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Cover image: Pictured is a Tasmanian devil (*Sarcophilus harrisii*), a carnivorous marsupial whose numbers are dwindling due to an infectious facial cancer called Devil Facial Tumor Disease. Webb Miller et al. sequenced the genome of devils from northwest and southeast Tasmania, spanning the range of this threatened species on the Australian island. The authors report that the sequences reveal a worrisome dearth of genetic diversity among devils, suggesting the need for genetically characterized stocks to help breed hardier devils that might be better equipped to fight diseases. See the article by Miller et al. on pages 12348–12353. Image courtesy of Stephan C. Schuster.

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Soils on exposed Sunda Shelf shaped biogeographic patterns in the equatorial forests of Southeast Asia

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The marked biogeographic difference between western (Malay Peninsula and Sumatra) and eastern (Borneo) Sundaland is surprising given the long time that these areas have formed a single landmass. A dispersal barrier in the form of a dry savanna corridor during glacial maxima has been proposed to explain this disparity. However, the short duration of these dry savanna conditions make it an unlikely sole cause for the biogeographic pattern. An additional explanation might be related to the coarse sandy soils of central Sundaland. To test these two nonexclusive hypotheses, we performed a floristic cluster analysis based on 111 tree inventories from Peninsular Malaysia, Sumatra, and Borneo. We then identified the indicator genera for clusters that crossed the central Sundaland biogeographic boundary and those that did not cross and tested whether drought and coarse-soil tolerance of the indicator genera differed between them. We found 11 terminal floristic clusters, 10 occurring in Borneo, 5 in Sumatra, and 3 in Peninsular Malaysia. Indicator taxa of clusters that occurred across Sundaland had significantly higher coarse-soil tolerance than did those from clusters that occurred east or west of central Sundaland. For drought tolerance, no such pattern was detected. These results strongly suggest that exposed sandy sea-bed soils acted as a dispersal barrier in central Sundaland. However, we could not confirm the presence of a savanna corridor. This finding makes it clear that proposed biogeographic explanations for plant and animal distributions within Sundaland, including possible migration routes for early humans, need to be reevaluated.

climate change | human migration | plant distribution | sea-level change

Together with the Amazon Basin, Congo Basin, and New Guinea, Southeast Asia's Sundaland forms one of the world's largest equatorial tropical forests (1). The present-day insular nature of this region is unrepresentative of the historical situation because most of the time the area formed a single landmass as a result of lowered sea levels associated with global cooling events (2–5). Despite this long history of land connections, there exists a marked biogeographic boundary between western (Malay Peninsula and Sumatra) and eastern (Borneo) Sundaland (3, 5, 6). These differences have been explained by a hypothesized north-south–oriented savanna corridor through the center of Sundaland that blocked dispersal of wet forest species (7–13). Although there is strong evidence for drier conditions within the region during the last glacial period (10, 12–15), the presence of a continuous north-south savanna corridor through the center of Sundaland remains controversial, and most coupled vegetation–climate reconstructions contradict this possibility (4, 16–20). Furthermore, the savanna-corridor hypothesis is based on the climatic conditions during glacial maxima when land area was maximal. This situation existed for only 17% of time during the last 250,000 y (2), making it unlikely that it is solely responsible for the observed biogeographic pattern in Sundaland.

Another explanation for the biogeographic boundary in central Sundaland relates to the soil conditions of the exposed sea floor (12). The current topsoil texture map of the region (21) shows that coarse-textured, often poorly drained soils are a common feature of the central part of the region (Fig. 1). These soils limit plant growth because they are extremely nutrient poor; they currently support peat swamp on poorly drained sites and heath forests on well-drained sites, both with a distinct species composition, generally low productivity, and poor diversity compared with the richer lowland forests on fine-textured, more nutrient-rich and better-drained soils (22). Sediments of the central Sunda Shelf sea bed also consist of these coarse-textured sands (12, 23, 24). Palynological data from east of Natuna Island (25) contain more common Poaceae pollen than any equatorial pollen sites do, suggesting that poorly drained areas of the Sunda Shelf were covered with extensive grass-dominated fresh-water swamps during periods of lowered sea levels. For most of the time, the connection between eastern and western Sundaland

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ECOLOGY

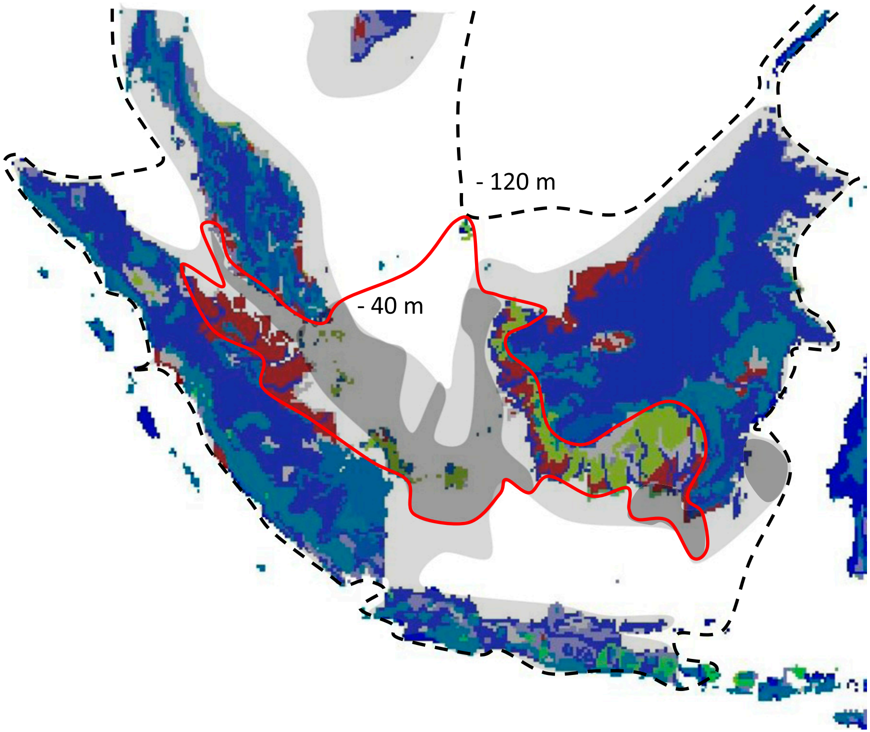

Fig. 1. Composite map of Sundaland. The green and red areas indicate currently exposed land areas with coarse sandy and/or badly drained soils. The light gray areas indicate the exposed sea bed at a sea-level lowering of 40 m, a situation that existed for more than 50% of the time during the last 250,000 y (2). The dark gray areas indicate the coarse sandy soils on this exposed seabed (12). The dashed black line indicates the maximum land area during the Last Glacial Maximum, when sea levels were lowered by ~120 m. The red line indicates the potential extent of the sandy soil dispersal barrier in central Sundaland.

ran through this coarse sandy exposed sea bed (Fig. 1) (2), which could have formed an enduring dispersal barrier to taxa ill adapted to these conditions.

Capitalizing on a unique database of 111 forest tree inventories from the region, we try to renew the discussion on the observed biogeographic differences between western and eastern Sundaland by testing both the climate and soil dispersal barrier hypotheses. Because a dispersal barrier based on soil properties assumes a different dispersal-limitation mechanism than one based on climate does, it should result in recognizable floristic signatures. A drier central Sundaland with a savanna corridor (hypothesis 1) should act as a filter blocking drought-intolerant tree species while letting drought-tolerant species pass, whereas a central Sundaland characterized by coarse-textured sandy soils (hypothesis 2) should block tree species adapted to fine-textured soils while letting taxa adapted to coarse soil pass. By looking at the drought and coarse-soil texture tolerance of the genera characteristic of floristic clusters that cross central Sundaland and those that are restricted to either side of it, we can thus gain insight into the processes that shaped the biogeographic patterns.

Results

The final floristic data set of 111 locations and 280 genera resulted in a dendrogram with 11 terminal clusters (Fig. S1), with 10 (5 unique) in Borneo, 5 (none unique) in Sumatra, and 3 (1 unique) in Peninsular Malaysia (Fig. 2). Five floristic clusters crossed the central Sundaland biogeographic barrier, and six were found either west or east of this boundary. For the floristic clusters that crossed the biogeographic boundary, we found 12 indicator genera versus 39 found for the clusters that did not cross (Dataset S1). The indicator genera of the crossing floristic clusters had a significantly higher coarse-soil tolerance than did the indicator genera of clusters that did not cross the biogeographic boundary [0.67 ± 0.15 versus 0.44 ± 0.18 (mean ± SD), for crossing and noncrossing indicator genera, respectively; F ratio = 16.9, P = 0.0002]. For drought tolerance, on the other hand, no significant difference was found [0.50 ± 0.16 versus 0.56 ± 0.21 (mean ± SD), for crossing and noncrossing indicator genera, respectively; F ratio = 1.0, P = 0.327].

Discussion

Soil Dispersal Barrier in Central Sundaland. Our results provide evidence that the exposed sea-bed soils may have played a role as dispersal barrier in central Sundaland. The special character and potential impact on plant species distributions of the currently submerged soils of central Sundaland have been noted before (4, 12) but have not yet been taken seriously as a dispersal barrier. A soil dispersal barrier also makes sense in a historical perspective because, unlike the hypothesized savanna corridor, the soil conditions would have been present in central Sundaland whenever sea levels dropped enough to expose the current shelf area. During the Pleistocene, this was the case for hundreds of thousands of years (2), more than enough time to cause a detectable biogeographic signal. Based on our reinterpretation of recent data (26), a likely vegetation type for the former soils of the submerged Sunda Shelf would have been heath forest on well-drained sandy soils, with kerapah peat swamps on poorly drained interfluves, and with herb-dominated swamp vegetation for areas that experienced some degree of climatic seasonality to the north, e.g., in the vicinity of Natuna. The region of the Java sea is more likely to have borne seasonal climate vegetation based on the palynological record from the southern part of the Makassar Straits, which shows the presence of widespread grass-dominated vegetation throughout the last glacial period (marine isotope stages 2–4, 16–74 ka) with extensive burning, as shown by charcoal records, from ~16 to 37 ka (27, 28). Heath forests and kerapah peats in the equatorial region between Sumatra and Borneo, herbaceous swamps in low-lying areas of the Natuna

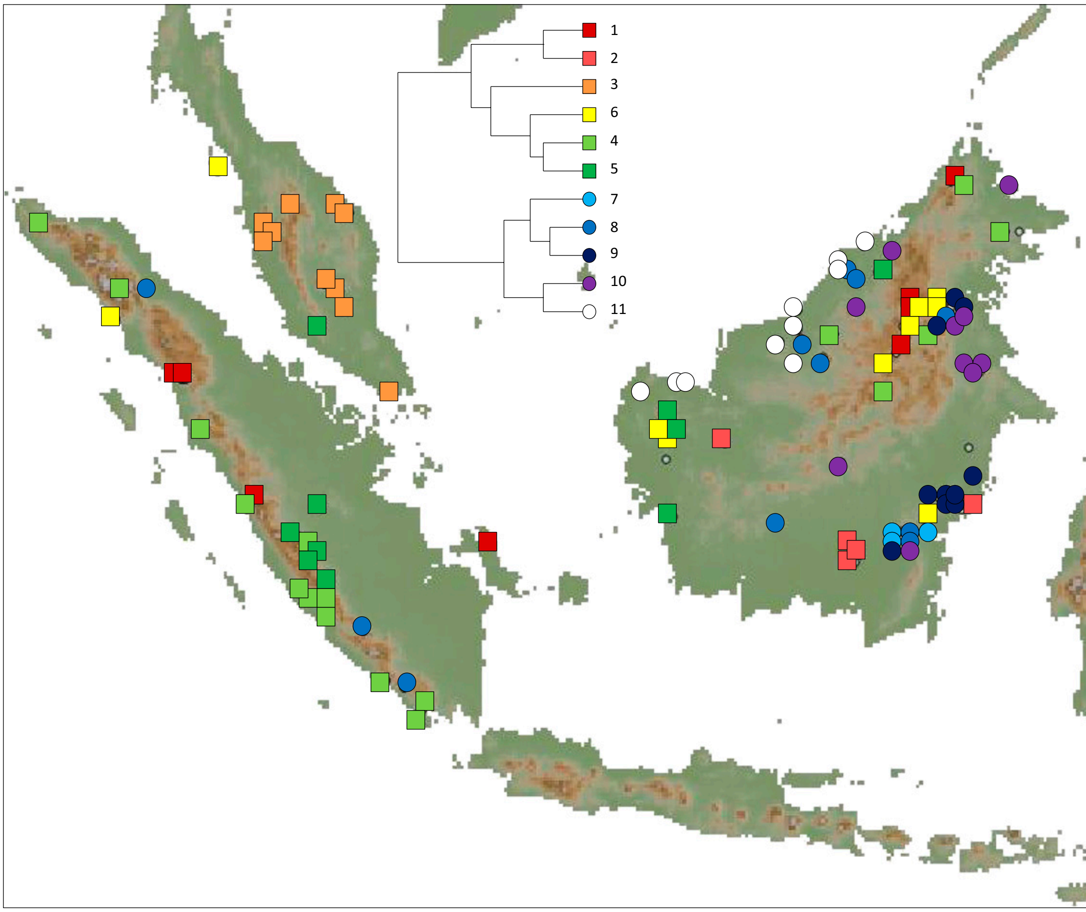

Fig. 2. Spatial distribution of the 111 forest inventory locations with their floristic affinities indicated by the color scheme in the dendrogram and the map.

region, and seasonal climate vegetation in the Java Sea area could have acted as a dispersal barrier for plants and animals not adapted to such soils or vegetation types. Indeed, current heath and swamp forests are characterized by a limited mix of tree species of the surrounding forests, resulting in much reduced diversity and productivity compared with lowland forests on fine-textured and richer soils (22, 29).

What About the Savanna-Corridor Hypothesis? On the other hand, our study provides no support for a continuous savanna corridor in central Sundaland, which is in accordance with most coupled vegetation–climate models (16–20), although the most recent historical vegetation reconstruction for this region (4) includes a savanna corridor in some models. However, this outcome could only be achieved by a priori forcing of a continuous corridor into these models (4). These outcomes do not mean that the savanna corridor did not exist because there is strong evidence for drier, savanna-like or seasonal conditions north and south of central Sundaland in the Pleistocene (10, 12–15, 30, 31). However, if it existed, it left no clear floristic evidence among current tree populations. One reason for this lack of evidence could be that the wetter climates that prevailed during interglacial periods have led to the disappearance of the drought-tolerant taxa from Borneo, Sumatra, and Peninsular Malaysia, thus erasing any floristic evidence for a savanna corridor in these areas. Another reason could be that, even if there was a continuous savanna corridor in central Sundaland, it probably occurred during conditions of maximum sea-level retreat. This situation existed for only short periods of time during the Pleistocene (2), making it unlikely that it is solely responsible for the observed biogeographic patterns in Sundaland.

Floristic Diversity Patterns in Sundaland. Another interesting outcome of our analysis is the high floristic diversity of Borneo compared with other Sundaland areas, with Borneo harboring 10 of the 11 identified floristic clusters (5 endemic), Sumatra 5 (none endemic), and Peninsular Malaysia only 3 (1 endemic). Even when Sumatra and Peninsular Malaysia are combined, they still only harbor 6 of the 11 identified floristic clusters, 5 of which are shared with Borneo. This pattern, which has recently also been demonstrated for bird species (6), probably largely reflects the longevity of everwet climate forests on Borneo (4, 28). Glacial–interglacial forest expansions and contractions seem to have had the most negative impact on lowland forests of Sumatra and Peninsular Malaysia because, compared with their present day potential extent, their size was small during glacial periods (3, 4). This small forest size might have resulted in the disappearance of some unique lowland floristic associations. Additionally, for parts of Sumatra and especially Peninsular Malaysia, considerably drier conditions existed during glacial periods (10, 12–15), which might have negatively affected their lowland everwet forest types. Borneo, on the other hand, has had a relatively stable everwet climate at its core and in most of the lowland coastal areas with the exception of the south and northeast, which might explain why it maintained so many unique lowland forest types (4, 12, 15, 28, 32).

Another possibility explaining the low floristic diversity of lowland forests on Sumatra could be related to the underrepresentation of eastern Sumatran locations, which might have affected our results because this area is one of the largest lowland forest regions within Sundaland. Unfortunately, it is also one of the most deforested areas within Sundaland, which means that getting inventory data from undisturbed forests of this region is almost impossible. Although older inventory studies probably exist, they are difficult to access because they are published in local reports. Therefore, Sumatra might eventually turn out to harbor more floristic diversity than is detected by our study.

Migration of Early Humans Through Sundaland. The presence of a savanna corridor in central Sundaland has been used as an argument for the rapid dispersal of early humans (between *ca.* 60,000 and 45,000 y ago) from mainland Southeast Asia and central Sundaland to Java and then onward to eastern Indonesia, Papua New Guinea, and Australia (12). However, the presence of swamps and heath forests in central Sundaland, as suggested by our study, would not favor this human-dispersal route because swamps and heath forests, aside from being hard to traverse, are generally low-productivity systems with limited wildlife and other edible products for hunter-gatherers (22). It would be more likely that humans used the coastal routes along Sundaland to reach Java and beyond (33, 34), especially because, during this period, large parts of central Sundaland would have been submerged by sea, leaving only a small land area in central Sundaland as a land connection (2).

Conservation Issues. Our study underlines the conservation importance of lowland forests because they contain floristic associations that are unique and among the most threatened in SoutheastAsia. In Borneo, only a fraction of the identified lowland forest types are protected (35). Moreover, they are mostly excluded from the Heart of Borneo program, which is especially focused on hill and montane forests. In Sumatra and Peninsular Malaysia, the ongoing loss of forest is critical (36, 37). In special need of conservation are kerapah swamps, which form one of the oldest plant communities in the region and can be followed back in time to the Oligocene. Throughout the region, there is considerable pressure to convert forests to oil palm, pulp, and other industrial plantations even though many deforested areas, especially in Sumatra, remain unused (38, 39). Additionally, existing lowland forest reserves, especially in Indonesia, provide no guarantee for good forest protection because remote-sensing studies have shown that serious forest degradation, fires, and even clearance are occurring within their boundaries (40, 41). Our results strongly underline the need to focus conservation priorities in Southeast Asia toward better protection of lowland forest systems before most of them have disappeared.

Methods

Floristic Analysis. We used tree inventory data for 111 locations across Sundaland (Fig. 2 and Dataset S2), which were centered on an underlying grid of $\sim$10 $\times$ 10 km that corresponded to our climate and soil layers (see below). Each of our locations thus represents the pooled trees from plots that fell within such grid cells. Most of these locations contained many morphospecies, making direct comparisons between locations based on species-level identifications impossible. Therefore, we based our floristic analysis on genera only, which not only improves the identification accuracy but has also been shown to reflect species-level floristic patterns well (42). For each location, we ranked genera from high to low abundance and selected the 30 most abundant genera for the floristic analysis because selection of a fixed number of genera makes floristic comparisons depend less on sample size. In cases where more than 30 genera were selected because of equal genus abundances, we randomly excluded genera from the lowest abundance class until we had selected 30 genera. In some cases, there were fewer than 30 genera present in a location. We decided to retain these locations because they usually represented low-diversity forest types such as heath, peat swamp, and montane forests. Overall, 30 genera represented between 54.8% and 100% of individuals from each inventory [77.7 $\pm$ 11.3% (mean $\pm$ SD)]. We used relative abundances of genera (number of individuals divided by total number of individuals in each inventory) to make the locations comparable. The final matrix, containing all locations and the relative abundances of their genera, was used in a cluster analysis (data were log 10-transformed to reduce impact of abundant genera) using minimal-variance clustering.

Indicator Genera Analysis. To determine the characteristic genera for each cluster in the floristic analysis, we used an indicator method (43). This method calculates an indicator value (IV) for each genus in predefined clusters (like the clusters identified by a floristic analysis). Only genera that have a high mean abundance and are present in the majority of locations of a cluster (and have low abundance and frequency outside of that cluster) will score a high IV. To test whether the observed IV of a genus in a cluster was significantly higher than could be expected based on a random distribution of individuals over the locations, the observed IV was compared with 999 randomly generated IVs. These random IVs were generated by a reallocation procedure in which the number of individuals per genus was randomly reshuffled over the locations (43). If the observed IV of a genus in a cluster fell within the top 5% of the random IVs (sorted in decreasing order), it was considered to deviate significantly from the random distribution. Indicator taxa were mapped on the dendrogram (Fig. S2).

Testing Indicator Taxa Drought and Coarse-Soil Tolerance. Drought and coarse-soil tolerance of genera were determined by sorting the 111 study locations by their annual rainfall (WorldClim, http://www.worldclim.org) and subsoil texture values taken from the Food and Agriculture Organization of the United Nations' *TERRASTAT: Global Land Resources GIS Models and Databases for Poverty and Food Insecurity Mapping* (21) (Fig. S3). Drought tolerance per genus was calculated as the abundance in the 50% driest sites divided by total abundance over all sites. Similarly, coarse-soil tolerance per genus was calculated as the abundance in the 50% coarsest soil sites divided by total abundance over all sites. Therefore, the higher the value (scaled between 0 and 1), the more tolerant a genus is to drought or coarse soil (the whole list is in Dataset S1). We then tested (one-way ANOVA) whether the means of the drought and coarse-soil tolerance values of the indicator taxa differed significantly between floristic clusters that crossed the dispersal barrier versus those that did not cross. Some indicator taxa occurred in several clusters. In those cases, we used only the data (cross or not cross central Sundaland) from the cluster where it scored its highest IV.

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