**Compound-specific carbon isotope records of vegetation and hydrologic change in
central Sulawesi, Indonesia, since 53,000 yr BP**

Satrio A. Wicaksono¹

James. M. Russell¹

Satria Bijaksana²

¹Department of Earth, Environmental, and Planetary Sciences, Brown University, BOX
1846, Providence, RI, 02912, USA

²Faculty of Mining and Petroleum Engineering, Institut Teknologi Bandung, Jalan
Ganesa 10, Bandung, Indonesia

*Author to whom correspondence should be addressed, Satrio.Wicaksono@Brown.edu,
+1-860-834-2981

Abstract

24 Lake Matano (2°29.1'S 121°20'E) in central Sulawesi, the deepest and one of the largest
25 lakes in Indonesia, provides an excellent opportunity to reconstruct long-term
26 hydrological and vegetation changes at the heart of the Maritime Continent within the
27 tropical Western Pacific Warm Pool. We measured the carbon isotopic composition of
28 terrestrial leaf waxes ($\delta^{13}\text{C}_{\text{wax}}$) in new sediment cores from Lake Matano to understand
29 regional variations in vegetation and their interactions with local and high latitude climate
30 forcings during the past 53 kyr. Variations in $\delta^{13}\text{C}_{\text{wax}}$ record the expansion and
31 contraction of C_3 versus C_4 vegetation as well as changes in plants' carbon and water use
32 efficiency and, by inference, regional hydroclimate. During Marine Isotope Stages 1 and
33 3, more negative $\delta^{13}\text{C}_{\text{wax}}$ values indicate that closed-canopy C_3 rainforests predominated
34 in Sulawesi, reflecting a wetter, less seasonal climate. In contrast, more positive $\delta^{13}\text{C}_{\text{wax}}$
35 values record a terrestrial ecosystem with more abundant open canopy vegetation and
36 possible expansion of C_4 grasses between 29 and 14 ka BP, indicating that during Marine
37 Isotope Stage 2, including the Last Glacial Maximum, the climate was more arid, likely
38 with increased precipitation seasonality, in central Sulawesi. Comparison of our record
39 with other paleovegetation and paleohydrological records from Sulawesi and nearby
40 islands suggests coherent long-term hydrological changes in central Indonesia that appear
41 to be sensitive to high latitude climate across glacial-interglacial boundaries. However,
42 variations in the amplitude of the response of vegetation to these glacial-interglacial
43 forcings highlight the importance of regional topographic control on climate and
44 vegetation and suggest an important role for higher elevations in maintaining rainforest
45 refugia during regionally arid time intervals when C_4 savannas and grasslands expanded
46 at lower elevations.

47

48 **Keywords:**

49 Precipitation; Monsoon; Vegetation; Biomarker; Carbon; Sulawesi; Maritime Continent;
50 Orbital-scale

51 **1. Introduction**

52

53 The Australian-Indonesian Monsoon (AIM) is the main variable controlling
54 Indonesia's hydroclimate (Aldrian and Susanto 2003), and is a globally important source
55 of energy and water vapor for the Earth's atmosphere (Qu et al. 2005). Understanding the
56 history of the Indonesian hydrology and the AIM is therefore of paramount importance to
57 understanding the role of the tropics in global climate change. In recent years a number of
58 new reconstructions have begun to illuminate the hydrologic history of Indonesia, also
59 known as the Maritime Continent. These records are based upon a variety of different
60 proxies including geochemical data from lake and marine sediment, proxies for past
61 vegetation, and speleothems (e.g. Carolin et al. 2013, Dubois et al. 2014, Gibbons et al.
62 2014, Niedermeyer et al. 2014, Russell et al. 2014). Unfortunately, many of these records
63 exhibit strong contrasts between different proxies and between different regions, and
64 implicate a number of different forcing mechanisms of past hydroclimatic variations. For
65 instance, some speleothem (Griffiths et al. 2009), foraminiferal records (Holbourn et al.
66 2005), and palynological data (e.g. Kershaw et al. 2006, Kershaw et al. 2011) suggest that
67 regional precipitation is controlled by precessional orbital forcing, whereby the AIM
68 oscillated between strong states and weak states during intervals of high and low seasonal
69 insolation. In contrast, recent plant biomarker study from Lake Towuti, situated in central

Sulawesi, exhibits little evidence of orbital precession and instead suggests that Northern Hemisphere high latitude climate forcings, in particular changes in ice volume, control regional precipitation changes across glacial-interglacial stages (Russell et al. 2014). While these differences could be attributed to variable sensitivities of different parts of Indonesia to climate forcings, at least in some cases such differences arise even over short spatial scales. For instance, speleothem records from Flores, one of the Lesser Sunda Islands in southeastern Indonesia, suggest a relatively wet Last Glacial Maximum (LGM) (Ayliffe et al. 2013), despite previous palynological evidence for aridity in southern Indonesia at that time (van der Kaars et al. 2000).

Understanding these differences will require detailed evaluation of individual proxy records and their sensitivities within a dense network of proxy reconstructions. On the proxy interpretation side, for instance, there is a growing realization that proxy records of precipitation isotopes, such as speleothems, often do not record changes in local rainfall amount, complicating hydroclimatic interpretation for the Maritime Continent (e.g. LeGrande and Schmidt. 2009, Lewis et al. 2010, Moerman et al. 2013). Similarly, vegetation records, which form the basis for many Indonesian climate reconstructions, exhibit complex relationships with hydroclimate. Both precipitation amount and precipitation seasonality, both linked to the AIM, are important determinants of vegetation distribution within the tropical Maritime Continent (Peel et al. 2007). In the present, the high annual precipitation rates –including high precipitation rates during the dry season– observed across most of the archipelago give rise to widespread lowland ever-wet rainforests and montane cloud forests at higher elevations (Göltenboth et al. 2006). These forest types predominate within the major Indonesian islands including

Sumatra, Kalimantan, Sulawesi and Papua. In contrast, C₄ grasslands and savannas are common in lowland regions where average annual rainfall is lower and seasonal variability in AIM rainfall (i.e. seasonality) is high, for example in Nusa Tenggara or the Lesser Sunda Islands and southeast Papua. In regions with moderate precipitation seasonality, such as southwestern Sulawesi and central and eastern Java, open-canopy C₃ monsoon forests are often observed (Göltenboth et al. 2006, Peel et al. 2007).

Recent plant biomarker records have highlighted important changes in the distribution of these ecosystems during and since the LGM, generally reflected by the expansion of drier, more seasonal vegetation regimes and climates during the LGM (Wurster et al. 2010, Dubois et al. 2014, Russell et al., 2014). However, floristic analyses of modern plants and several paleoenvironmental studies of floral and faunal assemblages indicate the presence of disjunct rainforest areas in some parts of the Maritime Continent during the LGM, highlighting the possible role of rainforest refugia in establishing the region's ecosystem diversity (Slik et al. 2003, Barton 2005, Moyle et al. 2011). Evidence for such refugia, coupled with robust evidence for regionally pervasive aridity, suggests significant heterogeneity in past changes in climate and vegetation and highlights important gaps in our understanding of the long-term stability of the regional rainforest ecosystems. Recent work has also highlighted the role that regional topography might play in controlling long-term changes in both rainfall amount and the types of vegetation present in different parts of the Maritime Continent since 25 kyr BP (Wurster et al. 2010, Niedermeyer et al. 2014). In light of this evidence, dense networks of proxy records are needed to determine robust signals of paleoclimate changes and to evaluate the processes that govern climate and vegetation heterogeneity in the Maritime Continent.

Here we present new compound-specific stable isotope records from Late Pleistocene and Holocene-aged sediments of Lake Matano in central Sulawesi, situated at the heart of the Maritime Continent within the tropical Western Pacific Warm Pool. The close proximity between Lake Matano and Lake Towuti allow us to evaluate the robustness of local to regional paleohydrologic signals from both lakes, as well as possible causes for differences between these records, with important implications for the interpretation of other local to regional reconstructions of Indonesian climate. Our reconstructions highlight linkages between the AIM and high-latitude forcings at orbital timescales. In addition, the heterogeneity of local hydrological and vegetation settings among records from central Indonesia during the past 50 kyr, including between Lakes Matano and Towuti, highlight the importance of orography in interpreting past vegetation and paleohydrologic records and provide new information about rainforest refugia during arid episodes in Indonesia.

2. Study Site

Lake Matano (2°29.1'S 121°20'E, 394 m asl) is located on the island of Sulawesi in central Indonesia (Figures 1, 2). The annual average precipitation near Lake Matano ranges from 2500 to 3000 mm (Figure 2) and occurs year-round, placing the region into the tropical rainforest climate category in the Köppen climate classification (Peel et al. 2007). Precipitation is highest in December-May, with peak precipitation of ~400 mm/month in April, and lower in June-November, with minimum precipitation in September of ~100 mm/month (Figures 1, 2). This seasonality is largely set by the AIM

and its interactions with the regional seas (Aldrian and Susanto 2003). During the rainy season (Dec-May), the Intertropical Convergence Zone (ITCZ) migrates southward to northern Australia and the northwesterly monsoon blows south across the equator, bringing moisture from the Northern Hemisphere sector of the Indian Ocean and the South Pacific to most of Indonesia (Aldrian and Susanto 2003, Gimeno et al. 2012). During the dry season (June-November), the ITCZ shifts north over Asia, and strong southeasterly flow cools the local oceans of the southern maritime continent, limiting convective activity (Aldrian and Susanto 2003). Precipitation in our study region increases with elevation; weather stations at higher altitudes record higher annual rainfall amounts (with the exception of one outlier; Figure 2). Precipitation seasonality also decreases with elevation, such that higher elevations experience year-round wetness.

Lake Matano is one of the five lakes forming the ancient Malili Lakes system, a set of large tectonic lakes in central Sulawesi. With a maximum depth of 590 m, this ultra-oligotrophic lake (Haffner et al. 2001) is the eighth deepest lake in the world (Lehmusluoto and Machbub 1997). Lake Towuti, the largest tectonic lake in Indonesia, lies at a lower elevation (319 m asl) approximately 10 km south of Lake Matano (Figure 2). Both lakes lie mostly in an iron-rich ultramafic ophiolite formation, except in the southwestern border of Lake Matano, where a limestone formation is located (Figure 2). The catchment area of Lake Matano, at 276 km², is steep and mountainous (maximum altitude: ~1340 m, mean altitude: ~650 m) as compared with that of Lake Towuti, and vegetation in Matano's catchment is dominated by closed canopy lowland C₃ rainforest (van Balgooy and Tantra 1986). At altitudes above 850 m, cloud forests including submontane and montane plant types are present, characterized by abundant Fagaceae

including *Lithocarpus* and *Castanopsis*, as well as mosses, ferns, orchids, and other epiphytic plants (Hope 2001, Culmsee et al. 2010).

3. Methods

Core IDLE-MAT10-2B (Figure 1, 2°31'10.52"S, 121°24'41.72"E, core length: 9.07 m) was collected from 137 m water depth using a Kullenberg piston corer in July 2010. The core was air freighted to the LacCore facility, University of Minnesota, where it was split, described, and logged for its major lithofacies. The age model for this core is based on radiocarbon (^{14}C) analyses of eight bulk sediment samples and two fragments of wood/plant macrofossils (Table 1). Comparison of bulk organic carbon and macrofossil ages from the same stratigraphic horizons yields an average ^{14}C lacustrine reservoir effect of approximately 975 ^{14}C years (Figure 3, Table 1), assuming that the plant materials reflect the atmospheric ^{14}C age at the time of their deposition. This reservoir effect is likely due to dissolved old carbon inputs resulting from the weathering of limestone deposits in Lake Matano's catchment. After correcting for this reservoir and converting corrected radiocarbon ages to calendar ages by applying the IntCal09 curve using the CALIB 6.0 program, we fit a third-order polynomial through the calibrated age points to construct the age model (Figure 3).

We measured 68 samples from the core for the carbon isotopic composition of long-chain *n*-alkanoic acids, terrestrial leaf waxes that are abraded from terrestrial biomass and transported to and preserved in lake sediments. Sediment samples were freeze-dried, homogenized with a mortar and pestle, and lipids were extracted using a

Dionex Accelerated Solvent Extractor. Alkanoic acids were separated from the total lipid extracts using aminopropyl column chromatography. The separated acids were methylated with acidified methanol of a known isotopic composition, and further purified via silica gel chromatography. The resulting fatty acid methyl esters (FAMES) were analyzed in at least duplicate via gas chromatography isotope ratio monitoring-mass spectrometry (GC-IR-MS) using a Thermo Delta V Plus at Brown University. We targeted long chain fatty acid homologues (between C₂₆ and C₃₂) because they are largely derived from terrestrial plants (Sachse et al. 2012) In this study, we report $\delta^{13}\text{C}_{\text{wax}}$ values of the C₂₈ homologue (Figure 3), the most abundant homologue in Matano sediments, after correcting for the isotopic composition of the methyl group added during methylation.

4. Results

The core is composed primarily of dark olive to reddish-brown slightly silty clay with no obvious disconformities, and radiocarbon dating indicates fairly continuous sedimentation rates over the past ~53 kyr BP of ~14 cm/kyr, similar to sedimentation rates in nearby Lake Towuti (Figure 3). During this time, $\delta^{13}\text{C}_{\text{wax}}$ varies between -44 and -33 ‰, averaging -38.5 ‰ (Figure 3). These values are similar to, but slightly more negative than waxes deposited over the same time period at Lake Towuti (Figure 4). The average difference between duplicates (n=56) in the $\delta^{13}\text{C}_{\text{wax}}$ of C₂₈ was 0.18 ‰, and the average standard error on samples measured in triplicate or greater (n=12) was 0.34 ‰ (Figure 3). The $\delta^{13}\text{C}_{\text{wax}}$ of C₂₈ and C₂₆ *n*-acid are strongly correlated ($r^2 = 0.79$, $p <$

0.001), as are the $\delta^{13}\text{C}_{\text{wax}}$ of C_{28} and C_{30} *n*-acid ($r^2 = 0.85$, $p < 0.001$), indicating that measurements on C_{28} are broadly representative of the isotopic composition of the long-chain waxes. The mean values of the $\delta^{13}\text{C}_{\text{wax}}$ for C_{26} and C_{30} *n*-acid are -36.6 and -34.4 ‰ respectively.

From ~53 to 31 kyr BP, i.e. much of Marine Isotope Stage 3 (MIS 3), $\delta^{13}\text{C}_{\text{wax}}$ averages -40.5 ‰. At 31 kyr BP $\delta^{13}\text{C}_{\text{wax}}$ rapidly transitions to more positive (^{13}C -enriched) values, and between ~28 to 14 kyr BP (i.e. during MIS 2) the average $\delta^{13}\text{C}_{\text{wax}}$ was -34.9 ‰. $\delta^{13}\text{C}_{\text{wax}}$ then shifts rapidly toward more negative (^{13}C -depleted) values and averages -38.8 ‰ in the Holocene, similar to the values observed during the later part of MIS 3 (Figure 4). The depleted modern $\delta^{13}\text{C}_{\text{wax}}$ values in Lake Matano are comparable to the $\delta^{13}\text{C}$ of modern soil samples ($n = 5$) taken around the Malili Lakes (average: -36 ‰, maximum: -38.6 ‰, minimum: -32.6 ‰). The long-term isotopic changes record a series of shifts in vegetation that show both similarities to and differences among other regional records, as discussed below.

5. Discussion

5.1 Interpretation of the $\delta^{13}\text{C}_{\text{wax}}$ proxy for vegetation and climate

In the tropics, $\delta^{13}\text{C}_{\text{wax}}$ is primarily interpreted to reflect changes in the relative abundance of plants using the C_3 and C_4 photosynthetic pathways (Vogts et al. 2009). The $\delta^{13}\text{C}$ of *n*-alkanes leaf waxes from C_4 plants, which include most tropical grasses, typically range from -14 ‰ to -27 ‰, while waxes from C_3 plants range between -29‰

231 and -42 ‰ (Bi et al. 2005, Chikaraishi and Naraoka 2007, Vogts et al. 2009). For n-
 232 alkanolic acid leaf waxes, the reported $\delta^{13}\text{C}_{\text{wax}}$ values for C_4 plants range from -19 ‰ to -
 233 26 ‰ and the values for C_3 plants range from -30 ‰ to -45 ‰ (Chikaraishi and Naraoka
 234 2007). $\delta^{13}\text{C}_{\text{wax}}$ can also vary due to changes in the efficiency of carbon and water
 235 utilization within C_3 and C_4 plants, often related to the effects of edaphic factors, such as
 236 soil, precipitation, humidity (Diefendorf et al. 2010). Globally, C_3 biomass exhibit a ~6
 237 ‰ enrichment across precipitation gradients from closed-canopy rainforest to more xeric
 238 ecosystems (Diefendorf et al. 2010). The average n-alkanes $\delta^{13}\text{C}_{\text{wax}}$ for C_3 plants in
 239 African rainforests are more negative (-36.9 ± 2.5 ‰) relative to C_3 plants in more xeric
 240 African ecosystems, at -33.5 ± 2.8 ‰, with waxes from some rainforest trees reaching
 241 $\delta^{13}\text{C}_{\text{wax}}$ as negative as -45‰ (Vogts et al. 2009).

242 Analyses of the $\delta^{13}\text{C}$ of n-alkanoic acids from surface marine sediments across the
 243 Maritime Continent and northwestern Australia suggest that $\delta^{13}\text{C}_{\text{wax}}$ is correlated strongly
 244 with rainfall seasonality as well as with average monthly precipitation (Dubois et al.
 245 2014). $\delta^{13}\text{C}_{\text{wax}}$ values observed in marine surface sediments from southwestern Indonesia,
 246 where C_4 grasslands and savannas are common, are enriched compared to those from
 247 wetter, less seasonal regions including Sulawesi. Southwestern Indonesia experiences a
 248 much more highly seasonal climate, marked by strong precipitation in boreal winter
 249 associated with a strengthened winter monsoon and southward migration of the ITCZ.
 250 These data show that $\delta^{13}\text{C}_{\text{wax}}$ tracks ecoclimate/biome classifications for the Maritime
 251 Continent at least partly, if not dominantly, through dry season water stress, which also
 252 would affect carbon use efficiency in C_3 forests. Thus, we interpret Lake Matano $\delta^{13}\text{C}_{\text{wax}}$

record as a proxy for changes in vegetation type, which is largely controlled by regional hydroclimate.

The long-term pattern of $\delta^{13}\text{C}_{\text{wax}}$ preserved in Lake Matano likely reflects catchment-wide transitions between closed-canopy rainforest and more open ecosystems, possibly incorporating C_4 grasses. During the MIS 3 and MIS 1, $\delta^{13}\text{C}_{\text{wax}}$ remained at about -38 ‰ (Figure 4), similar to the values recorded for closed-canopy rainforests in other regions (Vogts et al., 2009) and consistent with the present vegetation within the catchment. The 5.5 ‰-enrichment observed during MIS 2 indicates a shift toward more drought-tolerant ecosystems, and a drier, more seasonal climate after 30 kyr BP (Figure 4). The absolute values of $\delta^{13}\text{C}_{\text{wax}}$ we observe during the LGM (-35 ‰) do not require incorporation of C_4 grasses and instead could reflect more open, C_3 ecosystems with increased water stress. However, it is likely that this transition also saw at least limited expansion of C_4 grasses within the catchment. Discontinuous pollen data from mires located only 1.5 km from the southwestern shore of Lake Matano, indicate a substantial increase in Poaceae (grass) pollen between 35 and 17 ka (Hope 2001). Moreover, $\delta^{13}\text{C}_{\text{wax}}$ reconstructions from Lake Towuti suggest more enriched values during the LGM than observed at Lake Matano (-25 vs. -35 ‰, respectively) that are enriched relative to typical C_3 end-member $\delta^{13}\text{C}_{\text{wax}}$ values, implying expanded C_4 grasslands around Towuti only 10 km from our study area (Figure 4). Thus, we interpret the $\delta^{13}\text{C}_{\text{wax}}$ record at Lake Matano to reflect the prevalence of closed-canopy rainforest during MIS 3 and the Holocene, interrupted by the development of a more open C_3 forest with scattered C_4 grasses during late MIS3 and the LGM.

What might have caused these transitions? Atmospheric pCO₂ is known to affect vegetation type and $\delta^{13}\text{C}$, with low CO₂ concentrations favoring C₄ grasses relative to C₃ plants (Ehleringer et al. 1997). However, the patterns of changes from MIS 3 through the Holocene observed at our site is unlikely be explained solely by changes in CO₂ concentrations, as CO₂ concentrations were quite low during MIS 3 relative to the Holocene (Figure 6), yet our data suggest similar, if not more depleted $\delta^{13}\text{C}_{\text{wax}}$ in MIS 3 than in the Holocene. Temperature also likely influenced vegetation changes, and while high-altitude pollen taxa have been observed in relatively low elevation settings in the Maritime Continent (Kershaw et al. 2011), variations in Sulu Sea sea surface temperatures during the past 50 kyr, which might be indicative of synoptic temperature change in the region, also show relatively little contrast during MIS 2 and 3 followed by a much warmer Holocene (Figure 6), in contrast to the temporal pattern in our $\delta^{13}\text{C}_{\text{wax}}$ records. Furthermore, modern temperature gradients across the Maritime Continent are small and not correlated with changes in the relative abundance of C₃ and C₄ vegetation (Dubois et al. 2014). Lastly, sedimentary Ti concentrations in Lake Towuti, which indicate fluvial erosion and hence precipitation, show a temporal pattern that is strikingly similar to $\delta^{13}\text{C}_{\text{wax}}$ data, with high Ti concentrations indicating strong runoff during MIS 3 and the Holocene, and low concentrations reflecting drier conditions during MIS 2 (Russell et al. 2014). Therefore, we interpret the more enriched values between 29 and 14 kyr BP as indicative of a drier and more seasonal MIS 2.

5.2 Regional vegetation changes in central Sulawesi during the LGM

298 The long-term trend in $\delta^{13}\text{C}_{\text{wax}}$ in Matano is similar to that observed at Lake
 299 Towuti (Figure 4, Russell et al. 2014), demonstrating coherent vegetation and
 300 hydrological changes in central Sulawesi since 50 kyr BP. The two records do differ in
 301 their absolute values, particularly during the last glacial maximum, MIS 2, as well as
 302 during parts of MIS 3. During MIS 2, both lakes recorded a substantial ^{13}C -enrichment
 303 relative to the Holocene and MIS 3, but Towuti experienced a much larger enrichment
 304 compared to Matano. During MIS 3 and the Holocene, $\delta^{13}\text{C}_{\text{wax}}$ values are also more
 305 depleted at Lake Matano, although less so than at the LGM. The differences at the LGM
 306 reflect quite different terrestrial ecosystems likely related to regional climatic variations,
 307 perhaps controlled by topographic differences between the two lakes' catchments.

308 Despite the close proximity between Lake Towuti and Lake Matano, altitudinal
 309 and geomorphological differences led to a number of floristic and climatic contrasts
 310 between their catchments that could explain the different amplitudes of variation in
 311 $\delta^{13}\text{C}_{\text{wax}}$. Today, the catchment of Lake Towuti (area: $\sim 1200 \text{ km}^2$, maximum elevation:
 312 $\sim 1250 \text{ m}$, mean elevation: $\sim 500 \text{ m}$) is dominated by lowland rainforest, similar to what is
 313 found in Lake Matano's catchment below 850 m, and many of the flat river valleys
 314 surrounding Lake Towuti today are inhabited by mixed forest and C_4 grassland
 315 (BBKSDA Sulse 2011). In contrast, the steeper and higher mountain ranges encircling
 316 Lake Matano are home to lowland rainforests below 650 m, and submontane and
 317 montane rainforests above, in keeping with the increase in precipitation with elevation
 318 observed regionally (Fig. 2). Pockets of anthropogenic C_4 grasses are found near Lake
 319 Matano (Hope 2001). The large differences in $\delta^{13}\text{C}_{\text{wax}}$ between Matano and Towuti
 320 during the LGM suggest that the grasslands in the valleys around Towuti today expanded,

contributing to the substantial enrichment ($\sim 13\text{ ‰}$) of around Towuti (Figure 4), while Matano remained surrounded largely by C_3 ecosystems. We also note 1-2 kyr differences in the timing of $\delta^{13}C_{\text{wax}}$ transitions, in which Lake Towuti variations generally lead those of Lake Matano. During the last glacial termination, for instance, $\delta^{13}C_{\text{wax}}$ shifts toward more depleted values at Lake Towuti beginning at ~ 16 kyr BP, while values become more enriched beginning ~ 14 kyr BP at Matano. While this could reflect age model errors, it is also possible that this is due to the topographic differences. The presence of the many flat river valleys surrounding Lake Towuti could facilitate a relatively rapid expansion and contraction of C_4 grasses, while transitions at Matano are controlled by slower shifts related to both C_4 grass expansion and changes in C_3 tree composition.

Indeed, pollen-based vegetation reconstructions from the Wanda site near Lake Matano indicate that the period between 35 and 17 kyr was marked by an increase in Poaceae pollen relative to MIS 3 and the Holocene, supporting our inference of regionally drier and more seasonal conditions during MIS 2 (Hope 2001). In addition, the Wanda site also records increased *Castanopsis* and *Lithocarpus* pollen during the glacial MIS 2 (Hope 2001). While Poaceae indicates increasing aridity, which in itself might have driven the enrichment of $\delta^{13}C_{\text{wax}}$ during the glacial period, *Castanopsis* and *Lithocarpus* might indicate that colder, higher-altitude tree taxa migrated to lower elevation areas closer to Lake Matano, presumably due to cooler LGM temperatures. Fagaceae, including *Lithocarpus* and *Castanopsis*, is highly abundant in the high mountains around Lake Matano, as has been observed in other mountain forests across Sulawesi (Culmsee et al. 2010, Culmsee and Leuschner 2013). Interestingly, Fagaceae plants from settings comparable to our study site (i.e. having similar altitudes and

precipitation regimes) from the tropics and subtropics have lower $\delta^{13}\text{C}$ values than Fagaceae and other evergreen angiosperms (Read and Farquhar 1991, Wei et al. 2010, Du et al. 2014). The larger carbon isotope fractionation (by approximately 2 ‰) has been attributed to the relatively low water use efficiency requirements of Fagaceae in cool, moist submontane forest ecosystems in China (Du et al. 2014).

While the Wanda pollen record is highly discontinuous (Hope 2001), the long-term trends in $\delta^{13}\text{C}_{\text{wax}}$ in Matano are compatible with the pollen reconstruction from the Wanda site. Enriched $\delta^{13}\text{C}_{\text{wax}}$ during the LGM is compatible with grassland expansion observed at Wanda, and the more depleted $\delta^{13}\text{C}_{\text{wax}}$ values observed during the MIS 2/LGM at Lake Matano relative to Towuti suggest that the mountains surrounding Matano remained home to submontane and montane taxa. Downslope migration of these taxa during the LGM could have somewhat offset the enrichment in $\delta^{13}\text{C}_{\text{wax}}$ related to C_4 expansion. This suggests that the cooler temperatures at these higher elevations may have reduced water stress, and provided refugia to rainforests during the regionally dry conditions.

5.3. Altitudinal gradients in Indonesian vegetation and climate during the LGM

Given that precipitation is a primary factor controlling $\delta^{13}\text{C}_{\text{wax}}$ variations among modern C_3 ecosystems (Diefendorf et al. 2010) as well as variations between C_3 and C_4 ecosystems in the Maritime Continent (Dubois et al. 2014), we suggest that the differences in Matano and Towuti $\delta^{13}\text{C}_{\text{wax}}$ records may also be explained by rainfall variations with altitude within central Sulawesi. In the present, large-scale sea breezes are

thought to play an important role in maintaining modern montane cloud forests across the interior of Sulawesi and other Indonesian islands, which together make up the largest area of cloud forests in the world (Bruijnzeel 2001, van der Molen et al. 2006). Radar and TRMM observations above Sulawesi demonstrate that the sea breeze carrying moisture from the seas around the island often results in higher precipitation in mountainous central Sulawesi in the afternoon, especially during the wet season (Renggono 2011). Today, Matano's higher altitude and steeper slopes cause intense cloud cover development, resulting in higher rainfall amounts and less seasonality than near Towuti (Figure 2) and more extensive active montane cloud forests (Culmsee et al. 2010). The higher supply of soil water, combined with the more humid, cloudier microclimate near Matano is likely to result in relatively low year-round water use efficiency and a relatively large carbon isotope fractionation in vegetation near Matano compared to Towuti (e.g. Cernusak et al. 2013).

During the last glacial period, lowered sea level (i.e. increasing distance toward the island's center) combined with cooler sea surface temperature might be expected to reduce the strength of the sea breezes. However, Sulawesi's coastline is relatively steep, resulting in little shoreline migration during sea level lowstands as compared to other Indonesian islands. The large mountainous area in the center of the island would still have generated a strong orographic effect and attracted sea breezes, thus ensuring a relatively wetter region and cloud generation during all months of the year. At the same time, the relatively cooler surface and tropospheric temperatures during the LGM (e.g. Tripathi et al. 2014) should have depressed the condensation height. This is in keeping with downward migration of high-altitude taxa observed in pollen records from

intermediate elevations in central Sulawesi (Hope 2001) and other Indonesian islands (van der Kaars et al. 2000, van der Kaars et al. 2001). Within this context, the highlands of Sulawesi, including the higher altitude areas of Lake Matano's catchment, were thus likely to maintain elements of C₃ rainforests during the last glacial cycle.

The shifts in tropical rainfall variability above Sulawesi, as well as their altitudinal gradients, during the past 50 kyr are in agreement with the hydrological interpretation of many pollen and plant biomarker records from marine and terrestrial sites across the Maritime Continent. Marine sediment cores from the Aru Sea (Kershaw et al. 2006) and Banda Sea (van der Kaars et al. 2000) record reduced abundances of Pteridophyta and increased concentrations of charcoal from ~30 to 13.8 kyr, indicating less rainfall than present during MIS 2 in the eastern part of the archipelago. Highest pteridophyte and rainforest pollen concentrations occur during the Holocene and MIS 3, indicating that the interglacials were much wetter than glacial periods. The local vegetation around Rawa Danau, a lowland lake in Java, was dominated by grasses from ~28.7 to 16.7 kyr, indicating drier climate around the site during MIS 2 (van der Kaars et al. 2001). Records of n-alkane $\delta^{13}\text{C}$ measured from cave guano profiles from low elevation Batu cave in Peninsula Malaysia, and Makangit and Gangub caves on Palawan Island (Figure 5, Wurster et al. 2010), display substantial MIS 2 enrichment compared to Holocene values, indicating drier LGM/MIS 2 similar to our records. The much more enriched C₂₉ n-alkane $\delta^{13}\text{C}_{\text{guano}}$ values for the two Palawan caves compared to the C₂₈ n-alkanoic acid $\delta^{13}\text{C}_{\text{wax}}$ from central Sulawesi (Figure 5) is consistent with previous work demonstrating that long-chain n-alkane are in general enriched in ¹³C (up to ~7‰) relative to the corresponding long-chain n-alkanoic acids (Chikaraishi and Naraoka

2007). The enriched values for Palawan are also expected given the open-canopy characteristic of Palawan rainforests (Peel et al. 2007). Trends in our carbon isotope records, coupled with published pollen evidence in Central Sulawesi, are highly consistent with the $\delta^{13}\text{C}_{\text{wax}}$ records collected in Savu Sea, a basin surrounded by the Nusa Tenggara islands in southeastern Indonesia (Figure 4, Dubois et al. 2014). While the Savu record has reduced amplitude and appears to have less “noise” in $\delta^{13}\text{C}_{\text{wax}}$ compared to Matano and Towuti (Figure 4), possibly due to the much larger wax source areas and thus a more mixed signal, all three records indicate enriched $\delta^{13}\text{C}_{\text{wax}}$ during the LGM compared to the Holocene (Figure 4). The amplitude of $\delta^{13}\text{C}_{\text{wax}}$ change between the LGM and the Holocene in Savu is 2-3 ‰, similar to the shift observed at Matano (3-4 ‰), both much smaller than the shift observed at Lake Towuti (13 ‰) (Figure 4). However, $\delta^{13}\text{C}_{\text{wax}}$ values at Lake Towuti during MIS 2 were only 1 ‰ more enriched than the LGM values of Savu. Thus, we infer that grasslands or patches of grasslands dominated lowland areas in the Sulawesi-Nusa Tenggara corridor during the drier, more seasonal climate of the LGM, while the highlands supported C_3 ecosystems under cooler and moister conditions. In this context, it seems likely that the large modern gradients in precipitation and its seasonality that exist between Sulawesi and Nusa Tenggara developed during the last glacial termination. Importantly, our results also highlight the need for numerous records at regional to continental spatial scales to disentangle large-scale climatological signals trends from more regional patterns that can be influenced by orography.

In contrast to these low elevation records, there is also evidence for continuous ever-wet vegetation from many of Indonesia’s high elevation lakes (above 500 m asl).

Palynological data from Danau di Atas in Sumatra (1535 m asl, Newsome and Flenley 1988), Lake Hordorli in West Papua (780 m asl, Hope and Tulip 1994), as well as from peatlands in Kalimantan (35 m asl but flanked by mountain ranges as high as 2000 m, Anshari et al. 2004) suggest that the highlands and the interior of the Maritime Continent remained relatively wet during MIS 2. Similarly, n-alkanoic acid $\delta^{13}\text{C}_{\text{wax}}$ records from west Sumatra (Niedermeyer et al. 2014) and Tarakan Delta off east Kalimantan (Dubois et al. 2014), which are associated with catchments dominated by high elevation (>2000 m asl) mountain ranges, indicate wet conditions during the LGM. Interestingly, despite its low altitude, records from Niah cave in northern Borneo display little changes in $\delta^{13}\text{C}_{\text{guano}}$ values from the LGM through early Holocene (Wurster et al. 2010), suggesting that rainfall variability over Borneo during regionally dry LGM was not sufficient to result in the reduction of C_3 rainforests in Borneo –or northern Sundaland– lowlands (Dubois et al. 2014). Despite this observation, taken together, these low and high elevation records show that the vegetation gradients we observe in central Sulawesi reflect larger-scale altitudinal patterns observed across much of the Maritime Continent.

Based on the Maritime Continent pollen and biomarker records, we surmise that the phytogeography of the region's rainforests across glacial-interglacial boundaries is closely linked with both climatic and altitudinal factors. C_4 grasslands, which in present-day Maritime Continent islands occupy drier and highly seasonal areas in the lowlands (Whitten et al. 1987, Peel et al. 2007), were expanded into larger areas at the expense of lowland C_3 rainforests during the last glacial period. Meanwhile, higher elevation regions cooled and remained relatively wet, supporting C_3 ecosystems, and at least some montane taxa were also able to expand to intermediate altitudes. The maintenance of wetter, C_3

ecosystems at higher elevations indicates the significance of orographic precipitation and temperatures in reducing dry season water stress, thus providing favorable conditions to C_3 rainforest taxa. These data are in contrast to biome modelling studies suggesting that rainforests perhaps expanded into low elevation, exposed shelves during the LGM due to the availability of additional land area, which could support those rainforests given sufficient precipitation (Cannon et al. 2009), and instead highlight an important role for the higher elevations as rainforest refugia.

5.4. Climatic controls on central Indonesian rainfall since 53 kyr BP

Our data suggest that over the last 53 kyr BP, regional climate varied between wet conditions during MIS 3 and the Holocene, to dry and more seasonal conditions from 30 to ~14 kyr BP. This history is very similar to recent reconstructions from Lake Towuti (Figure 4, Russell et al. 2014), as well as other Sulawesi records including Lake Tondano (Dam et al. 2001), where lower lake levels record drying during the LGM. Together with vegetation-based biomarker records from Makangit and Gangub caves (Wurster et al. 2010) as well as biomarker and pollen data from Savu Sea (Dubois et al. 2014), we surmise that a drier and more seasonal climate than present was a robust MIS 2 feature across Sulawesi and the islands north and south of Sulawesi. Indeed, the strong similarity between $\delta^{13}C_{wax}$ data from Lakes Matano and Towuti indicate a regionally robust response to climate forcing.

The records from Sulawesi, however, do not entirely agree with other regional paleoclimate data derived from $\delta^{18}O$ of speleothems and planktic foraminifera. Variations

in speleothem $\delta^{18}\text{O}$ from Gunung Buda in northern Borneo (Figure 5, Partin et al. 2007, Carolin et al. 2013) have been interpreted to demonstrate that regional precipitation is controlled primarily by precessional orbital forcing and was only weakly affected by glacial-interglacial transitions. Similarly, shorter speleothem $\delta^{18}\text{O}$ records from Liang Luar in Flores suggest a wet LGM in contrast to other southwest Indonesian records (Figure 5, Ayliffe et al. 2013). Planktic foraminifera-derived $\delta^{18}\text{O}$ of seawater ($\delta^{18}\text{O}_{\text{sw}}$) proxy records from offshore western Sumatra (Mohtadi et al. 2014), off south Java (Mohtadi et al. 2011), and the Savu Basin (Gibbons et al. 2014), indicate relatively little glacial-interglacial hydrologic changes during the Late Pleistocene-Holocene. These $\delta^{18}\text{O}_{\text{sw}}$ records were interpreted to reflect basin-scale sea surface salinity changes driven by either river runoff from the surrounding islands or changes in regional currents or atmospheric circulation.

These discrepancies highlight the possibility that vegetation-based $\delta^{13}\text{C}$ and speleothem/seawater $\delta^{18}\text{O}$ proxy data may record different seasonal hydroclimatic signals of the AIM (Dubois et al. 2014). Given that $\delta^{13}\text{C}_{\text{wax}}$ is a function of both mean precipitation and dry season intensity and duration (Dubois et al. 2014, this study), it is possible that the $\delta^{13}\text{C}_{\text{wax}}$ data in Savu Basin records a stronger dry season (Dubois et al. 2014), while $\delta^{18}\text{O}$ data from Liang Luar records a stronger wet season (Griffiths et al. 2009, Ayliffe et al. 2013). Meanwhile, the foraminifera used to generate the $\delta^{18}\text{O}_{\text{sw}}$ records, *G. ruber*, has been shown to record annual instead of seasonal mixed layer conditions (Mohtadi et al. 2011), such that the mean average conditions measured by $\delta^{18}\text{O}_{\text{sw}}$ might reflect little glacial-interglacial change. While these factors might explain these discrepancies, the $\delta^{13}\text{C}_{\text{wax}}$ at Matano and Towuti record expanded C_4 ecosystems

signifying a stronger/longer dry season at the same time that Ti concentrations in Towuti sediments decline (Russell et al. 2014). As surface runoff and fluvial erosion are primarily driven by peak precipitation (i.e. wet season), our data suggest reductions in both wet and dry season, and therefore mean annual, precipitation. Alternatively, the discrepancies might be explained by additional factors controlling $\delta^{18}\text{O}$ proxy data in this region, in particular the possibility that different moisture sources and precipitation trajectories change the isotopic composition of the rainfall (LeGrande and Schmidt 2009, Lewis et al. 2010, Carolin et al. 2013). Finally, it is also possible that the apparent discrepancies might point to strong regional hydroclimatic gradients that existed in Indonesia during MIS 2/LGM. The northern Borneo cave and sites used in the $\delta^{18}\text{O}_{\text{sw}}$ studies are situated at the peripheries of the Maritime Continent, and the southern sites are situated near the southernmost limit of present-day ITCZ migration across Indonesia, which might be more sensitive to precessional orbital forcing. In contrast, the $\delta^{13}\text{C}_{\text{wax}}$ records from Palawan and Sulawesi are located near the center of the Maritime Continent where ever-wet conditions and proximity to the Pacific Ocean and its overlying atmosphere might make the area more sensitive to global temperatures and boundary conditions. Additional records from northern Indonesia could help to evaluate this possibility.

The new data from Matano, combined with other biomarker records from Savu (Dubois et al 2014) and Palawan (Wurster et al. 2010) (Figure 5), corroborate the finding of Russell et al. (2014) that the variations in central Indonesian hydroclimate are most strongly correlated to changes in ice volume (Figure 6). There is little relationship between our proxy data and insolation forcing in the tropics as highlighted by the lack of

21-kyr precessional insolation cycles in our Matano data. However, the $\delta^{13}\text{C}_{\text{wax}}$ records from both Lakes Matano and Towuti appear to show correlations with the regional sea surface temperature (SST), the concentration of atmospheric greenhouse gases (GHG), the Sunda Shelf areal exposure, and the extent of Northern Hemisphere ice sheets (Figure 6). Among these, the Matano records most closely track the timing of significant Laurentide ice sheet growth during late MIS 3 (Figure 6). Regional SST records show similar temperatures during MIS 3 and MIS 2 and the Sunda Shelf had nearly similar exposed area between 53 and 12 kyr BP, whereas changes in the GHG concentrations between portions of MIS 3 and MIS 2 cannot wholly explain the variations observed in our $\delta^{13}\text{C}_{\text{wax}}$ (Figure 6), suggesting the relatively minor influence of these three forcings compared to that of ice sheet volume and topography. Indeed, modeling studies show that a relatively small change in ice sheet thickness might significantly increase the Hadley mass transport above the Pacific and shift the mean position of the ITCZ southward (e.g. Lee et al. 2014). In this light, the regional MIS 2 drying observed across central Maritime Continent could result from orographic forcing by the Laurentide ice sheet, which perturbed the tropical Pacific atmospheric circulation and subsequently drove the migration of intense precipitation to the south of central Indonesia.

6. Conclusions

Late Pleistocene and Holocene sediments from Lake Matano in central Sulawesi reveal a paleovegetation and paleohydrological history that is consistent with similar records from the region, in particular the vegetation record from Lake Towuti, which lies

at a lower elevation approximately 10 km south of Lake Matano. Together, $\delta^{13}\text{C}_{\text{wax}}$ from Lakes Matano and Towuti indicate that grassland and open canopy forest ecosystems expanded during a more arid and seasonal MIS 2, including during the LGM, whereas closed-canopy rainforest ecosystems predominated in central Sulawesi during MIS 1 and MIS 3, when the climate was wetter and less seasonal. The distinct glacial-interglacial shifts observed in central Sulawesi records during the past 50 kyr are likely due to the sensitivity of Maritime Continent hydroclimate to changes in global climate boundary conditions, and particularly remote high latitude forcings associated with ice volume and thickness. Given the importance of Lake Towuti as the site of an upcoming International Continental Drilling Project, which will attempt to reconstruct regional hydroclimate and vegetation history during the past 650 kyr or longer (Russell and Bijaksana 2012), the similar histories between the two lakes during the past 50 kyr strongly suggest that the climate proxy records of Lake Towuti are representative of the regional hydroclimate at the heart of the Western Pacific Warm Pool.

Within this framework, $\delta^{13}\text{C}_{\text{wax}}$ from Lake Matano are more depleted than those of Lake Towuti, and Lake Matano experienced a lesser enrichment in $\delta^{13}\text{C}_{\text{wax}}$ than Lake Towuti during late MIS 3 and MIS 2. We suggest that the local topographic setting in Sulawesi had a significant impact on local climatic and/or plant type variations across glacial-interglacial timescales, whereby the cooler, wetter climates at the higher elevations surrounding Lake Matano supported C_3 ecosystems during a regionally drier time period. This is consistent with the interpretation of multiple vegetation-based reconstructions from high and low altitude regions within the Maritime Continent, and

suggests an important role for mountains in maintaining rainforest elements in the Maritime Continent during glacial-interglacial cycles.

Acknowledgements

We acknowledge financial support from the National Science Foundation (NSF-EAR-1144623) to James M. Russell. We thank Anders Noren, Nigel Wattrus, Sinyo Rio, and Gerald Tamuntuan for field assistance, and PT Vale Indonesia for logistical support during our field work. Rafael Taroza, Yongsong Huang, Bronwen Konecky, and Cassandra Costa are thanked for laboratory assistance and for discussions on interpretations of these data. Research permits to conduct fieldwork on the Malili Lakes were granted by the Indonesian Ministry of Research and Technology (RISTEK). We also thank two anonymous reviewers who provided substantial feedback on an earlier version of the manuscript and two other reviewers for the later version of the manuscript.

References

- Aldrian, E. and R. D. Susanto (2003), Identification of three dominant rainfall regions within Indonesia and their relationship to sea surface temperature, *Int. Jour. of Clim.*, 23, 1435-1452.
- Anshari, G., A.P. Kershaw, S. van der Kaars, and G. Jacobsen (2004), Environmental change and peatland forest dynamics in the Lake Sentarum area, West Kalimantan, Indonesia. *Journal of Quaternary Science*, 19, 7, 637-656.

596 Ayliffe, L., M. Gagan, J.-x Zhao, R.N. Drysdale, J.C. Hellstrom, W.S. Hantoro, M.L.
 597 Griffiths, H. Scott-Gagan, E St Pierre, J.A. Cowley, and B.W. Suwargadi
 598 (2013), Rapid interhemispheric climate links via the Australasian
 599 monsoon during the last deglaciation, *Nature Communications*, 4, 1-6.
 600 Barton, H. 2005. The case for rainforest foragers: the starch record at Niah Cave,
 601 Sarawak. *Asian Perspectives*, 44, 56–72.
 602 BBKSDA Sulsel (2011), Statistik BBKSDA Sulsel, Ditjen PHKA Kementerian
 603 Kehutanan. Makassar.
 604 Bi, X., G. Sheng., X. Liu, C. Li, and J. Fu (2005), Molecular and carbon and hydrogen
 605 isotopic composition of n-alkanes in plant leaf waxes, *Organic Geochemistry*
 606 36, 1405–1417.
 607 Bruijnzeel, L.A. (2001), Hydrology of tropical montane cloud forest: a reassessment.
 608 *Land Use and Water Resources Research* 1, 1.1-1.18.
 609 Cannon, C.H., R.J. Morley, and A.B.G. Bush (2009), The current refugial rainforests of
 610 Sundaland are unrepresentative of their biogeographic past and highly
 611 vulnerable to disturbance, *Proc Natl Acad Sci USA* 106(27), 11188–11193
 612 Carolin, S., K.M. Cobb, J.F. Adkins, B. Clark, and A. Tuen (2013), Varied response of
 613 western tropical Pacific hydrology to abrupt climate changes, *Science*,
 614 doi:10.1126/science.1233797.
 615 Cernusak, L.A., N. Ubierna, K. Winter, J.A.M. Holtum, J.D. Marshall, and G.D.
 616 Farquhar (2013), Environmental and physiological determinants of carbon
 617 isotope discrimination in terrestrial plants, *New Phytologist* doi:
 618 10.1111/nph.12423.

619 Chikaraishi, Y. and H. Naraoka (2007), $\delta^{13}\text{C}$ and δD relationships among three n-alkyl
620 compound classes (n-alkanoic acid, n-alkane and n-alkanol) of terrestrial
621 higher plants. *Org. Geochem.* 38, 198-215

622 Culmsee, H. and C. Leuschner (2013), Consistent patterns of elevational change in tree
623 taxonomic and phylogenetic diversity across Malesian mountain forests,
624 *Journal of Biogeography* 40, 10, 1997-2010.

625 Culmsee, H., C. Leuschner, G. Moser, and R. Pitopang (2010), Forest aboveground
626 biomass along an elevational transect in Sulawesi, Indonesia, and the role of
627 Fagaceae in tropical montane rain forests, *Journal of Biogeography*, 37, 960-
628 974.

629 Dam, R., J. Fluin, P. Suparan, and S. van der Kaars (2001), Palaeoenvironmental
630 developments in the Lake Tondano area (N. Sulawesi, Indonesia) since 33,000
631 yr BP. *Palaeogeography, Palaeoclimatology, Palaeoecology* 171, 147–183.

632 Diefendorf, A.F., K.E. Mueller, S.L. Wing, P.L. Koch, and K.H. Freeman (2010) Global
633 patterns in leaf ^{13}C discrimination and implications for studies of past and
634 future climate. *Proc Natl Acad Sci USA* 107(13), 5738–5743.

635 Du, B., C. Liu, H. Kang, P. Zhu, S. Yin, G. Shen, J. Hou, and H. Ilvesniemi (2014),
636 Climatic Control on Plant and Soil $\delta^{13}\text{C}$ along an Altitudinal Transect of
637 Lushan Mountain in Subtropical China: Characteristics and Interpretation of
638 Soil Carbon Dynamics, *PLOS One*. DOI: 10.1371/journal.pone.0086440

639 Dubois N., D.W. Oppo, V. Galy, M. Mohtadi, S. van der Kaars, J. Tierney, Y. Rosenthal,
640 T. Eglington, A. Lückge, and B. Linsley (2014), Indonesian vegetation

641 response to changes in rainfall seasonality over the past 25,000 years. *Nature*
 642 *Geoscience* 7, 513-517.

643 Ehleringer, J. R., T.E. Cerling, and B.R. Helliker (1997), C₄ photosynthesis, atmospheric
 644 CO₂, and climate. *Oecologia* 112, 285–299.

645 Gibbons F., D.W. Oppo, M. Mohtadi, Y. Rosenthal, J. Cheng, Z. Liu, and B.K. Linsley
 646 (2014), Deglacial $\delta^{18}\text{O}$ and hydrologic variability in the tropical Pacific and
 647 Indian Oceans. *Earth and Planetary Science Letters* 387, 240-251.

648 Gimeno, L., A. Stohl, R. M. Trigo, F. Dominguez, K. Yoshimura, L. Yu, et al. (2012),
 649 Oceanic and terrestrial sources of continental precipitation. *Rev. Geophys.* 50,
 650 RG4003. doi: 10.1029/2012RG000389

651 Göltenboth, F., Langenberger, G., and Widmann, P (2006) Forest systems. In:
 652 Timotius, K.H., Milan, P.P., Margraf, J (eds.) *Ecology of Insular Southeast*
 653 *Asia: The Indonesian Archipelago*, Elsevier.

654 Griffiths M. L., R. N. Drysdale, M. K. Gagan, J.-X. Zhao, L. K. Ayliffe, J. C. Hellstrom,
 655 W. S. Hantoro, S. Frisial, Y. -X. Feng, I. Cartwright, E. St. Pierre, M. J.
 656 Fischer, and B. W. Suwargadi (2009), Increasing Australian-Indonesian
 657 monsoon rainfall linked to early Holocene sea-level rise, *Nature Geoscience*,
 658 2, 636-639.

659 Haffner, G. D., P. E. Hehanussa, and D. Hartoto (2001), The biology and physical
 660 processes of large lakes of Indonesia, p. 183–194. In M. Munawar and R. E.
 661 Hecky [eds.], *The great lakes of the world: Food web, health and integrity*.
 662 Backhuys.

663 Holbourn, A., W. Kuhnt, H. Kawamura, Z. Jian, P. Grootes, H. Erlenkeuser and J. Xu
 664 (2005), Orbitally paced paleoproductivity variations in Timor sea and
 665 Indonesian throughflow variability during 460 kyr. *Paleoceanography*, 20, PA
 666 3002.

667 Hope, G. S. (2001), Environmental change in the Late Pleistocene and later Holocene at
 668 Wanda Site, Soroako, South Sulawesi, Indonesia, *Palaeogeogr. Palaeoclim.*
 669 *Palaeocl.*, 171, 129145.

670 Hope, G. and Tulip, J. (1994), A long vegetation history from lowland Irian Jaya,
 671 Indonesia. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 109, 385-398.

672 Kalnay et al. (1996), The NCEP/NCAR 40-year reanalysis project, *Bull. Amer. Meteor.*
 673 *Soc.*, 77, 437-470.

674 Kershaw, A. P., S. van der Kaars, P. Moss, B. Opdyke, F. Guichard, S. Rule, and C.
 675 Turney (2006) Environmental change and the arrival of people in the
 676 Australian region. Before Farming (online version) 2006/1 article 2.

677 Kershaw, A.P., S. van der Kaars. and J.F. Flenley (2011), The Quaternary history of far
 678 eastern rainforests (2nd Edn.). In: Bush, M.B., Flenley, J.F. and Gosling,
 679 W.D. (Eds.) *Tropical Rainforest Responses to Climate Change*. Springer-
 680 Verlag, Berlin Heidelberg, pp. 85-123.

681 Lee, S.-Y., J.C.H. Chiang, and P. Chang (2014), Tropical Pacific Response to
 682 Continental Ice Sheet Topography, *Climate Dynamics*, DOI:
 683 10.1007/s00382-014-2162-0.

684 LeGrande, A.N. and G.A. Schmidt (2009), Sources of Holocene variability of oxygen
 685 isotopes in paleoclimate archives, *Clim Past*, 5, 441-455.

686 Lehmusluoto, P. and B. Machbub (1997), National Inventory of the Major Lakes and
 687 Reservoirs in Indonesia, Expedition Indodanau Technical Report, Revised
 688 Ed., Research. Inst. For Water Res. Dev., Min. of Public Works, Rep. of
 689 Indonesia, and Dept. of Limnology and Env. Protection, University of
 690 Helsinki, Finland, Helsinki.

691 Lewis, S. C., A. N. LeGrande, M. Kelley, and G. A. Schmidt (2010), Water vapour
 692 source impacts on oxygen isotope variability in tropical precipitation
 693 during Heinrich events, *Climate of the Past*, 6, 325– 343.

694 Moerman, J.W., K.M. Cobb, J.F. Adkins, H. Sodemann, B. Clark, and A. Tuen (2013),
 695 Diurnal to interannual rainfall oxygen isotope variations in northern Borneo
 696 driven by regional hydrology. *Earth and Planetary Sciences Letter*, 369, 108-
 697 119.

698 Mohtadi, M., D. W. Oppo, S. Steinke, J. W. Stuut, E. C. Hathorne, J. Groeneveld, D.
 699 Hebbeln, and A. Lückge (2011), Glacial to Holocene swings of the
 700 Australian-Indonesian monsoon, *Nature Geoscience*, 4, 540-544.

701 Mohtadi, M., M. Prange, D.W. Oppo, R. De Pol-Holz, U. Merkel, X. Zhang, S. Steinke,
 702 and A. Lückge (2014), North Atlantic forcing of tropical Indian Ocean
 703 climate. *Nature* 509, 76-80.

704 Monnin, E., A. Indermühle, A. Dällenbach, J. Flückiger, B. Stauffer, T.F. Stocker, D.
 705 Raynaud, and J.-M. Barnola. 2001. Atmospheric CO₂ concentrations over the
 706 last glacial termination. *Science*, 291, 112-114.

707 Moyle, R. G., S.S. Taylor, C.H. Oliveros, H.C. Lim, C.L Haines, M.A. Rahman, and F.H.
 708 Sheldon. 2011. Diversification of an endemic Southeast Asian genus:

709 phylogenetic relationships of the spiderhunters (Nectariniidae), *The Auk*,
 710 128, 777–788.
 711 Newsome, J. and J. R. Flenley (1988), Late Quaternary vegetation history of the Central
 712 Highlands of Sumatra. II.: Palaeopalynology and Vegetational History. *J.*
 713 *Biogeog.*, 15, 555-578.
 714 Niedermeyer E.M., A.L. Sessions, S.J. Feakins, and M. Mohtadi (2014), Hydroclimate of
 715 the western Indo-Pacific Warm Pool during the past 24,000 years.
 716 *Proceedings of the National Academy of Science* 111, 9402-9406.
 717 Partin J. W., K. M. Cobb, J. F. Adkins, B. Clark, and D. P. Fernandez (2007), Millennial-
 718 scale trends in west Pacific warm pool hydrology since the Last Glacial
 719 Maximum, *Nature*, 449, 452-455.
 720 Peel, M. C., B.L. Finlayson, and T.A. McMahon (2007), Updated world map of the
 721 Köppen– Geiger climate classification, *Hydrol. Earth Syst. Sci.*, 11, 1633–
 722 1644.
 723 Petit, J.R., J. Jouzel, D. Raynaud, N.I. Barkov, J.-M. Barnola, I. Basile, M. Benders, J.
 724 Chappellaz, M. Davis, G. Delayque, M. Delmotte, V.M. Kotlyakov, M.
 725 Legrand, V.Y. Lipenkov, C. Lorius, L. Pépin, C. Ritz, E. Saltzman, and M.
 726 Stievenard. (1999), Climate and atmospheric history of the past 420,000 years
 727 from the Vostok ice core, Antarctica, *Nature* 399, 429-436.
 728 PT Vale Indonesia (unpubl.) Data from weather station near the Malili Lakes.
 729 Qu, T., Y. Du, J. Strachan, G. Meyers and J. Slingo (2005), Sea surface temperature and
 730 its variability in the Indonesian region. *Oceanography* 18, 50–61.

731 Read, J. and G. Farquhar (1991), Comparative studies in Nothofagus (Fagaceae). I. Leaf
 732 carbon isotope discrimination, *Functional Ecology* 5, 684-695.

733 Renggono, F. (2011) Pola Sebaran Hujan di DAS Larona (in Indonesian). *Jurnal Sains*
 734 *dan Teknologi Modifikasi Cuaca*, 12, 1, 17-24.

735 Russell, J. and S. Bijaksana (2012), The Towuti Drilling Project: Paleoenvironments,
 736 Biological Evolution, and Geomicrobiology of a Tropical Pacific Lake.,
 737 *Scientific Drilling*, 14, 68-71.

738 Russell, J.M., H. Vogel, B.L. Konecky, S. Bijaksana, Y. Huang, M. Melles, N. Wattrus,
 739 K. Costa, and J.W. King (2014), Glacial forcing of central Indonesian
 740 hydroclimate since 60,000 y B.P., *Proc Nat Ac Sci USA*,
 741 doi:10.1073/pnas.1402373111.

742 Sachse, D, I. Billault, G.J. Bowen, Y. Chikaraishi, K.H. Freeman, C.R. Magill, F.A.
 743 McInerney, M.T.J. van der Meer, P. Polissar, R.J. Ribons, J.P. Sachs, H.-L.
 744 Schmidt, A.L. Sessions, J.W. White, J.B. West, and A. Kahmen (2012),
 745 Molecular paleohydrology: interpreting the hydrogen-isotopic composition of
 746 lipid biomarkers from photosynthesizing organisms. *Annu. Rev. Earth Planet.*
 747 *Sci.*, 40, 221–249.

748 Slik, J. W. F., A.D. Poulsen. et al. (2003), A floristic analysis of the lowland
 749 dipterocarp forests of Borneo, *Journal of Biogeography*, 30, 1517–1531.

750 Stott, L., A. Timmermann, and R. Thunell (2007), Southern Hemisphere and deep-
 751 seawarming led deglacial atmospheric CO₂ rise and tropical warming. *Science*
 752 318(5849), 435–438.

753 Tierney, J.E., D.W. Oppo, A.N. LeGrande, Y. Huang, Y. Rosenthal, and B.K. Linsley
 754 (2012), The influence of Indian Ocean atmospheric circulation on warm pool
 755 hydroclimate during the Holocene epoch. *J. Geophys. Res.*, 117, D19108,
 756 doi:10.1029/2012JD018060.

757 Tripathi, A.K., S. Sahany, D. Pittman, R.A. Eagle, J.D. Neelin, J.L. Mitchell, and L.
 758 Beaufort (2014), Modern and glacial tropical snowlines controlled by sea
 759 surface temperature and atmospheric mixing. *Nature Geoscience*, 7, 205–
 760 209 doi:10.1038/ngeo2082.

761 van Baalgoy, M.M.J and I.G.M. Tantra (1986) The vegetation in two areas in Sulawesi,
 762 Indonesia. *Bulletin Penelitian Hutan*, Special Edition, pp. 1-61.

763 van der Kaars, S., D. Penny, J. Tibby, J. Fluin, R. Dam, and P. Suparan (2001) Late
 764 Quaternary palaeoecology, palynology and palaeolimnology of a tropical
 765 lowland swamp: Rawa Danau, West Java, Indonesia. *Palaeogeography*,
 766 *Palaeoclimatology, Palaeoecology*, 171, 185–212.

767 van der Kaars, S., X. Wang, A.P. Kershaw, F. Guichard, and D.A. Setiabudi (2000) A
 768 Late Quaternary palaeoecological record from the Banda Sea, Indonesia:
 769 Patterns of vegetation, climate and biomass burning in Indonesia and northern
 770 Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 155, 135–
 771 153.

772 van der Molen, M.K., A.J. Dolman, M.J. Waterloo and L.A. Bruijnzeel (2006), Climate is
 773 affected more by maritime than by continental land use change: a multiple-
 774 scale analysis. *Global and Planetary Change*, 54, 128-149.

775 Vogts, A., H. Moossen, F. Rommerskirchen, and J. Rullkötter (2009), Distribution
 776 patterns and stable carbon isotopic composition of alkanes and alkan-1-ols
 777 from plant waxes of African rain forest and savanna C₃ species. *Organic*
 778 *Geochemistry*, 40, 1037-1054.

779 Waelbroeck, C., L. Labeyrie, E. Michel, J.C. Duplessy, J. McManus, K. Lambeck, E.
 780 Balbon, and M. Labracherie (2002), Sea-level and deep water temperature
 781 changes derived from benthic foraminifera isotopic records. *Quaternary*
 782 *Science Reviews*, 21, 295-305.

783 Wei, Z., X. Jibin., C. Jixiu, Z. Yanming, M. Qiaohong, O. Jun, C. Ying, Z. Zhiguo, and
 784 L. Wei (2010), Bulk organic carbon isotopic record of lacustrine sediments in
 785 Dahu swamp, eastern Nanling mountains in South China: implication for
 786 catchment environmental and climatic changes in the last 16,000 years,
 787 *Journal of Asian Earth Sciences*, 38, 162–169.

788 Whitten, T., M. Mustafa and G.S. Henderson (1987), *The Ecology of Sulawesi*. Gadjah
 789 Mada University Press, Yogyakarta, Indonesia. Republished by Periplus, Hong
 790 Kong, 2002.

791 Wurster, C.M., M.I. Bird, I.D. Bull, F. Creed, C. Bryant, J.A.J. Dungait, and V. Paz
 792 (2010), Forest contraction in north equatorial Southeast Asia during the Last
 793 Glacial Period, *Proceedings of the National Academy of Sciences*, USA, 107,
 794 15508–15511.

Figure 9

NCEP/NCAR Reanalysis 1980-2010 Climatology

Figure 1

Surface Precipitation Rate (mm/day)

Figure 3

Figure 4

Figure 5

Figure 6

Table 1

ID	Material	Depth (m)	¹⁴ C Age	± ¹⁴ C	Reservoir correction (¹⁴ C years)	Reservoir corrected ¹⁴ C Age	Calib-rated age (yr BP)
2B-1-107.5	bulk	0.40	4610	30	977.53	3632	3944
2B-1-109	wood/plant	0.41	3680	80	n/a	3680	4020
2B-2-51.5	bulk	1.26	10250	50	977.53	9272	10453
2B-3-1.5	wood/plant	2.23	15900	60	n/a	15900	19168
2B-3-5.5	bulk	2.27	17100	70	977.53	16122	19457
2B-3-94	bulk	3.15	21600	90	977.53	20622	24835
2B-4-47.5	bulk	4.18	28000	130	977.53	27022	31064
2B-5-23	bulk	5.30	33900	280	977.53	32922	37008
2B-6-54.5	bulk	6.62	42100	330	977.53	41122	44629
2B-7-16	bulk	7.74	46000	460	977.53	45022	48391

Figure 1. Surface precipitation rates for December to May and June to November from NCEP/NCAR Reanalysis (Kalnay et al. 1996). Locations of our study site and other sites/records discussed in the text are shown on the map: 1) Makangit Cave, 2) Gangub Cave, 3) Niah Cave, 4) Gunung Buda Cave, 5) Tarakan Delta, 6) Lake Matano, 7) Lake Towuti, 8) Liang Luar Cave, 9) Savu Basin.

Figure 2. (A) Geological map of the Malili Lakes region. Core locations in both lakes are indicated with red stars. Locations of weather stations near the lakes are shown on the map. (B) Monthly mean precipitation for eight weather stations near Lakes Matano and Towuti (PT Vale Indonesia, unpublished) from 1997 to 2006. (C) Average annual precipitation for those weather stations plotted against their elevations. A trend line is fitted to the data, omitting one outlier (Timampu). (D) Seasonality index (difference between the average rainfall during the wettest and driest months divided by the mean monthly rainfall) for those weather stations were computed and plotted against their elevations. A trend line is fitted to the data, omitting one outlier (Palumba).

Figure 3. Age-depth profile, $\delta^{13}\text{C}$ of C_{28} n-alkanoic acids ($\delta^{13}\text{C}_{\text{wax}}$) data, and lithostratigraphic description of Lake Matano's Core 2B. 1-sigma errors for $\delta^{13}\text{C}_{\text{wax}}$ measurements are plotted.

Figure 4. $\delta^{13}\text{C}_{\text{wax}}$ from Lakes Matano and Towuti in central Sulawesi and Savu Basin near the Nusa Tenggara islands. Dashed lines represent a Gaussian smoothing of the data to emphasize long-term trends.

Figure 5. Comparison of Lake Matano $\delta^{13}\text{C}_{\text{wax}}$ record with other $\delta^{13}\text{C}$ records of regional vegetation. From top to bottom: 1) Northern Borneo/Gunung Buda $\delta^{18}\text{O}$ record, ice volume-corrected (Partin et al. 2007 and Carolin et al. 2013), 2) C_{29} n-alkane $\delta^{13}\text{C}_{\text{guano}}$ from Makangit on Palawan Island (Wurster et al. 2010), 3) C_{29} n-alkane $\delta^{13}\text{C}_{\text{guano}}$ from Gangub on Palawan Island (Wurster et al. 2010), 4) Matano $\delta^{13}\text{C}_{\text{wax}}$ (this study), 5) Savu $\delta^{13}\text{C}_{\text{wax}}$ (Dubois et al. 2014), 6) Flores/Liang Luar $\delta^{18}\text{O}$ record, ice volume-corrected (Griffiths et al. 2009, Ayliffe et al. 2013).

Figure 6. Comparison of Lake Matano $\delta^{13}\text{C}_{\text{wax}}$ records with climate forcings. From top to bottom: 1) Mg/Ca sea surface temperature record from Celebes Sea (Stott et al. 2007), 2) CO_2 concentration record from Dome C and Vostok, Antarctica (Monnin et al. 2001, Petit et al. 1999), 3) areal shelf exposure of Sunda Shelf, obtained by applying sea level fluctuations data to Sunda Shelf bathymetry, as described in Russell et al. (2014), 4) sea level fluctuations, as a proxy for global ice volume, derived from benthic foraminifera oxygen isotopes, as described in Waelbroeck et al. (2002), 5) Matano $\delta^{13}\text{C}_{\text{wax}}$ (this study).

Table 1. Calibrated and reservoir-corrected ages used to determine the age model for core MAT10-2B. The reservoir correction is based on the average of two interpolated paired ages.