher elevation tropical conifers (predominantly *Phyllocladus*), and reduction of fire activity in the landscape, suggests onset of peak humidity at the site. This potentially reflects a local expression of the Holocene Climate Optimum – supported by the similarly timed regeneration of dense lowland forest in Tondano record (Dam et al., 2001).

The subtle change in the Mid- to Late- Holocene vegetation, including expansion of seasonal/secondary taxa over lowland forest taxa and declining abundance of mid- to upper-montane conifers from ~5 to 4 cal. kyrs BP suggests declining humidity and/or heightened anthropogenic activity at the site. Both a drying (lake shallowing) and anthropogenic (forest disturbance) signal are also evident in the Lake Tondano record over the same period (from 5 cal. kyrs BP), suggesting that this change is regionally synchronous (Dam et al., 2001). The interpretation of a drier climate is supported by a slight recovery of *Gymnostoma* pollen and decline of *Phyllocladus* pollen, suggesting contraction of the elevation range of the latter. However, the timing of this change also coincides with Austronesian migration into island south-east Asia (after ~4.5 cal. kyrs BP) as interpreted from archaeological records from Sulawesi (Brandão et al., 2016; Bulbeck, 2018). A need for additional palaeoenvironmental indicators and increased chronological control on the records is thus necessary to disentangle drivers of Mid-to-Late Holocene floristic change.

A second, potentially clearer indicator of intensified human activity at the site is the decline in lake edge *Pandanus* and increase of ground ferns from ~2 cal. kyrs BP, which occurs in concert with the expansion of a potential cultivated plant – *Garcinia celebica* – in the record. The timing of this shift is consistent with other palaeoecological records for the island (Kirleis et al. 2010), as well as the

archaeological record, which indicates population increase in Sulawesi from ~2 cal. kyrs BP, associated initially with the expansion of farming settlements (2.5 to 2 cal. kyrs BP) and, later, the establishment of the iron industry (from ~1.5 cal. kyrs BP) (Bulbeck, 2018).

4.6.2 Comparison with regional climatic records

4.6.2.1 *The Late Pleistocene*

The presence of a drier climate at a local and regional scale during the Late Pleistocene is supported by a series of records from Lake Towuti – directly adjacent to Lake Lantoa (Costa et al., 2015; Russell et al., 2014; Vogel et al., 2015) – and a record from Lake Tondano in north-east Sulawesi (Dam et al., 2001) (site locations shown on Fig. 1; records summarised on Fig. 7). By-in-large, these data indicate high-latitude (vs. orbital forcing) of the Wallacean climate as discussed in Russell et al. (2014).

Lake level proxy data for Lake Towuti indicate rising waters from ~16 to 11 cal. kyrs BP (Vogel et al., 2015), while sedimentological (trace element) and geochemical data presented in Costa et al. (2015) and Russell et al. (2014) indicate onset of increased soil erosional input to Lake Towuti at ~15 cal. kyrs BP and ~14 cal. kyrs BP, respectively (Fig. 7). The proxies considered in the latter two of these studies reflect onset of heightened catchment erosion after the LGM due to increased precipitation. This observation appears contradictory with the geochemical erosional proxies and sedimentation rates constructed for Lake Lantoa, which suggest faster sedimentation to the lake basin during dry vs. humid climate phases (i.e. the Pleistocene vs. the Holocene). The discrepancy between these basins can be accounted for by the combination of 1) increased exposure of catchment soils under a (semi-)seasonal, periodically burnt forest canopy vs. a rainforest canopy, and 2) the predominantly catchment fed- vs. riverine fed- sediment source for Lake Lantoa vs. Lake Towuti.

At a regional scale, the presence of a dry MIS 2 is evidenced by sedimentological and diatom lake level proxies from Lake Tondano (Dam et al., 2001). These data show a slightly later onset of increased effective moisture and lake deepening, from ~13 to 11 cal. kyrs BP (Dam et al., 2001). However, given that the timing of the LGM in this lake edge record (~33 to 13 cal. kyrs BP) derives from a shift from lacustrine- to terrestrial- sourced sediments, the 13 cal. kyrs BP date captures the time that the coring site was flooded, very likely postdating the initial onset of lake water level rise.

In addition to an overall drier climate, MIS 2 also appears to be characterised by increased seasonality. For instance, the high concentration of Fe in the presently meromictic Lake Towuti between ~35 and 14 cal. kyrs BP suggests frequent lake water overturn (and oxygenation of the surficial lake sediments) (Costa et al., 2015) (Fig. 7). Within the context of this deep lake (present max. depth of 205m (Russell et al., 2014)), this is interpreted to represent a more pronounced/longer dry season, where low humidity and low cloud cover drive high evaporation and long-wave heat loss from the surficial waters

that in turn cool the lake, weaken the pycnocline, and trigger mixing (Costa et al., 2015). These data support our interpretation of a well-mixed (albeit much shallower) Lake Lantoa in MIS 2 (Fig. 7). The extended duration of mixing in Lantoa (to the Holocene boundary) in comparison to Towuti is presumably associated with the shallowness of the basin, making the basal waters less sensitive to a stable state shift from well-mixed to infrequently mixed.

Though there is evidence for increased humidity in Wallacea from approximately ~16 to 14 cal. kyrs BP, there is no clear expression of distinct, northern hemisphere driven Bølling-Allerød (BA) interstadial warming (~14.7-12.9 cal. kyrs BP) or subsequent Younger Dryas (YD) cooling (~12.9 to 11.7 cal. kyrs BP) in the Lantoa lake level record. This supports observations made in Russell et al. (2014).

4.6.2.2 The Holocene

Lake level data from Towuti (Costa et al., 2015; Russell et al., 2014; Vogel et al., 2015) indicate water level (and hence hydroclimatic) stabilisation from 11 cal. kyrs BP. Aside from evidence for lake level lowering from the Tondano site at ~4 cal. kyrs BP (Dam et al., 2001), none of these records provide evidence for a Holocene Climate Optimum in Wallacea between ~8 and 5 cal. kyrs BP as suggested from the Lantoa pollen data. Ti runoff proxies from Towuti (Russell et al., 2014), conversely, suggest humid conditions between ~10 to 8 cal. kyrs BP and ~4 and 0 cal. kyrs BP (Fig. 7). The discrepancy between the Towuti sediment and Lantoa vegetation records may relate to dense forest reducing the amount of sediment available for runoff erosion between 10 and 4 cal. kyrs BP and, in the case of the Late Holocene, increased mineral erosion associated with intensified human activity.

4.6.3 Comparison with regional vegetation and fire records

4.6.3.1 The Late Pleistocene

Pollen records that provide insight into compositional vegetation dynamics in Wallacea are highly compressed (Dam et al., 2001), sampled at a low temporal resolution (van der Kaars et al., 2000) or only cover the Late Holocene (Biagioni et al., 2015a; Biagioni et al., 2015b; Hope, 2001). As consequence, much of what we know about floristic responses to the dynamic climate of the region between the LGM and the MIS 2-Holocene boundary is informed by $\delta^{13}\text{C}_{\text{wax}}$ records (Russell et al., 2014 - Lake Towuti; Wicaksono et al., 2015 - Lake Matano; Wicaksono et al., 2017- Mandar Bay). These data, which capture the transition between C_3 ($\delta^{13}\text{C}_{\text{wax}}$ depleted) and C_4 ($\delta^{13}\text{C}_{\text{wax}}$ enriched) plant dominance in the landscape, are typically used to interpret state shifts between forested (C_4 plant poor) and more open, grassy (C_4 plant rich) habitats. Though variable in magnitude, the Sulawesi $\delta^{13}\text{C}_{\text{wax}}$ records are interpreted to show the expansion of C_4 -rich vegetation during the LGM (Russell et al., 2014; Wicaksono et al., 2015), and gradual reorganisation to a C_3 dominated landscape between 18 and 10 cal. kyrs BP (Russell et al., 2014), 14 to 10 cal. kyrs BP (Wicaksono et al., 2015) and from ~15 cal. kyrs BP (Wicaksono et al., 2017) (Fig. 7). This is taken to represent the expansion of open-canopy

forest (Russell et al., 2014; Wicaksono et al., 2015) or savanna (Wicaksono et al., 2017) in the lowlands during the LGM, and subsequent reorganisation to closed forest. *Prima facie*, these data are comparable with the Lake Tondano MIS 2 pollen record (Dam et al., 2001), which, though highly compressed and likely incomplete between 33 and 13 cal. kyrs BP, shows the expansion of grass alongside sedge and Moraceae pollen during the LGM. The authors of this study, however, note that this signal may only be capturing an extra-local, lake-edge wetland assemblage, hence providing limited information on the surrounding forest composition.

There are some important differences between the Lake Lantoa pollen record and past interpretations of vegetation change inferred from local and regional $\delta^{13}\text{C}_{\text{wax}}$ records. Importantly, while there appears to be slight opening of the forest in the Lake Lantoa catchment, an ultramafic seasonal forest vs. open habitat appears to persist in the region from as early as 16.6 cal. kyrs BP. This aligns with the offshore Banda Sea pollen record, which indicates that the LGM landscape was characterised by the persistence of a periodically burnt, monsoonal, lower-montane forest (van der Kaars et al., 2000). Importantly, these data suggest resilience of forest to a drier, more seasonal climate, contrasting with the interpretation of climatically sensitive lowland Wallacean forests posed by Wicaksono et al. (2017). This hints at the fact that the lacustrine $\delta^{13}\text{C}_{\text{wax}}$ records (Russell et al., 2014; Wicaksono et al., 2015), which show higher $\delta^{13}\text{C}_{\text{wax}}$ enrichment than the Mandar Bay record (Wicaksono et al., 2017) during the LGM, may, as with the Lake Tondano record, be capturing a local wetland vs. regional vegetation signal.

The Banda Sea and Lantoa pollen data do, however, suggest plasticity in forest composition, with a drier, seasonal landscape subject to burning favouring expansion of seasonal taxa and Casuarinaceae (*Gymnostoma*), and contraction of fire-sensitive, moisture reliant gymnosperms. The onset of increasingly humid conditions after the LGM appears to encourage the gradual expansion of gymnosperms and ultramafic adapted rainforest taxa and decline in terrestrial grasses. This broad compositional shift is relatively well aligned with the Banda sea pollen record (van der Kaars et al., 2000) and the pre-17 cal. kyrs BP (LGM) vs. post 5.5 cal. kyrs BP (Holocene) Wanda mire record (Hope, 2001) (though fire activity remains high in the Holocene portion of the Wanda mire record).

4.6.3.2 The Holocene

While limited in either temporal or taxonomic resolution, $\delta^{13}\text{C}_{\text{wax}}$, pollen and charcoal data that capture Holocene landscape processes in Sulawesi reveal similar overarching patterns to those observed in the Lantoa record. Both $\delta^{13}\text{C}_{\text{wax}}$ and pollen records indicate the expansion of closed forest both locally and at a regional scale (Dam et al., 2001; Hope, 2001; Russell et al., 2014; van der Kaars et al., 2000; Wicaksono et al., 2015; Wicaksono et al., 2017). This includes increased representation of

pteridophytes (Dam et al., 2001; van der Kaars et al., 2001), lowland rainforest taxa (Dam et al., 2001; Hope, 2001; van der Kaars et al., 2001), and mid- to upper montane coniferous forests (van der Kaars et al., 2000).

The Lantoa, Tondano, and Banda Sea charcoal records indicate that, in contrast with MIS 2, fire appears to have been minimal in the Early- and Mid- Holocene landscape (Dam et al., 2001; van der Kaars et al., 2001). Regional discrepancies in fire activity in the Late Holocene in Sulawesi (e.g. moderate fire activity at Tondano (north-east Sulawesi) and Lore Lindu (Central Sulawesi) simultaneous to low fire activity at Lantoa), are attributable to the differential impacts of coupled human-ENSO drivers on the landscape (Biagioni et al., 2015a; Biagioni et al., 2015b; Dam et al., 2001). However, floristic evidence for heightened forest management at Lantoa in the absence of fire is curious, and requires further interrogation using a higher-spatiotemporal resolution analysis of Malili lake records.

5 Conclusion

This research presents one of the first detailed records of fire and lowland vegetation dynamics in Wallacea during a period of significant climatic change from the LGM to the Holocene. Additionally, it presents a palaeoclimate record of lake redox cycling that compliments pre-existing findings from the region, notably that the hydroclimate is influenced by glacial scale forcing.

Our data demonstrate that during the Late Pleistocene (~16.6 to 12.0 cal. kyrs BP), the landscape was characterised by the presence of fire, and a more seasonal, drier hydroclimate than is present during the Holocene. These conditions appear to have supported a slightly open ultramafic forest with a seasonal element while limiting the available range for moisture-demanding tropical conifers. Our pollen data suggest a relatively abrupt transition to rainforest at ~14.4 cal. kyrs BP, coincident with the timing of Bølling-Allerød warming. However, this event has not been well constrained in other records from Wallacea and requires further interrogation. Transition of the climate towards increasingly humid conditions in the Holocene, appears to have precluded forest burning after ~12.0 cal. kyrs BP – a trend that appears to be regionally consistent across Sulawesi. The combination of a wetter hydroclimate with fire suppression facilitated gradual replacement of the seasonal forest with ultramafic forest in the lowlands, and expansion of tropical coniferous forest in the uplands. Our data suggest the possible manifestation of the Holocene Climate Optimum in Sulawesi between ~8 and 5 cal. kyrs BP. There is some evidence for intensification of human activity in the local landscape from ~2 cal. kyrs BP, coincident with the timing of population increase in Sulawesi as reconstructed from the archaeological record (Bulbeck, 2018).

There is a significant contrast between the LGM pollen record presented in this study, and the $\delta^{13}\text{C}_{\text{wax}}$ records reconstructed from adjacent lake basins presented in Russell et al. (2014) and Wicaksono et al. (2015). The Lantoa data suggest lowland forest resilience to a drier, more seasonal LGM, while the leaf wax records imply sensitivity of tropical rainforest to an open forest/ savanna state shift under the same conditions. Resolving this issue is of consequence given the dramatic impact that forest stability vs. sensitivity under a changing climate has with respect to carbon sequestration and other global- to local- scale ecosystem service provision – a research priority identified within the IPCC AR5 (2014). Furthermore, our findings bring into question the northern extent of the proposed LGM south-east Asian “savanna-corridor”, which currently extends into central Sulawesi in the vicinity of Lake Lantoa (Bird et al., 2005; Heaney, 1991). In order to resolve this discrepancy, additional palynological work examining a regional floristic signal (as would be the case for the large Lake Towuti and Lake Matano basins), and a continuous MIS 3 to MIS 1 record is required to fully ascertain the widespread lowland vegetation response to the LGM climate.

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