

Glacial forcing of central Indonesian hydroclimate since 60,000 y B.P.

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The Indo-Pacific warm pool houses the largest zone of deep atmospheric convection on Earth and plays a critical role in global climate variations. Despite the region's importance, changes in Indo-Pacific hydroclimate on orbital timescales remain poorly constrained. Here we present high-resolution geochemical records of surface runoff and vegetation from sediment cores from Lake Towuti, on the island of Sulawesi in central Indonesia, that continuously span the past 60,000 y. We show that wet conditions and rainforest ecosystems on Sulawesi present during marine isotope stage 3 (MIS3) and the Holocene were interrupted by severe drying between ~33,000 and 16,000 y B.P. when Northern Hemisphere ice sheets expanded and global temperatures cooled. Our record reveals little direct influence of precessional orbital forcing on regional climate, and the similarity between MIS3 and Holocene climates observed in Lake Towuti suggests that exposure of the Sunda Shelf has a weaker influence on regional hydroclimate and terrestrial ecosystems than suggested previously. We infer that hydrological variability in this part of Indonesia varies strongly in response to high-latitude climate forcing, likely through reorganizations of the monsoons and the position of the intertropical convergence zone. These findings suggest an important role for the tropical western Pacific in amplifying glacial–interglacial climate variability.

tropical Pacific | paleoclimate | geochemistry | paleoecology

Three major zones of deep atmospheric convection energize the Earth's moisture and energy budgets: tropical Africa, the Amazon, and the Indo-Pacific. Convection over the Indo-Pacific warm pool (IPWP) is by far the largest of these, and exerts enormous influence on global climate through its role in coupled ocean–atmosphere circulation (1, 2) and its influence on the concentration of atmospheric water vapor, which is the Earth's most important greenhouse gas (3). Despite the region's importance, variations in Indo-Pacific hydroclimate on orbital timescales remain poorly constrained.

Climate models and theory predict that Indo-Pacific hydrology responds strongly to, and interacts with, glacial–interglacial climate variations (4–6). This prediction is partly borne out by terrestrial sedimentary records that suggest widespread drying across the IPWP during the Last Glacial Maximum (LGM; refs. 7, 8) between 19,000 and 26,000 y ago (9). Unfortunately, many of these records are relatively short and discontinuous, limiting their utility to detect the relationship between regional climate change and global forcing. New, long, high-resolution oxygen isotopic ($\delta^{18}\text{O}$) records from speleothems from northern Borneo paint a very different picture of Indo-Pacific paleoclimate, suggesting that orbital-scale changes in regional convection are dominantly controlled by changes in equatorial insolation driven by orbital precession (10). On the other hand, marine sedimentary runoff records from southern Java imply little change in IPWP hydrology at glacial–interglacial timescales (11). Given this disagreement, new records—especially long proxy records that respond strongly to precipitation—are needed to understand

the response of Indo-Pacific climate to glacial–interglacial climate change and forcing.

Indonesia lies at the center of the IPWP and has thousands of lakes, the sediments of which represent a largely untapped archive of the region's hydrologic history. Here we present a 60 thousand y (ky) B.P. record of IPWP hydrology from the sediments of Lake Towuti, located on the island of Sulawesi in central Indonesia (Fig. 1). Lake Towuti is the largest tectonic lake in Indonesia, and at 205 m depth, its sediments preserve perhaps the longest and most continuous terrestrial record of climate available from the region. In 2007–2010, we recovered 13 sediment piston cores from Lake Towuti; here we focus on the most continuous radiocarbon-dated stratigraphy from core TOW10-9B (*Material and Methods* and Fig. S1 and Tables S1 and S2).

Study Site and Proxy Interpretations

Sulawesi lies at the center of the humid, unstable air mass overlying the IPWP, and its climate responds strongly to large-scale changes in regional atmospheric circulation and sea surface temperature associated with the Australian–Indonesian summer monsoon (AISM). The Lake Towuti basin receives ~2,700 mm of precipitation annually and is surrounded by dense closed-canopy rainforest (12). This region experiences a wet season from December to May when the intertropical convergence zone (ITCZ) migrates southward over Indonesia (13). During this

Significance

Climate variability in the tropical western Pacific exerts enormous influence on global climate, yet its history remains poorly constrained. We present the region's first continuous terrestrial sedimentary record of surface hydrology and vegetation spanning the last 60,000 y based upon geochemical data from Lake Towuti, Indonesia. Our data demonstrate that wet conditions and rainforest ecosystems present during the Holocene and during marine isotope stage 3 were interrupted by severe drying between ~33,000 and 16,000 y B.P., when high-latitude ice sheets expanded and global temperatures cooled. These findings indicate an important role for glacial boundary conditions in pacing tropical western Pacific climate change, and highlight the potential for the western Pacific to amplify global climate change during glacial–interglacial cycles.

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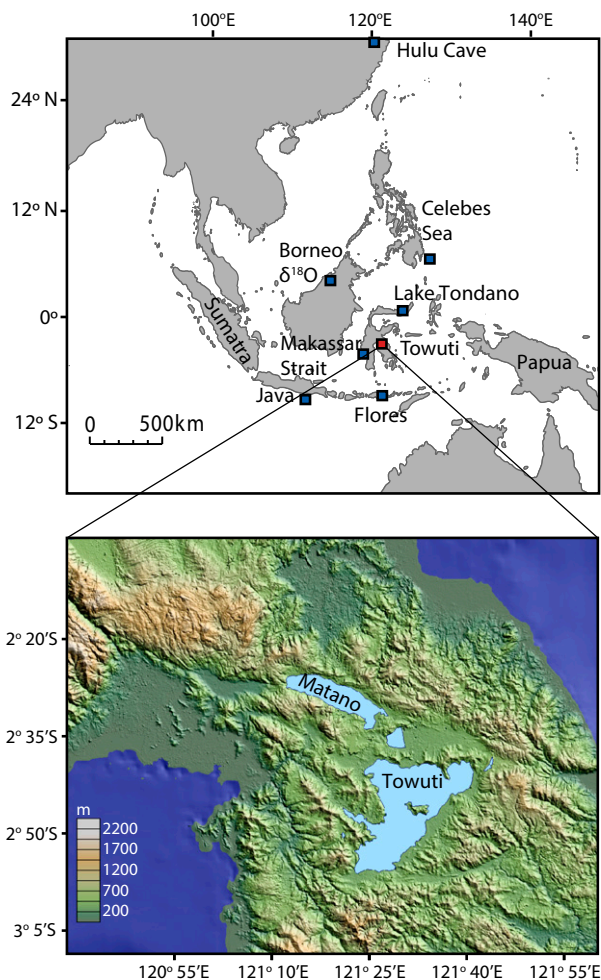


Fig. 1. (Upper) A map of Indonesia showing the location of Lake Towuti and regional records discussed in the text. (Lower) A regional map showing the location of Lake Towuti (2.5°S, 121.5°E) within central Sulawesi.

season strong northerly flow associated with the AISM, warm sea surface temperatures, and strong local convective activity (14) maintain regional precipitation at >250 mm/mo. Precipitation falls below 200 mm/mo from July to October, when much of southern and central Indonesia experiences a dry season (13). During this time, the ITCZ is displaced northward, and cool sea surface temperatures and strong southeasterly flow associated with the east Asian summer monsoon suppress regional convective activity (14).

Our paleoclimate record is based on high-resolution core scanning and organic geochemical analyses to reconstruct changes in surface runoff and terrestrial vegetation (*Materials and Methods*). We performed X-ray fluorescence (XRF) elemental scanning augmented by discrete analyses of elemental concentrations to correct for water content effects to determine sedimentary Ti content (Figs. S2 and S3), which is used to reconstruct climate-driven changes in clastic inputs to sedimentary basins (15). Ti provides a relatively simple and redox-insensitive proxy for the integrated processes of rainfall, erosion, and fluvial discharge from Towuti's ~1,500 km² catchment.

We also measured the carbon-isotopic composition of long-chain, even-numbered *n*-alkanoic acids ($\delta^{13}C_{wax}$), a main component of plant epicuticular waxes (*SI Materials and Methods* and Fig. S4). The $\delta^{13}C_{wax}$ is primarily used to distinguish between plants using C₃ and C₄ photosynthetic pathways (16) because C₄

plants use a CO₂-concentrating mechanism that improves their photorespiration and water-use efficiency relative to C₃ plants (17). The $\delta^{13}C$ of epicuticular waxes from C₄ plants, which are mainly tropical and warm season grasses, typically range from -14‰ to -26‰, and waxes from C₃ plants range between about -29‰ and -38‰ (18–20). Precipitation is the dominant control on the distribution of C₃ and C₄ plants through much of the tropics, such that $\delta^{13}C_{wax}$ has been widely used to reconstruct past changes in tropical hydroclimate (21, 22).

In modern plants, $\delta^{13}C_{wax}$ varies not only due to changes in plants' photosynthetic pathways, but also due to the influence of edaphic factors (water availability, temperature) (23) and plant biome structure (closed-canopy vs. open-canopy forest; ref. 24). Wetter conditions permit more efficient leaf-gas exchange and stronger fractionation against ¹³CO₂, and carbon recycling under closed-canopy forest can cause carbon-isotopic depletion of CO₂ (25). Recent global surveys of the $\delta^{13}C$ of vegetation indicate these processes can cause ~6‰ depletion in the $\delta^{13}C$ of leaf matter in tropical rainforests relative to more xeric C₃ ecosystems, and ~4‰ depletion in tropical rainforests relative to drier, tropical deciduous forests (23). Thus, we interpret more depleted $\delta^{13}C_{wax}$ to represent C₃ forests growing in wet conditions; whereas, enriched $\delta^{13}C_{wax}$ reflects a drier climate and increasing C₄ grasses.

Vegetation changes on glacial–interglacial timescales, including changes in C₃ and C₄ plant communities, are controlled not just by precipitation, but also temperature, atmospheric CO₂ concentrations, soil moisture, and other environmental factors (26). Similarly, sedimentary Ti concentrations are affected by changes in lake levels, soil chemical weathering, and other processes that affect clastic sediment deposition and erosion. Despite these differences, sedimentary Ti concentrations and $\delta^{13}C_{wax}$ in Lake Towuti exhibit coherent orbital-scale variations over much of the past 60 ky B.P. (*SI Materials and Methods* and Fig. S5), demonstrating that the glacial–interglacial variability in these proxies is mostly driven by changing precipitation.

Results

Ti concentrations and $\delta^{13}C_{wax}$ show strong glacial–interglacial variability over the past 60 ky B.P. (Fig. 2). Low Ti concentrations indicate reduced precipitation at ~60 ky B.P., during late marine isotope stage (MIS) 4, followed by an abrupt rise in Ti at ~58 ky B.P. reflecting a shift toward wetter conditions. At the base of our record, $\delta^{13}C_{wax}$ averages -32.4‰, and exhibits an abrupt ~4‰ depletion at 58 ky B.P., synchronous with the rise in Ti. This ¹³C depletion could result either from a reduction in the abundance of C₄ grasses, or from an increase in precipitation that altered the structure of C₃ forests in Lake Towuti's catchment, confirming an abrupt onset of wet conditions at the MIS 4/3 boundary. Ti concentrations are high and $\delta^{13}C_{wax}$ averages -37.8‰ between ~58 and 39 ky B.P., recording a wet climate and closed-canopy rainforest in central Sulawesi during much of MIS3 (*SI Materials and Methods*). Ti concentrations fall, and $\delta^{13}C_{wax}$ becomes somewhat more enriched, beginning ~39 ky B.P., followed by an abrupt transition at ~33 ky B.P. to relatively dry conditions. The $\delta^{13}C_{wax}$ averages -25.0‰ between 30 and 18 ky B.P., indicating substantial C₄ grass expansion during the LGM.

Ti concentrations are low during the LGM and reach a minimum at 16 ± 0.4 ky B.P., coincident with Heinrich event 1 (H1; Fig. 3) (27), providing additional evidence of the significance of H1 to tropical hydroclimate (28). Heinrich events 3 and 4 are also associated with declines in Ti concentrations, and aridity at Lake Towuti ~60 ky B.P. could be correlated to H6, one of the strongest Heinrich events in the North Atlantic (29). However, we see no clear evidence for H2 or H5, nor do we see evidence for the Younger Dryas, which appears to have had a limited impact over much of Indonesia (8). The expression of all six Heinrich events of the past 60 ky B.P. in speleothem $\delta^{18}O$ from

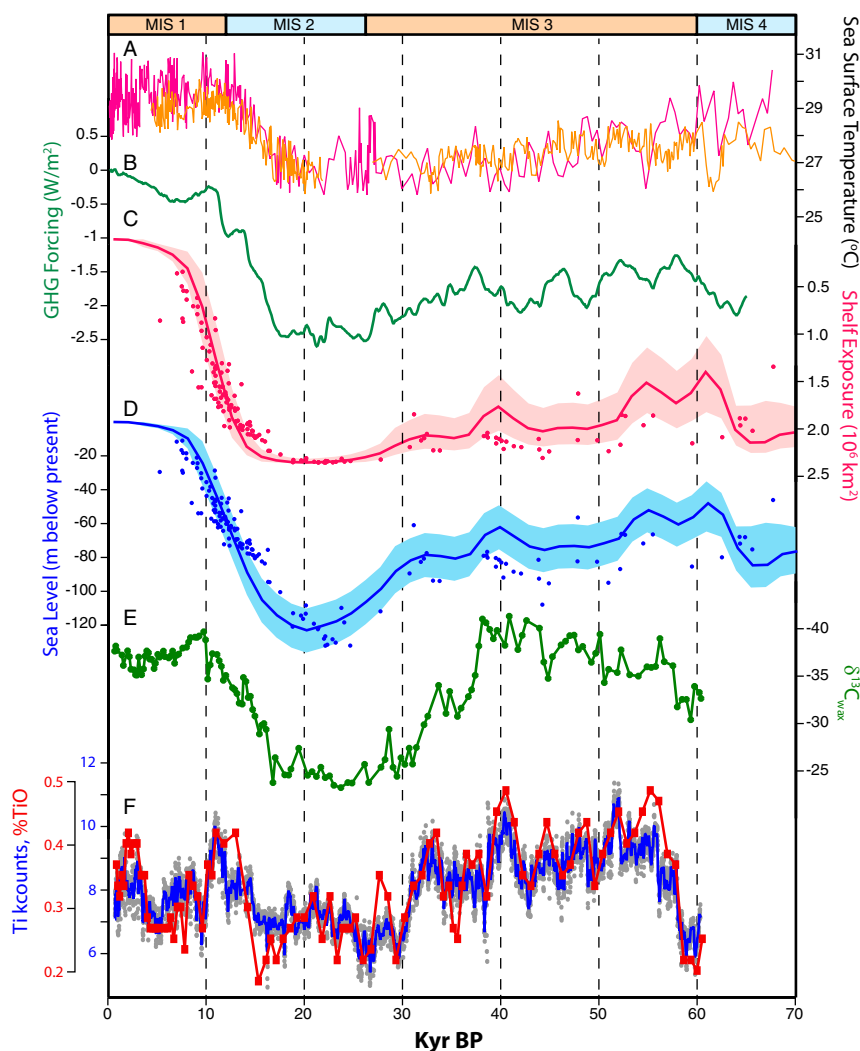


Fig. 2. A comparison of proxy data from Lake Towuti to global and regional climate forcings. (A) Sea surface temperature reconstructions from the tropical western Pacific [Celebes Sea (44) in pink and the Sulu Sea (45) in orange]; (B) radiative forcing from greenhouse gases (46). (C) Areal exposure history of the Sunda Shelf, calculated from sea level reconstructions applied to shelf hypsography using sea-level records from 2D (*SI Materials and Methods*). (D) Global sea level as proxy for ice volume, reconstructed from benthic $\delta^{18}\text{O}$ [blue line (47)] and globally distributed corals [blue dots (48)]. (E) The $\delta^{13}\text{C}_{\text{wax}}$ from Lake Towuti. (F) Ti in sediments from Lake Towuti measured by scanning XRF (gray dots are individual measurements, blue line is a 10-point running average), and flux-fusion ICP-AES (red).

Borneo (11), to the north of our site, coupled with the variable expression of Heinrich events in our record from Sulawesi, could reflect latitudinal gradients in the regional sensitivity of Indo-Pacific hydrology to millennial-scale forcing from the North Atlantic. This is perhaps related to variations in the strength and/or underlying mechanisms of the Heinrich events themselves and their ability to perturb regional rainfall.

Ti concentrations abruptly increase at 14.8 ± 0.38 ky B.P., synchronous with the abrupt onset of wetter conditions recorded in speleothem $\delta^{18}\text{O}$ records from China (30) (Fig. 3A). The $\delta^{13}\text{C}_{\text{wax}}$ reaches its Holocene average of -37.1‰ at 11 ± 0.28 ky B.P., recording the development of closed-canopy tropical rainforest that persists today. Ti concentrations are also high in the early Holocene, but fall during the mid-Holocene. The $\delta^{13}\text{C}_{\text{wax}}$ exhibits a muted but simultaneous mid-Holocene enrichment of $\sim 1.5\text{‰}$, indicating that the mid-Holocene reduction in precipitation implied by sedimentary Ti was insufficient to strongly perturb the region's rainforests under Holocene boundary conditions. Both proxies indicate a return to moist conditions in the late Holocene, similar to records from southern Indonesia (11,

29) and likely related to intensification of the austral summer monsoon (11).

Discussion

Our most significant findings are the existence of a very wet climate during much of MIS3 and the Holocene, interrupted by abrupt transitions to and from a dry LGM. No prior record from Sulawesi contains sediments covering the LGM, let alone the past 60 ky. However, sediment cores from the shoreline of Lake Tondano, North Sulawesi (Fig. 1), suggest a wet climate ca. 35 ky B.P., a moist early Holocene, and a discontinuity from ~ 31 to ~ 13 ky B.P. interpreted to reflect low lake levels (31), a history very similar to that of Lake Towuti. Even more discontinuous palynological records from the Wanda peatland, near Lake Towuti, suggest rainforest predominated during late MIS3 and the Holocene and grasslands expanded during the late LGM (12), supporting our interpretation of $\delta^{13}\text{C}_{\text{wax}}$. Shorter but high-resolution reconstructions from marine sediments offshore from western Sulawesi suggest a moistening trend from the late glacial into the Holocene (32). Thus, our data appear compatible with

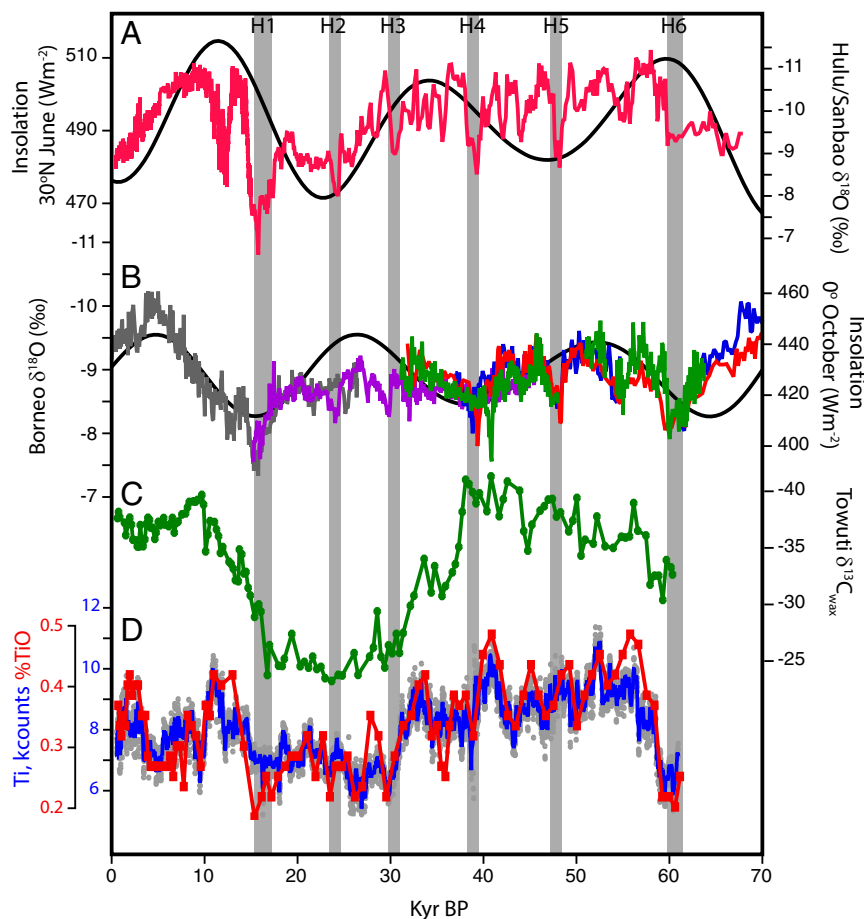


Fig. 3. A comparison of proxy data from Lake Towuti to paleoclimate records from nearby regions. Vertical gray bars indicate the timing of Heinrich events 1–6. (A) Hulu/Sanbao cave $\delta^{18}\text{O}$ records from China (29). (B) Borneo cave $\delta^{18}\text{O}$ records corrected for ice volume effects on seawater $\delta^{18}\text{O}$; different colors indicate different speleothems (10). (C) The $^{13}\text{C}_{\text{wax}}$ from Lake Towuti; (D) sedimentary Ti in Lake Towuti, as in Fig. 2. Gray shaded bars designate Heinrich events as dated in Hulu/Sanbao.

existing reconstructions from Sulawesi, and suggests a strong response of regional climate to glacial–interglacial forcings over the past 60 ky B.P.

In contrast, recently published speleothem $\delta^{18}\text{O}$ records from northern Borneo exhibit relatively little glacial–interglacial variability (Fig. 3), and instead suggest that boreal fall insolation at the equator, and hence precessional forcing, plays a dominant role in Indo-Pacific precipitation and convection (10) (Fig. 3B). These differences could suggest significant heterogeneity in LGM climate over Indonesia and the climate responses of these regions to remote and local forcings. Although the precise mechanisms that link changes in October insolation to Borneo $\delta^{18}\text{O}$ on orbital timescales are not known (10), in the present day seasonal and interannual precipitation variability in northern Borneo and our site are not strongly correlated. Borneo experiences little to no precipitation seasonality, and the austral winter precipitation minimum in central Sulawesi is characteristic of much of central and southern Indonesia (13). Moreover, variability in the $\delta^{18}\text{O}$ of precipitation at Borneo is most strongly correlated to precipitation variations over the oceans north of Borneo and Indonesia, and weakly or not correlated to precipitation variability in central and southern Indonesia (33). However, as there is widespread evidence for aridity during the LGM in Indonesia (7, 8), it is also possible that the $\delta^{18}\text{O}$ –precipitation amount relationship was weakened during the LGM, perhaps due to the effects of competing processes such as changes in precipitation sources, moisture trajectories, and

upstream convective effects (10). Indeed, precessional forcing is least evident in Borneo $\delta^{18}\text{O}$ during MIS2, which could reflect the effects of strong glacial forcings.

Our record alone cannot reconcile these differences, yet the wet climate we observe during much of MIS3 and the Holocene, interrupted by abrupt transitions to and from a dry LGM, has important implications for the mechanisms controlling climate variability in this region. This history suggests that the climate of Sulawesi is highly sensitive to glacial–interglacial forcings, and that the region may experience nonlinear, threshold responses to changes in global climate boundary conditions. Climate modeling studies indicate that IPWP hydrology could respond to a variety of glacial–interglacial forcings including regional processes, particularly exposure of the Sunda Shelf during sea level minima (34), as well as global forcings, including changes in global temperature and atmospheric greenhouse gas concentrations (GHGs) and remote forcing from ice sheet albedo and topography (5, 6). All of these forcings reached their minima or maxima during the LGM, potentially triggering threshold responses in regional hydroclimate. Because of their short nature, most previous proxy reconstructions have only evaluated the impacts of these forcings across the last glacial termination, when large and nearly synchronous changes in shelf exposure, temperature and GHGs, and ice volume complicate the attribution of precipitation changes. Our long, continuous record from Lake Towuti sheds light on the impacts of these forcings

across a broader range of changing boundary conditions of the past 60 ky B.P.

Previous work suggests that the exposure of the Sunda Shelf could play an important role in transmitting glacial–interglacial signals from the high latitude to the IPWP (30, 35). In many climate model simulations, the exposed land cools strongly relative to the ocean, and, together with reductions in atmospheric latent heating and humidity due to the replacement of ocean with land, weakens atmospheric convection and induces widespread drying over Indonesia (34). Although Sunda Shelf exposure during sea level lowstands could contribute to the dry conditions we observe on Sulawesi during the LGM, the history of shelf exposure is very different from the pattern of climate variability we observe at Lake Towuti. In particular, the shelf had nearly the same exposed area during the LGM and MIS3 (Fig. 2C; 2.3 vs. 1.9×10^6 km², respectively), yet we observe large differences in Sulawesi hydrology between these stages. Thus, shelf exposure alone did not trigger the threshold responses in rainfall that we observe at Towuti. Rather, to explain our observations this mechanism would necessitate large threshold responses in regional rainfall to small changes in the area of exposed land. This possibility has not been investigated in climate models. Moreover, although Sulawesi is not connected to the Sunda shelf and its climate might be less sensitive to shelf exposure, the Borneo $\delta^{18}\text{O}$ record also shows little influence of shelf exposure despite the location of that site on Sundaland (10). Taken together, these data suggest shelf exposure alone cannot impose a dry climate across this region.

Alternatively, Sulawesi hydrology could be highly sensitive to changes in global temperature, GHGs, and/or remote forcing by the ice sheets. Lower GHGs reduce precipitation rates in convective regions such as the IPWP through their control on global temperatures and atmospheric water vapor concentrations (4, 35, 36), yet climate model experiments suggest that average tropical precipitation declined by only $\sim 10\%$ during the LGM (35). Although our data cannot precisely quantify past precipitation changes, the shift from rainforest to more open terrestrial ecosystems almost certainly requires a $>10\%$ reduction in regional precipitation in light of the global distribution of C₄ grasslands. The IPWP could have experienced a stronger GHG-driven reduction in precipitation than the tropical mean due to regional temperature and humidity changes; however, regional sea surface temperature records indicate similar temperatures during MIS3 and MIS2 (Fig. 2A) when Towuti experienced large changes. Thus, although GHG forcing may have contributed to drying at Lake Towuti, it is unlikely to be the primary forcing of the pattern of hydrologic change observed between MIS3 and the Holocene.

On the other hand, the drying observed at Lake Towuti from late MIS3 to the LGM closely tracks changes in global ice volume (Fig. 2D; ref. 9), suggesting a strong remote forcing by the Northern Hemisphere ice sheets during the LGM. Indeed, glacial–interglacial variations in proxy data from Lake Towuti are most strongly correlated to changes in ice volume/sea level among these glacial–interglacial forcings (Table S3). Climate modeling studies indicate that both albedo and orographic forcing by the LGM ice sheet can alter tropical Pacific climate. Albedo forcing can alter the interhemispheric thermal gradient, shifting the ITCZ southward (37), and topographic forcing can alter westerly flow over the North Pacific, intensify northern trade wind circulation, and also force the ITCZ to migrate southward (6). The change in tropical winds and moisture convergence shift the locus of western tropical Pacific precipitation southward from equatorial sites such as Lake Towuti.

Although threshold responses of tropical Pacific precipitation to ice sheet forcing have not been explicitly investigated in modeling studies, the Pacific climate has been shown to be extremely sensitive to differences in ice sheet topography. Simulations of the

LGM climate with the Community Climate System Model 3 with differing ice sheet topography can produce very different patterns of atmospheric circulation and temperature over the northern Pacific as well as differences in tropical Pacific SST gradients (38). Given this sensitivity, we suggest that the growth of the Laurentide Ice Sheet during late MIS3 and MIS2 could have triggered a threshold response of the Pacific ITCZ, causing the abrupt changes we observe in Lake Towuti's hydrology. Northwesterly flow from the east Asian winter monsoon, which is also sensitive to remote forcing from the northern ice sheets, strengthened during late MIS3 and the LGM (39), and could also contribute to a southward shift in the locus of precipitation in the region, suppressing rainfall during Sulawesi's rainy season. Although much of northern Australia was dry during the LGM (8), speleothem records from Flores do suggest a southward shift of the ITCZ during the LGM (40), as does a wet MIS2 climate observed at Papua New Guinea (41). Existing data are too sparse to fully document the spatial patterns of IPWP climate during the last 60 ky B.P., and it is certainly possible that the threshold behavior we observe in Sulawesi could result from nonlinear interactions between multiple glacial–interglacial forcings. However, these regional patterns suggest that dynamical changes in the atmospheric circulation, potentially driven by northern high-latitude ice sheet forcing, exert a strong influence on orbital-scale changes in western tropical Pacific precipitation, as suggested by climate modeling experiments (4). Future modeling experiments could better assess thresholds and nonlinear interactions among these forcings in the western Pacific.

Our data also highlight the importance of glacial–interglacial changes in hydroclimate in structuring the vegetation on Sulawesi, one of the most biologically complex and diverse regions on Earth. Glacial–interglacial sea level variations are thought to play a dominant role in the phytogeography of this region through the expansion of land surface areas available for terrestrial ecosystems during Sunda Shelf exposure (42, 43). Indeed, modeling studies of Indonesian biomes suggest that wet evergreen lowland forests are currently in a refugial stage due to the flooding of the Shelf and geographic constraints on plant distributions (42). This stands in contrast to regions in which glacial climate change drove ecological bottlenecks. Our $\delta^{13}\text{C}_{\text{wax}}$ data challenge this prediction, and instead shows that Sulawesi rainforest contracted substantially in a relatively arid glacial climate. This would suggest that glacial–interglacial variations in both climate and geography play an important role in structuring Southeast Asian evergreen forests, which may migrate between climate refugia during glacial and geographic refugia during interglacials.

Records of surface runoff and vegetation from Lake Towuti highlight the strong sensitivity of Sulawesi hydrology and ecosystems to glacial–interglacial climate forcing and particularly forcing from the high-latitude ice sheets. The similarity of regional climate during the Holocene and MIS3, and the abrupt transitions into and out of MIS2, implies that central Indonesian hydrology can exhibit nonlinear, threshold responses to glacial climate forcing, tipping rapidly between wet interglacial and dry glacial climates. Although existing records are inadequate to fully evaluate the history of Indo-Pacific hydrology at glacial–interglacial timescales, such behavior, if widespread, could amplify climate change and ice sheet growth during glaciations through atmospheric water vapor feedbacks and help to synchronize abrupt temperature changes during glacial transitions.

Materials and Methods

Sediment cores were recovered from Lake Towuti using a modified Kullenberg piston corer with core-site selection guided by a high-resolution seismic stratigraphy. Sediment core IDLE-TOW10-9B (abbreviated TOW-9) was recovered from 154 m water depth and is 1,156 cm long. The age model for core TOW-9 is based on 23 radiocarbon dates yielding average sedimentation rates of 19 cm ky⁻¹ (SI Materials and Methods). We carried out high-resolution

elemental analysis using an ITRAX XRF core scanner equipped with a Cr tube. Selected samples were also prepared for elemental analysis using flux fusion and measured on an inductively coupled plasma atomic emission spectrometer (FF-ICP-AES). Ti counts measured by XRF were corrected for water content variations and other matrix effects and show a strong correlation to Ti concentrations measured by FF-ICP-AES (*SI Materials and Methods*).

We also measured the carbon isotopic composition ($\delta^{13}\text{C}$) of long-chain *n*-alkanoic acids (C_{26} , C_{28} , and C_{30}), components of terrestrial leaf waxes. Lipids were extracted by accelerated solvent extraction (Dionex) with $\text{CH}_2\text{Cl}_2\text{:MeOH}$ (9:1). Alkanoic acids were purified from the resulting extract, methylated, and the fatty acid methyl esters were analyzed by gas

chromatography–isotope ratio mass spectrometry (*SI Materials and Methods*). All $\delta^{13}\text{C}_{\text{wax}}$ data are corrected for the isotopic composition of the methyl group added during methylation. The pooled SE of samples measured in triplicate or greater is 0.47‰. See *SI Materials and Methods* for detailed analytical procedures.

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