The current refugial rainforests of Sundaland are unrepresentative of their biogeographic past and highly vulnerable to disturbance

Charles H. Cannon[a,b,1], Robert J. Morley[c,d], and Andrew B. G. Bush[e]

[a]Key Lab of Tropical Forest Ecology, Xishuangbanna Tropical Botanic Garden, Chinese Academy of Sciences, Yunnan 666303, People's Republic of China; [b]Deptartment of Biological Sciences, Texas Tech University, Lubbock, TX 79409-3131; [c]Palynova, Littleport, Cambs CB6 1PY, United Kingdom; [d]Department of Geology, Royal Holloway University, Egham, Surrey TW20 0EX, United Kingdom; and [e]University of Alberta, Department of Earth and Atmospheric Sciences, Edmonton, AB, Canada T6G 2R3

Edited by Robert May, University of Oxford, Oxford, United Kingdom, and approved May 8, 2009 (received for review October 4, 2008)

Understanding the historical dynamics of forest communities is a critical element for accurate prediction of their response to future change. Here, we examine evergreen rainforest distribution in the Sunda Shelf region at the last glacial maximum (LGM), using a spatially explicit model incorporating geographic, paleoclimatic, and geologic evidence. Results indicate that at the LGM, Sundaland rainforests covered a substantially larger area than currently present. Extrapolation of the model over the past million years demonstrates that the current "island archipelago" setting in Sundaland is extremely unusual given the majority of its history and the dramatic biogeographic transitions caused by global deglaciation were rapid and brief. Compared with dominant glacial conditions, lowland forests were probably reduced from approximately 1.3 to 0.8 × 10^6 km^2 while upland forests were probably reduced by half, from approximately 2.0 to 1.0 × 10^5 km^2. Coastal mangrove and swamp forests experienced the most dramatic change during deglaciations, going through a complete and major biogeographic relocation. The Sundaland forest dynamics of fragmentation and contraction and subsequent expansion, driven by glacial cycles, occur in the opposite phase as those in the northern hemisphere and equatorial Africa, indicating that Sundaland evergreen rainforest communities are currently in a refugial stage. Widespread human-mediated reduction and conversion of these forests in their refugial stage, when most species are passing through significant population bottlenecks, strongly emphasizes the urgency of conservation and management efforts. Further research into the natural process of fragmentation and contraction during deglaciation is necessary to understand the long-term effect of human activity on forest species.

lowland evergreen rainforest | paleoclimate simulation | upland evergreen rainforest

The Southeast Asian continent has one of the most complex geological histories in the world (1–3). The product of an ongoing collision between 2 ancient continents separated by an island archipelago (4, 5), several distinct centers of biological diversity can be identified within a small geographic range (Indochina, Sundaland, Wallacea, and Papuasia), demarcated by the Isthmus of Kra (6) and Wallace's Line (7). During the Quaternary Period, cyclical climate changes have affected the region in 2 ways: sea level change (8) modified total land area (9) while climate change affected the geographic distribution and elevational zonation of forest types (10). These land area dynamics may have had an impact on global climate as well, potentially affecting the ENSO cycle (11). Understanding the historical spatial dynamics of forest distribution plays a crucial role in the ability to predict community response to future change (12, 13).

Here, we have generated a distribution model of Sundaland rainforest at the Last Glacial Maximum (LGM) by combining paleontological constraints (5) with the results of a numerical simulation of paleoclimate (14). Using conservative estimates for the distinction between evergreen and seasonal forest, we present maximum, median, and minimum scenarios of lowland evergreen rainforest (LERF) at the LGM. These scenarios represent the interactions among precipitation levels in the paleoclimate simulation, equatorial temperature change (15), and assumptions about the vegetation lapse rate (10). These scenarios compare 3 distinct vegetation zones: coastal-swamp (0–10 m elev.), lowland (10–400 m elev.), and upland (1,000–2,000 m elev.). The dynamics of these 3 vegetation zones should be viewed as changes in the distribution of general bioclimatic envelopes, to which specific taxa would respond differently, depending on their dispersal ability and niche breadth. We also address the issue of whether a dry/seasonal climate corridor existed across Sundaland during the glacial periods (16, 17) by modeling the median scenario with and without a continuous belt of evergreen rainforest at the equator. We then extrapolate these scenarios over 2 time scales (the last glacial cycle and the past million years) to create dynamic models of rain forest change.

By generating spatially explicit historical models of evergreen rainforest distribution, we provide a robust approach for examining the pace and scale of change in rainforest extent and fragmentation through the Quaternary glacial cycles. Using this approach, we addressed 4 main questions: 1) How did the distribution of forest type, particularly evergreen vs. seasonal forest, differ at the LGM from current conditions? 2) How sensitive is the model to parameter assumptions? 3) How did the historical dynamics of 3 distinct vegetation zones differ through the last glacial cycle? and 4) How representative is the current biogeographic setting, given historical conditions?

Results

Forest Distribution at the Last Glacial Maximum. In the maximal and median scenarios, lowland evergreen rainforest (LERF) primarily existed as a large central block on the exposed shelf and encircling the coast of the current island of Borneo (Fig. 1). In the minimal LERF scenario (Fig. 1*D*), this block was dissected by the incursion of upland conditions centered on interior mountain ranges. Overall, our model was quite sensitive to the interaction between vegetation lapse rate and the mean temperature change as these 2 factors cause almost all of the differences between the maximal and median scenarios, while

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Author contributions: C.H.C., R.J.M., and A.B.G.B. designed research; C.H.C., R.J.M., and A.B.G.B. performed research; C.H.C. contributed new reagents/analytic tools; C.H.C. and R.J.M. analyzed data; and C.H.C., R.J.M., and A.B.G.B. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

[1]To whom correspondence should be addressed. E-mail: chuck@xtbg.ac.cn.

This article contains supporting information online at www.pnas.org/cgi/content/full/0809865106/DCSupplemental.

www.pnas.org/cgi/doi/10.1073/pnas.0809865106

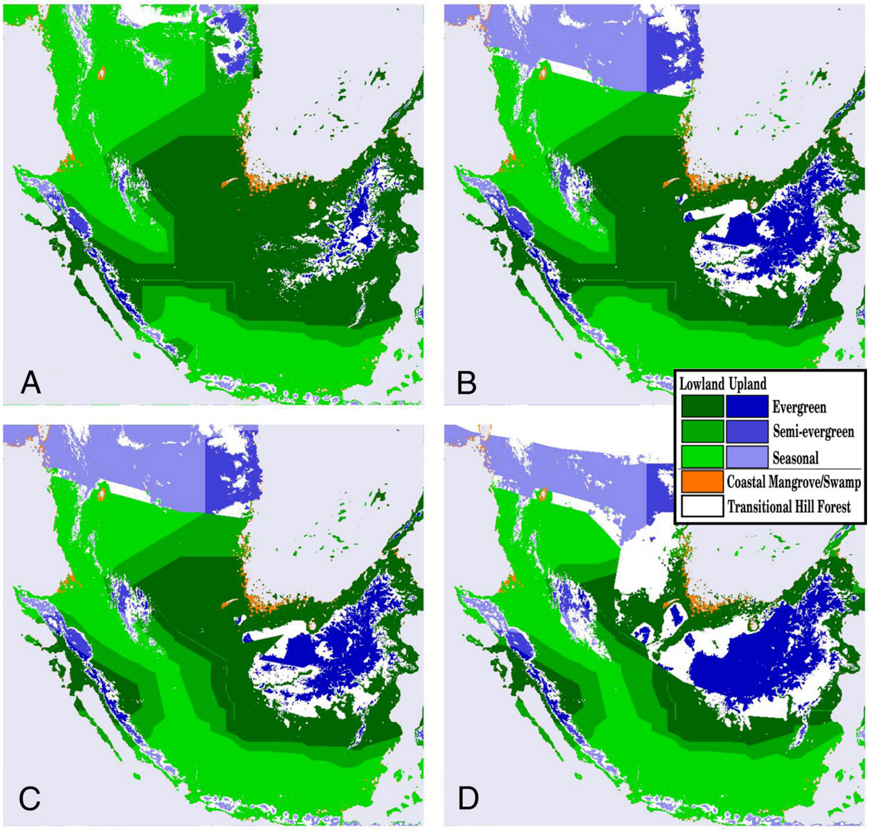

Fig. 1. Distribution of 3 distinct forest types at the Last Glacial Maximum, given different model parameters. (*A*) Maximum lowland evergreen rainforest (LERF) extent; (*B*) median LERF extent with ''closed corridor''; (*C*) median LERF with ''open corridor''; (*D*) minimum LERF. White areas represent transitional ''hill'' forests. Model parameters are given in the Methods.

changes in precipitation only made a difference under the more extreme model conditions.

In all LGM scenarios, coastal-swamp evergreen forests (CSEF) were restricted to the outer margins of the shelf, as the coastline was positioned beyond the shelf margin. The CSEF were greatly reduced in area, with a negligible fraction of "core" area (Fig. 2). Both LERF and upland evergreen rainforest (UERF) area were substantially greater than current conditions, under most model scenarios (Fig. 2). In the minimal LERF scenario, these 2 vegetation zones experience a dramatic but brief change in total area, largely due to global cooling and the large vegetation lapse rate assumed in that scenario. Core area for LERF was greater in all scenarios, reaching almost 80% in the maximal and median scenarios. Core area in the UERF at the LGM was also substantially greater in these scenarios.

Comparison of the simulation maps with historical data (Fig. S1) suggests that a vegetation lapse rate of 166 m/ΔC° and an equatorial temperature change of −3 °C was probably the most

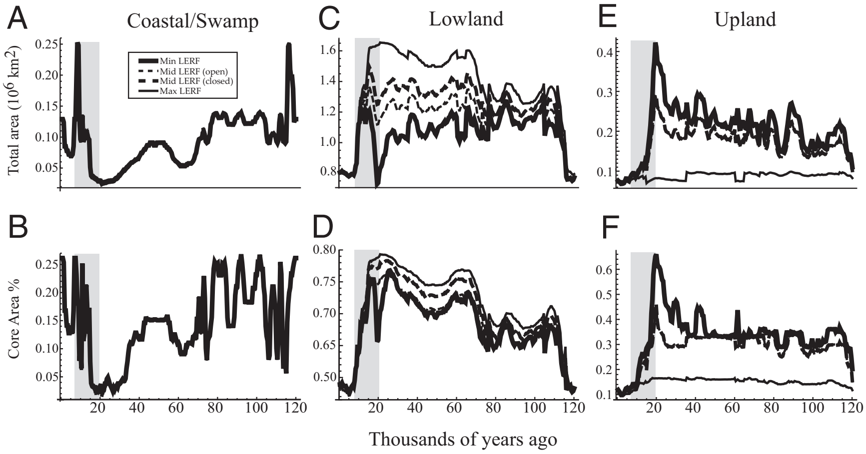

Fig. 2. Biogeographic dynamics of 3 vegetation zones over last glacial cycle (present to 120 kya), given different model parameters. (*A* and *B*) coastal; (*C* and *D*) lowland; (*E* and *F*) upland. Top row illustrates total land area of each forest type. Second row illustrates the percentage of that area in a ''core'' zone (10-km radius minimum). Gray box indicates period of sea level change from LGM to interglacial conditions. Model parameters are given in the *Methods*.

accurate scenario. This scenario agreed with observed increase of montane indicator pollen seen in the historical record of the Mahakam catchment (eastern Borneo) taken from the Papalang-10 deep sea core (18) and the presence of seasonal vegetation at the LGM in southern Kalimantan (19, 20).

Forest Distribution Through the Last Glacial Cycle. Coastal/swamp evergreen rainforests (CSEF) experienced the most dynamic biogeographic history of the 3 forest types examined (Fig. 2 *A* and *B*). At the peak of the LGM, when sea levels fell below the shelf margin, mangroves were restricted to a very narrow belt along coastlines, reflected in palynological records from deep sea cores by the very low representation of mangrove pollen at this time (18). There would have been very few opportunities for freshwater swamp forests in coastal regions at this time, except along incised valleys. However, many coastal swamp taxa would have maintained widespread inland distributions on poorly drained interfluves on watershed or kerapah peats (5), and in kerangas vergtation, which share many taxa with coastal peat swamp forests (6). As the shelf began to flood, especially from 11 to 9 Ka, CSEF would have experienced a dramatic but relatively brief expansion. Since about 8 Ka, coastal forests have roughly remained in their present positions, with the extent of mangroves, freshwater alluvial and peatswamps being determined by the patterns of progradation of individual river deltas following the Holocene transgression. CSEF also experienced a sudden and complete geographic relocation over hundreds of kilometers (Fig. 2 *A* and *B*) during the flooding, as the coastline retreated quickly across the shelf, coupled with an equally dramatic change in core area from minimal at the LGM to maximal at the time of the flooding of Sundaland. Different model scenarios had almost no impact on CSEF dynamics.

For LERF, total area and core area was substantially greater than current conditions for all scenarios (Movies S1–S4) through the vast majority of the last glacial cycle (Fig. 2 *C* and *D*), with the presence of an open corridor of seasonal forest having relatively little impact. In the maximal model, LERF exhibited 3 stages of increase in total and core area at approximately 110Kya, 95Kya, and 70Kya, corresponding primarily to greater exposure of the shelf due to lowering sea levels. In the minimal scenario, with an extreme vegetation lapse rate and 3 °C cooling, a sharp and very brief decline in area was apparent at the LGM, which represents the only time in the model when LERF total area dropped below current conditions. Even at this point, core area remained substantially greater.

While the amplitude of UERF response in the maximal LERF scenario (thin black line in Fig. 2*E* and *F*) was quite small, both total and core area were much greater in the median and minimal LERF scenarios. Both areas both experienced a gradual upward trend through the last glacial cycle, with a fairly dramatic peak at the LGM. In general, the distribution of UERF was very sensitive to the interaction between temperature change and vegetation lapse rate. Currently, UERF are highly fragmented, with roughly ten percent of total area found in a core area (Fig. 2*F*), which is extremely unusual given the conditions through the last glacial cycle. Core area was 30% greater in the max and median scenarios.

LERF Distribution Through the Last Million Years. As lowland evergreen rainforest (LERF) is the most valuable and vulnerable forest type in Southeast Asia, particularly in terms of biodiversity (21), we limited further study to this combination of forest and vegetation type. The extrapolation of our model to include the detailed reconstruction of historical climate and sea level change over the last million years (22) strongly indicates that LERF has undergone a succession of dramatic expansions and contractions (Fig. S2), with minimal distributions occurring at periods of *highest* sea levels, and by inference, *highest* ambient temperatures. This result is largely independent of model parameters, although the scale of difference between the "mean" historical condition and current condition does change considerably (Fig. 3). For Sundaland Asia therefore, it is imperative to view current rain forest distributions as refugial, with "glacial" distributions not only being the norm, but also with the most widespread LERF for the whole of the last million years.

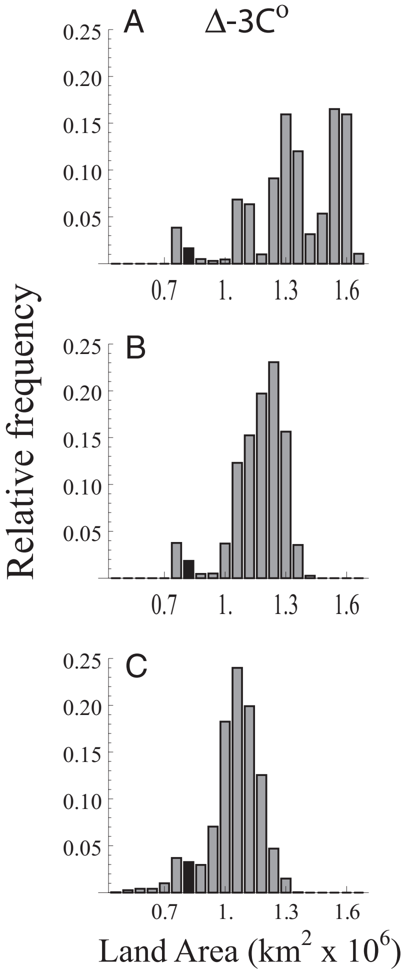

Fig. 3. Frequency distribution of tropical lowland evergreen forest land area over the last million years given −3C° change at the equator. (*A*) maximal LERF; (*B*) median LERF; and (*C*) minimum LERF scenario. The single black bar in each graph indicates the position of current situation.

Discussion

Refugial Dynamics. Our model results clarify several aspects about the historical dynamics of Southeast Asian rainforests which have not been adequately addressed before. Given the interplay of sea level, land distribution, and climate change over the last million years, the current interglacial biogeographic condition present in Sundaland is unrepresentative of the predominantly "glacial" past. The glacial scenario must be considered the "norm," characterized by cooler global climate, slight general reduction in precipitation, significantly lower sea levels, and greatly expanded land area with the exposure of the Sunda Shelf, which supported widespread LERF and UERF. Interglacials, on the other hand, with high sea levels breaking land areas up into islands and peninsulas, and with reduced LERF and UERF distributions, are the exception.

The powerful influence of refugial dynamics through the Quaternary Period on current distribution patterns of natural variation has been well documented in Europe (23, 24). In comparison to north latitude and equatorial African (13, 25) dynamics, they are reversed in the equatorial Sundaland archipelago. While European boreal biota were confined to the southern peninsulas fringing the Mediterranean Sea, rain forests in the Sunda Shelf area would have been at their maximum. Therefore, the transition from glacial to interglacial climatic conditions in the recent past led to a major contraction in forest cover and continuity. The Sundaland forests are currently in their refugial stage.

While a robust knowledge exists about how populations expand and migrate into areas with newly appropriate climate (12, 23, 26), very little is known about the retreat of populations and communities into refugial areas, particularly with respect to tropical communities. The Sundaland region could serve as a powerful model system for the largely unexplored but important questions about refugium formation. One question which could be directly tested is whether the refugium formation process is a truncation event, in which diversity external to the core area is simply lost, or whether it is an absorption event, where external diversity may become cryptically and temporarily incorporated into the refugium. While the conversion of forests by human activity is clearly a truncation event, where diversity outside the remnant area is simply lost, do forest remnants created over longer time scales through natural processes assimilate and concentrate diversity from a much wider landscape?

Biogeographic Dynamic of Different Vegetation Zones. While the 3 vegetation zones modeled (coastal/swamp, lowland, and upland) represent distinct communities in the current forests of Southeast Asia, sharing little overlap in species composition (6, 27, 28), the Sundaland forests at the LGM, particularly those on the newly exposed shelf, may have been substantially different in composition and structure. The dispersal capacity (29) and niche breadth of forest trees (27, 30) varies considerably at the landscape scale. This variance in dispersal capacity would lead to a complex distribution of forest tree species related to topography, prevalent wind, and the behavior of vertebrate seed dispersers.

Additionally, a number of abiotic factors are not included in our model, including relative light absorption properties and landscape scale geomorphological processes. Soils are particularly important in structuring forest communities (31). The repeated submersion and exposure of soils on the shelf would have probably affected their structure and fertility significantly. The evolution of these soils, after exposure, and their interaction with advancing forests would have been important but nothing is known about these dynamics. Our results are primarily limited to the spatial distribution of these 3 broad categories of forest type and vegetation zone and do not address specific taxonomic composition, physiological characteristics, and physical structure of these paleoforests.

Given these shortcomings in the model, the 3 vegetation zones obviously experienced substantially different biogeographic dynamics. Coastal-swamp forests have gone through repeated and complete geographic relocations of several hundreds of kilometers with each sea level oscillation (Fig. 2 *A* and *B*), with a major but brief spike in extent and connectivity immediately preceding the flooding and exposure of the main shelf. Given that the western region of the CSEF at the LGM, near northern Sumatera (Fig. 1), is relatively close to current CSEF, this forest would have experienced substantially less geographic relocation in comparison to these forests along the western coast of Kalimantan. Comparative studies in community composition and regional genetic diversity between these 2 areas could provide direct insight into the effects of these dynamics of forced migration.

Lowland and upland evergreen forest respond to the refugial dynamics in similar fashion, with maximal extent during glacials and minimal during interglacials (Fig. 2 *C*–*F* and Fig. S2). This dual expansion of forest types is possible because the declining temperature lowers the elevational zonation between upland and lowland forest, while the exposure of the shelf creates more lowland area onto which the lowland forest can retreat. These 2 vegetation types do respond to the different scenarios in opposite fashion. In the maximal LERF scenario (Fig. 1*A*), total area of UERF changes only slightly through the entire glacial cycle while total area of LERF varies over a 2-fold range. In the minimal scenario (Fig. 1*D*), these dynamics are reversed and the proportional change in UERF is substantially greater, representing a 3- and 4-fold change, respectively. These differences in historical dynamics represent different hypotheses about historical population sizes, particularly for specialist organisms in each vegetation type, and should be detectable in the geographic distribution of genetic variation (32, 33) and in the community level composition of different species and ecological characteristics (34).

Seasonal Climate Corridor. Historical evidence for a Quaternary seasonal climate corridor across the Sunda Shelf is most clearly suggested from palynological analyses from a poorly dated "mid" Quaternary locality near Kuala Lumpur (16, 35) and is supported from both geomorphological and biogeographical considerations (17). The palynological locality, formed by a thin lacustrine deposit from the "Old Alluvium", yielded abundant *Pinus* and Poaceae pollen, suggests open woodland vegetation surrounding the site. Overall, the paleo-evidence for seasonal climates does not demonstrate whether seasonal vegetation occurred as a continuous corridor between north and south portions of the shelf. Due to this uncertainty, both "open" and "closed" corridor scenarios were modeled.

Although these 2 conditions only marginally affect total land area of LERF on the Sunda Shelf through the last glacial cycle, a seasonal corridor would have had significant biogeographic effects, as it would have separated LERF into 2 geographic units. Molecular evidence in apes (36–38) and elephants (39) indicate a deep temporal separation between these 2 units. Additionally, these 2 units would have been substantially different in size, with the eastern block centered on the present island of Borneo much larger than the western block centered on Sumatera. The eastern block would also have possessed a much larger and continuous connection to the Asian continent, particularly the megadiverse areas of Indochina. These differences between the 2 major biogeographic units of LERF on the Sunda Shelf can be used to generate rigorous and testable biogeographic hypotheses.

Conclusions

The biogeographical dynamics suggest 2 major themes: 1) current distribution of evergreen rain forests are not representative of their historical distribution over the past million years and 2) the vegetation zones experienced substantially different biogeographical histories, providing an ideal model system of testing fundamental hypotheses about community assembly processes and historical population sizes. Given the life history strategies of rainforest trees, where lifespan frequently exceeds 2 centuries (40), the interglacial interludes of the Quaternary Period comprise periods of rapid change and occupy less than 10% of the past million years (Fig. 3). Phylogeographic evidence from the region indicates that the forest communities are quite old and that the main vicariance events occurred before the Pleistocene (41, 42). The refugial community dynamics illustrated here have thus had little impact on the geographic distribution of DNA sequence variation. This result indicates that forest species do have the ability to respond and persist through these dramatic biogeographic filters. While most tropical ecologists seek explanations for species co-existance based upon a fit between current selection pressures and community composition (43), the historical effects of these dramatic and recent biogeographic events probably play a major role in local landscape level community composition (34).

In terms of conservation and future dynamics of these forests, the glacial/interglacial cycle seek of reduction and fragmentation has been doubly reinforced and expanded by the conversion of forest to other land uses, particularly in the lowlands (44). Further fragmentation and reduction of these lowland forests can only further imperil already vulnerable populations. Given the great diversity currently found in the Southeast Asian forests (45), natural mechanisms and processes must exist which allow these communities to survive the dramatic historical biogeographic events of the past. The use of spatially detailed historical models to test various assumptions about these mechanisms and processes in the great natural laboratory of Southeast Asia will greatly enhance our understanding of future response to climate change and development, and will provide insight into how to best mitigate the ongoing conversion and degradation of these megadiverse forests.

Methods

Land Area Model. Topographic and bathymetric data were downloaded from the National Geophysical Data Center of the National Oceanic and Atmospheric Administration, U.S. Department of Commerce, using their Design-A-Grid Web facility. The area of interest of this study was defined as 15.30N/94.55E, 15.30N/119.25, 8.15S/94.55E, and 8.15S/119.25. The data were extracted as a simple raster from the global ETOPO2 2′ database. The sea level change record for the Sunda Shelf region for the glacial-interglacial transition was extracted from a regional study (8) while R. Bintanja kindly provided the reconstructions of global sea level and temperature change through the past million years (22). The Bintanja data, 100-year increments, was simplified to 500-year increments by taking the 500-year average around each 500-year mark. The Hanebuth data (8) was simply spliced onto the Bintanja data at 20,500 years ago. To estimate the distribution and total area of dry land at each point in the time series, we directly linked the bathymetric data to the sea level change estimate for each point in the time series. The margin of error (roughly 10 m) will only affect our estimates of coastal forest distribution.

Paleoclimate Simulations for LGM. Mean monthly precipitation and temperature were simulated for current land area conditions and at the Last Glacial Maximum for the Sunda Shelf region using a global coupled atmosphere-ocean general circulation model (GCM) developed at the Geophysical Fluid Dynamics Laboratory in Princeton, NJ (14). The model simulates the global evolution of the atmosphere, ocean, and sea ice as well as their interactions at a spatial resolution of approximately 2° in latitude and 3.75° in longitude. This model was chosen because of its effectiveness at simulating tropical ENSO patterns currently dominating the Pacific Ocean and its ability to produce a paleo-ENSO that concurs with paleoclimate proxy data (11) and which is an important element in the climatic features of the region. To examine the range of variability in the model, we took the mean and 1 standard deviation (both plus and minus) of monthly precipitation from 75 years of simulated data. Simulated values were interpolated between the GCM grid points to create rasters for both precipitation and temperature with equal geographic resolution to the land area model. We therefore used 4 different climatic rasters: 1 for current conditions, 1 for the mean model, and 1 each for plus and minus 1 standard deviation of the model.

Modeling Forest-Type Distribution at the LGM. We defined 3 different major tropical forest types: evergreen, semievergreen, and seasonal forests, using relatively simple climatic definitions. Given the narrow latitudinal extent of our area of interest., temperature ranges always remained within general definitions of ''tropical,'' so forest type was defined based on precipitation. All points on the climatic rasters with at least 1,900-mm annual rainfall were classified as ''evergreen.'' This threshold for precipitation is substantially higher than early estimates by tropical biologists (6), so the distribution of evergreen forest climate in our model should be a conservative estimate. We chose this higher threshold because it more closely fit the historical palynological record at several points. Semievergreen conditions were defined as 1,100 to 1,900 mm of total annual rainfall, while seasonal to dry conditions were below 1,100 mm total annual rainfall.

Modeling Vegetation Types at the LGM. The current distribution of 3 major vegetation zones were modeled at the equator using strict topographic definitions: coastal [land area 0–10 m above sea level (asl)]; lowland (land area 10–450 m asl); and upland (1,000–2,200 m asl). This model does not include the transitional ''hill'' forests between 450–1,000 m asl. We chose to limit our analysis to lowland and upland areas as defined here to focus on distinct vegetation zones. To incorporate the response of vegetation zones to local temperature change, we calculated vegetation lapse rate using 4 values (83, 124, 166, and 207 m/ΔC°), based upon a review for the region (10). Because this vegetation response rate was estimated for forests at 1,000 m asl, the response of lowland forest was adjusted by 40%. The interpolated values for temperature change, relative to the equator, were used to model the amount of elevational change in vegetation zonation, based upon the 4 vegetation lapse rates. The estimated temperature change was then multiplied by the lapse rate and added to the absolute elevation of that location for each model condition. While the temperature difference between current and LGM conditions were similar to other model results, we examined 2 different levels of temperature change at the LGM: the decline in temperature at the equator produced by the mean model and 2 times this value (roughly −3 C°).

Incorporating Historical Evidence. The initial simulation model results obviously conflicted with some aspects of the historical record of climatic conditions during the Quaternary Period (17). The geographic resolution of the coupled atmosphere-ocean general circulation model is quite coarse and does not incorporate local topographic effects. So, to improve the model, we updated the historical record and reviewed our current state of knowledge (Fig. S1). After evaluating the evidence, anchor points were added at critical geographic locations to the climate simulations to enforce seasonally dry conditions found in the historical record of the Late Quaternary, the position of the seasonal/everwet climate boundary at the LGM in southern Kalimantan being particularly important in this respect (Fig. S1). These anchor points were then incorporated into the vegetation simulations to enforce local climatic effects. To examine the effect of a ''seasonal climate corridor'' across the Sunda Shelf during Quaternary glacials, 2 options were also incorporated into the model: a ''closed'' and an ''open'' corridor model. In the ''closed'' model, only well-supported historical evidence for seasonally dry conditions was used, which do not fulfill the requirements for a continuous corridor. In the ''open corridor'' model, 2 additional points were added to the anchor points to create a continuous corridor of seasonal/dry forest. Preliminary results indicated that the model results were particularly sensitive to the interaction between temperature change and vegetation response rates, so further dynamic modeling examined the minimal, median, and maximal results for each of the 2 estimates of temperature change at the LGM, given the different vegetation response rates. These 4 model conditions were as follows: **Max LERF** (GMC + 1sd, −83m VR, −1.4 C°, closed corridor), **Median-closed LERF** (GCMmean, −166m VR, −3 C°, and closed corridor), **Median-open LERF** (GCMmean, −166m VR, −3 C°, and open corridor), and **Min LERF** (GCM-1sd, −207m VR, −3 C°, and open corridor).

Dynamic Modeling of Historical Conditions. Using the current and LGM conditions as proxies for the extremes of climatic change through the Quaternary Period, we interpolated the distribution of major forest and vegetation types by creating a ''step raster'' for precipitation and temperature change separately by assuming a linear rate of change between extremes of sea level and temperature change. These step rasters were then used to extrapolate the spatial dynamics over the last glacial/interglacial cycle (LGC = 120,000 years ago until present) and the last million years by multiplying the change in sea level and temperature at each 500-year step in the historical record. The historical record for sea level change was taken directly from the combined Hanebuth-Bintanja record as described above, while temperature change was taken from the Bintanja record. Instead of taking direct measures from the Bintanja record, we simply constrained the extremes of temperature change to be within the simulated values from our GCM model of LGM conditions. This modulation of the temperature change record would preserve the timing of temperature changes but maintain them to be within those observed for the region. Because the geographic distribution of coastal forests were affected only by sea level change, this vegetation type was calculated simply as the land area within 10 m of reconstructed sea levels at each point in the time series.

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