Journal of Tropical Ecology

www.cambridge.org/tro

Research Article

Cite this article: Anirudh NB, van Veen FJF, Ripoll-Capilla B, Buckley BJW, Erb WM, Niun MA, Maimunah S, Makur KP, Armadiyanto, Estrada E, Boyd NS, Cheyne SM, Santiano, Namaskari N, Husson SJ, Randi A, Seaman DJI, Deere NJ, Supriatna J, Struebig MJ, and Harrison ME (2025). Lowland heath forests of Indonesian Borneo: ecological value and conservation challenges. *Journal of Tropical Ecology*. **41**(e19), 1–11. doi: https://doi.org/10.1017/S0266467425100084

Received: 28 October 2024
Revised: 19 May 2025
Accepted: 22 May 2025

Keywords:
Kerangas; Kalimantan; tropical forest; edaphic; flora; Southeast Asia; Sundaland; ecoregion

Corresponding authors: Namrata B. Anirudh, Mark E. Harrison;
Email: namrata.b.anirudh@gmail.com; m.e.harrison@exeter.ac.uk;

Lowland heath forests of Indonesian Borneo: ecological value and conservation challenges

Namrata Biligeri Anirudh[1], Frank J.F. van Veen[2], Bernat Ripoll-Capilla[3], Benjamin J.W. Buckley[4], Wendy M. Erb[5], Mariaty A. Niun[6], Siti Maimunah[7], Kristana Parinters Makur[8], Armadiyanto[8], Erik Estrada[8], Nicholas S. Boyd[4], Susan M. Cheyne[3,4], Santiano[8], Nityasa Namaskari[8], Simon J. Husson[3], Agusti Randi[9], Dave J.I. Seaman[10], Nicolas J. Deere[10], Jatna Supriatna[1], Matthew J. Struebig[10] and Mark E. Harrison[2,3,11]

[1]Faculty of Mathematics and Natural Sciences, Department of Biology, Universitas Indonesia, Depok, Indonesia; [2]Centre for Geography and Environmental Science, University of Exeter, Penryn, UK; [3]Borneo Nature Foundation International, Penryn, UK; [4]School of Humanities and Social Sciences, Oxford Brookes University, Oxford, UK; [5]K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Cornell University, Ithaca, USA; [6]Faculty of Agriculture and Forestry, Universitas Muhammadiyah Palangka Raya, Palangka Raya, Indonesia; [7]Faculty of Forestry, Instiper Yogyakarta, Yogyakarta, Indonesia; [8]Yayasan Borneo Nature Indonesia, Palangka Raya, Indonesia; [9]Nusantara Climate Initiatives, Jakarta, Indonesia; [10]Durrell Institute of Conservation and Ecology, University of Kent, Canterbury, UK and [11]School of Geography, Geology and the Environment, University of Leicester, Leicester, UK

Abstract

Heath forests, or known locally as kerangas, in Indonesia and Malaysia form a distinct and understudied ecoregion. We document the distribution and ecological significance of the largest extent of kerangas in Kalimantan, Indonesian Borneo. We mapped 16,586 km^2 of kerangas to the nearest one square kilometre across Kalimantan, showing a significant reduction from previous estimates. About 19% of this area exists as a poorly documented mosaic landscape in Central Kalimantan's Rungan-Kahayan region. Here, peat-based forests transition to heath and dipterocarp forests, making it difficult to reliably classify these forests for conservation planning. Using remote sensing and tree plot data, we identified three forest types—kerangas, low pole, and mixed swamp. Vegetation structure is influenced by soil, topography, and hydrology, while peat depth and elevation affect species diversity. Our findings indicate that these forests are dynamic ecosystems with diverse vegetation communities adapted to peat as well as sandy soils. Lowland heath forests in Rungan-Kahayan exhibits higher tree densities compared to other Bornean heath forests, reflecting unique ecological adaptations to challenging environments. Despite covering just 3% of Kalimantan's forest area, these ecosystems remain largely unprotected, facing threats from land conversion and fire. Our study highlights the ecological complexity of kerangas and underscores the urgent need for targeted conservation and further research on these forests.

Introduction

Habitats shaped by distinctive geological and extreme edaphic conditions are biodiversity hotspots that support highly specialised and often threatened species adapted to harsh, nutrient-poor soils (Hulshof and Spasojevic 2020). Soil properties play a crucial role in driving plant species composition, with complex geologies contributing to global biodiversity (Myers *et al.* 2000). Examples such as the limestone grasslands of Europe (Köhler *et al.* 2005), the white sand soils of Guyana (Fine and Baraloto 2016), and ultramafic and karst ecosystems in tropical regions (Garnica-Díaz *et al.* 2023; Geekiyanage *et al.* 2019) highlight how soil composition fosters habitat specialisation and endemism. While environmental heterogeneity is central to structuring these ecosystems (Trethowan *et al.* 2024), the mechanisms underlying plant diversity and adaptation in such soils remain poorly understood, especially in certain regions of the tropics. Despite their global distribution, these habitats are often overlooked in macroecological studies, which tend to prioritise climatic gradients over geodiversity (Gaston and Blackburn 2000). Heathlands in Southeast Asia are one such habitat that highlights the ecological significance of these underappreciated systems.

Heathlands are characterised by perennial sclerophyllic plants thriving on highly acidic and nutrient-poor sandy soils and represent some of the most diverse ecosystems globally (Adeleye *et al.* 2021; Proctor *et al.* 1983a). This unique combination of soil properties supports high levels of local endemism and species turnover along environmental gradients (Keith *et al.* 2014).

CAMBRIDGE
UNIVERSITY PRESS

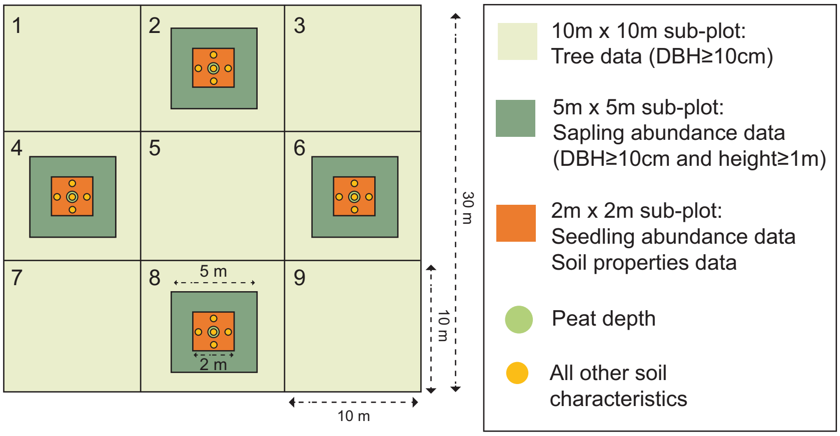

Figure 1. Vegetation plot structure and sampling methodology to record biotic and abiotic data.

Heathlands are particularly extensive in tropical regions, where they often form transitional habitats from flooded river basins to drier forests, notably in the lowlands of Brazil, Colombia, Peru, and Venezuela (Coomes and Grubb 1996), parts of the Guyanas (Adeney *et al.* 2016), and coastal West Africa (Proctor 1999). The origin of these ecosystems dates to the Pleistocene, arising from sediment aggradation during periods of lower sea levels and drier climates (Thorp *et al.* 1990), and influenced by subsequent climatic variations and indigenous land-use practices (Adeleye *et al.* 2021; McWethy *et al.* 2017).

Heathlands in the Sundaland biodiversity hotspot of western Indonesia and Malaysia form a distinct and poorly documented ecoregion known locally as '*kerangas*' (Dinerstein et al. 2017). These habitats exhibit a distinctive coexistence of typical heathland vegetation dominated by shrubs and trees (Davies *et al.* 2004), forming unique forest formations (Sprecht and Womersley 1980). The lowland kerangas forests of Borneo are particularly notable, sharing characteristics with high elevation or coastal heath forests, but differing markedly in their habitat structure (Ikbal *et al.* 2023). These forests exhibit substantial variation in hydrology (De Graaf *et al.* 2009) and can comprise tall, closed canopies, stunted, dry savannah-like open canopies or wet kerangas conditions (Kartawinata 1980; MacKinnon 1996). Central Kalimantan in Indonesia hosts the most extensive kerangas habitats, often appearing as patches within mixed dipterocarp forests or as stunted lower montane forests (Ashton 2014). Heterogeneous formations and the lack of a clear definition owing to several variations of this habitat type have made it challenging to document kerangas forests accurately both ecologically and geographically. Attempts to classify kerangas have been based on varying soil properties (Langner *et al.* 2015; Saxon and Sheppard 2010). Early assessments (Brünig 1974; MacKinnon 1996) are based on gross estimations limited by technology and remote sensing information, potentially misrepresenting them as dipterocarp forests, swamps, or degraded areas.

Despite extensive studies on the floristic and soil characteristics of kerangas elsewhere in Borneo (Brünig 1974, Din *et al.* 2015, Newbery and Proctor 1984, Riswan and Kartawinata 1991), documentation of the various formations in Kalimantan remains limited. This lack of focus results in a significant knowledge gap compared to more humid ecosystems like peatlands and dipterocarp forests. Redundant or inaccurate classification and estimation of kerangas, compounded by significant land use change in Indonesia (Gaveau *et al.* 2014), further complicates reliable mapping and effective spatial planning. The ecological value and importance of kerangas forests hence remain relatively unacknowledged, and as a result, there is insufficient representation within protected areas or conservation management more broadly (Giesen *et al.* 2018; Trethowan *et al.* 2024).

Kerangas ecosystems face considerable threats from deforestation, land conversion, invasive plants, and recurrent fires, exacerbated by hydrological changes and increased nitrogen and sulphur deposition (Jambul *et al.* 2020; Tuah *et al.* 2020). These factors make kerangas particularly vulnerable, leading to potential transformations into open savannahs with sparse shrub and grass cover (Din *et al.* 2015). Such changes result in severe biodiversity loss, threatening specialist organisms and complex ecological interactions (De Graaf *et al.* 2009). The ongoing fragmentation heightens edge effects and the influence of surrounding land cover types (Piessens *et al.* 2006). Given the long recovery time for these forests and past challenges in re-establishing native vegetation (Riswan 1982), prioritising research and conservation strategies is crucial.

Here we revise the current distribution of kerangas across Kalimantan by spatially reassigning and reclassifying kerangas from available maps and spatial layers. We then focus on the kerangas-mosaic landscape in Central Kalimantan, using vegetation plot data to highlight the biotic and abiotic characteristics that differentiate between habitat types in the mosaic. Emphasising floristic composition and sub-habitat differences, our goal is to establish baseline information to facilitate further research and inform conservation strategies for this critical habitat type in Indonesia.

Study area

Our vegetation study was focused on the Mungku Baru Education and Research Forest (MBERF), in Central Kalimantan, spanning ~ 50 km^2 of forest area managed by a local university (*Universitas Muhammadiyah Palangkaraya*). MBERF lies within the Rungan-Kahayan River catchment area, north of the provincial capital, Palangka Raya (Figure 1). The landscape encompasses 4,729 km^2, comprising largely forests without strict protection status, small forest areas under the social forestry scheme of Indonesia, and peat swamps under the Peatlands Moratorium. The landscape ranges between 30 and 85 m above sea level and is represented by peat swamps in the south to lowland mixed dipterocarp forests to the north. MBERF lies in the northern part of this landscape and features relatively undisturbed mosaic kerangas and swamp habitats, bordered by oil palm plantations, logging concessions, and artisanal gold mines. The site is watered by blackwater tributaries of the Rakumpit River. During the study (2016–2020), the region received rainfall ranging from 48 to 556 mm (BPS, 2024).

Methods

Mapping kerangas across Indonesian Borneo

Previous estimates of the heath forest extent on Borneo are > 20 years old, and significant land-cover changes have occurred since (Sari *et al.* 2023; Stibig *et al.* 2014). Hence, we conducted spatial analysis using current and available forest cover and soil layers to provide an updated representation of the heath forest distribution across Indonesian Borneo. Additionally, we examined the representation of kerangas in protected areas by overlaying maps from the World Conservation Monitoring Centre with the forest cover data from Indonesia's Ministry of Environment and Forestry (see Supplementary Table 1).

Mapping habitat types in the Rungan-Kahayan landscape

To create Land Cover and Habitat Classification maps for the Rungan-Kahayan landscape, we used cloud-free Landsat 8 OLI/TIRS imagery (July 2017) and ran the 'Habitat-Types' model via the semi-automatic classification QGIS plugin (Congedo 2021). A 654-band composite was produced with pre-processing atmospheric correction and pan-sharpening for the following pre-defined categories: stunted kerangas on white soil, kerangas on black soil, low pole, mixed swamp/riverine, secondary disturbed, scrub/grassland, clearing/forest gap, and bare soil/sand. To enhance thematic clarity in the post-classification process and reduce speckle noise, we applied a minimum patch threshold of 6, which was determined through iterative model testing and accuracy assessments. This helped remove isolated misclassified pixels and eliminate noise and minor features, ensuring that only ecologically relevant habitat patches were maintained, consistent with best practices for minimum mapping units (Jensen 2005). The threshold ensured that only habitat patches with a minimum contiguous area or pixel density above this value were retained. Additionally, a four-neighbour connectivity rule was applied to ensure accurate grouping of adjacent pixels, avoiding the merging of distinct habitat patches that are spatially adjacent but not functionally connected. This is a more conservative approach, particularly important in mapping heterogeneous landscapes (Turner *et al.* 2015).

We gathered habitat data from 1,064 ground-verification points along line transects spaced ~ 100 m apart, covering different habitat types and transitions. At each point, we recorded habitat type (adapted for a kernagas mosaic from habitat differentiation in peatlands by Page *et al.* (1999)), canopy height, canopy cover, soil type, topography, hydrology, and undergrowth within a 5-m radius (see Supplementary Table 2 for variable categorisation). Ground-truth validated habitats were rasterised to obtain pixel values. Finally, we performed a post-processing accuracy assessment by running a confusion matrix to validate the spatial layer against the ground-truth data (Rwanga and Ndambuki 2017).

Constructing vegetation plots

Between 2016 and 2020, we established 56 vegetation plots in MBERF using a stratified random sampling design. Plot locations were concentrated in the southwest region of MBERF due to inaccessibility to other parts and good representation of habitat types mapped in our initial habitat mapping (see Supplementary Table 5). Plots were 30 ×30 m in size and contained nested subplots (Figure 1). Trees ≥ 10 cm diameter at breast height (DBH = 1.3 m above the ground) were identified, measured, and tagged, and maximum tree height was recorded using a clinometer in all 10 × 10 m subplots. Within four 5 × 5 m subplots, we recorded the abundance of tree saplings (trees <10 cm DBH, ≥ 1 m height), orchids, lianas, pitcher plants, pandans, and palms, as well as the percentage cover of tussocks, ferns, grass, and other ground vegetation. For seedling abundance and soil properties, we created nested plots of 2 × 2 m to measure soil properties such as peat depth (cm), soil moisture (%), soil pH, and slope. For a detailed description of equipment and methods used for soil sampling, see Supplementary Table 3.

Data analysis

For all analyses below, we consider three main habitat types based on our habitat analysis. We combine black and white soil kerangas and refer to it as 'kerangas,' aggregate stream edge and swamp habitats as 'mixed swamp,' and retain low pole forest.

Tree species were identified in the local language (*Bahasa Dayak Ngaju*) and simultaneously assigned their corresponding Latin names by a field botanist. The compiled species list was subsequently validated by a senior botanist and cross-checked against the rWCVP package (Brown *et al.* 2023), ensuring accuracy of the species' binomial names.

Stem density (richness)

To reliably compare between habitat subtypes in the broad-scale habitat classification, we standardised the number of species per square kilometre using the formula

$$\textit{Stem density per species} = (S_{ij}/\sum S_j)/\mathrm{km}^2$$

$$\textit{Total stem density/habitat} = \sum S_j/\mathrm{km}^2$$

where S_{ij} is the number of stems of species i in habitat j and S_j is the total number of species in habitat j.

Cluster analysis and ordination

To evaluate the variation in tree species composition between the three habitat types, we conducted a cluster analysis. We calculated pairwise Bray-Curtis dissimilarity coefficients (ranging from 0 to 1, with higher values indicating greater dissimilarity) to capture differences in plant community composition across plots within and between habitat types. A dendrogram was constructed to visualise the dissimilarity matrix, arranging plots based on their similarity in tree species composition. To determine whether dissimilarity in tree species composition was greater between different habitats than within them, we conducted an Analysis of Similarity (ANOSIM) test (Clarke and Green 1988) on the community data using the 'vegan' package in R (Oksanen *et al.* 2024).

To test which habitat predictors best explain species composition between habitat types, we conducted nonmetric multidimensional scaling (NMDS) on tree species as a function of peat depth, elevation, soil moisture, soil pH, and biomass. Aboveground biomass was calculated using DBH and tree height for each plot in the study area using the 'BIOMASS' package in R (Réjou-Méchain *et al.* 2017).

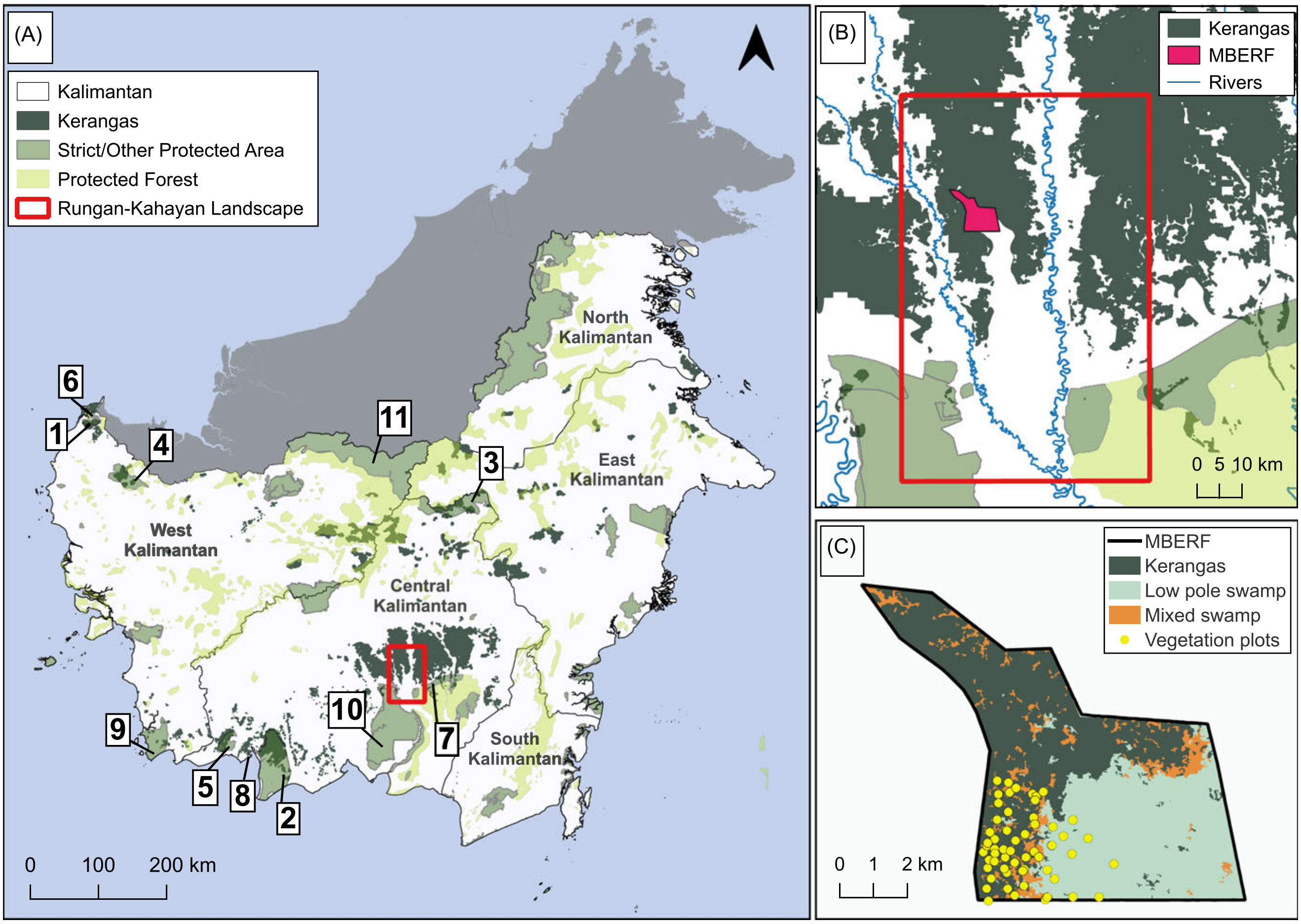

Figure 2. A. Distribution of kerangas in Kalimantan, Indonesia, based on available spatial data. Numbers 1–11 correspond to the list of protected areas in Supplementary Table 4. **B.** Distribution of kerangas within and surrounding the Rungan-Kahayan landscape in Central Kalimantan. **C.** Study site (MBERF) indicating habitat mosaic with kerangas cover.

Diversity

Tree species diversity for habitat type was calculated using the iNEXT package in R (Chao *et al.* 2014) for all tree species ≥ 10 cm DBH. We calculated diversity using sample-based extrapolation with diversity orders q1, q2, and q3, representing Hill numbers, and 100 bootstraps. We used 84% confidence intervals (MacGregor-Fors and Payton 2013), as they offer practical advantages for ecological inference. Specifically, when comparing group means, non-overlapping 84% CIs approximate a statistical significance level of $p < 0.05$, making them more intuitive for visual assessment of meaningful differences. Data were extrapolated to a common sample size of 100 plots in each comparison.

Structural differences

Multinomial logistic regression was performed using the ‘multinom’ function from the ‘nnet’ package in R (Venables and Ripley 2002) to analyse the relationship between tree height and DBH (independent variable) with the three main habitat types (dependent variables). Basal area was excluded from the model after testing for collinearity.

All spatial analyses were performed using QGIS v3.6, and quantitative analyses were conducted in Rv3.3.

Results

Mapping kerangas across Indonesian Borneo

We identified that kerangas forests cover approximately 16,586 km² across Indonesian Borneo. Kalimantan has 35,849 km² of strictly protected forests in national parks and wildlife reserves (IUCN categories Ia, Ib, and II) and 82,396 km² of other protected areas (IUCN categories III–VI), of which heath forests constitute only 2.4% and 21.9%, respectively. Overall, only 3.7% of kerangas across Kalimantan are within strict protection zones (Figure 2). The largest extent is in the Central Kalimantan province, comprising 76.8% of Indonesian Borneo’s heath forests, albeit fragmented amongst six protected areas (Figure 2; Supplementary Table 4).

Mapping habitat types in the Rungan-Kahayan landscape

The habitat model accuracy assessment confirmed that habitat classification from satellite imagery was moderately reliable across the landscape (**K** = 0.5). The classification performed well compared to randomly assigning values, although the low kappa value may affect confidence in spatial conclusions, especially for certain habitat types (see Supplementary Table 5 for percentage cover and accuracy achieved for each classified habitat type).

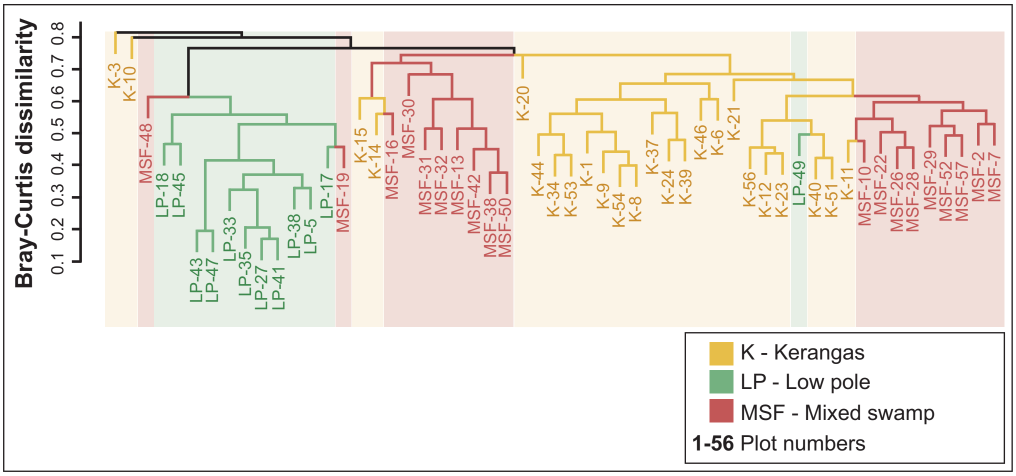

Figure 3. Dendrogram showing clusters of tree species based on the Bray-Curtis dissimilarity index between three main habitat classifications.

The model discriminated nine habitat types with an overall classification accuracy of 82% and a producer's accuracy for kerangas (82%), low pole swamp (73%), and mixed swamps (48%). This allowed us to assign the percentage coverage of each habitat type across the landscape and within our study area. The most dominant habitat types in both our study site and the larger landscape were kerangas (33.9% in MBERF and 25.7% in the landscape).

Vegetation plots

We recorded 3,950 trees across 56 vegetation plots, representing 176 distinct taxa (Figure 2). Only trees identified to at least the genus and/or species level were included in the analysis ($N = 102$); unidentified individuals were excluded. Where multiple individuals within the same genus showed clear morphological differences but could not be confidently assigned to a specific species, they were treated as distinct species-level taxa for the purposes of analysis. Based on the abiotic and biotic data obtained from the forest plots, we were able to strengthen habitat differentiation through spatial analyses and confirm distinguishable features of the main habitat types. The presence and distribution of these habitats are determined by soil characteristics, hydrological regimes, and surface topography, as reported below. They represent a forest continuum with variations, gradients, and transitional habitats. For a detailed description of each of the main dominant habitat subtypes, refer to Supplementary Text 1.

Stem density

Apart from certain genera that are exclusive to or highly dominant to certain habitat types, such as *Gymnostoma*, *Agathis*, *Endospermum*, and *Gluta* in kerangas, *Combretocarups* and *Dactylocladus* in low pole, and *Cratoxylum*, *Tetractomia*, *Litsea*, and *Nephelium* in mixed swamp habitats, most species were common taxa across all habitat types, although differing in their relative stem densities. However, the most common taxa across the study site, found in every habitat type, were Myrtaceae (*Syzygium* sp.), Calophyllaceae (*Calophyllum hosei*), and *Dipterocarpus borneensis*. (See Supplementary Table 6 for a list of species with stem densities per habitat.)

Cluster analysis and ordination

Cluster analysis using ANOSIM tests revealed that tree species dissimilarity was significantly greater between the three habitat classes than within them ($R = 0.44, p < 0.05$). This suggests that the three habitat types exhibit clear differences in tree species composition, despite constituting a mosaic of interspersed habitats (Figure 3).

The NMDS analysis in two dimensions yielded a stress value of 0.22, indicating a moderate fit for the data (Figure 4). The ordination revealed key environmental gradients that correlated with tree community structure in the forest mosaic. Peat depth had the most influence on community composition, followed by elevation and biomass. Specifically, average peat depth correlated with tree species in low pole and mixed swamp, indicating these two habitats have a deeper peat layer relative to kerangas. Conversely, more elevated (~ 60 m asl) areas support species typical of kerangas habitat (see Supplementary Text 1). Soil pH influenced species composition in mixed swamps the most, where plots in this habitat type were characterised by higher pH values. This is given by a significant negative correlation between peat depth and soil pH ($r = -0.33; p = 0.01$). As expected, the effect of average peat depth on differentiating habitat types based on species composition was opposite to that of elevation.

Diversity

The extrapolated asymptotic diversity profile indicates that there is distinct separation in tree species richness between habitat types, given by the absence of any overlap of the 84% confidence intervals for each habitat (Figure 5). Overall, mixed swamp has the highest diversity across all q-values, suggesting a more even distribution of species within the habitat. Low pole habitat has a remarkably lower diversity of tree species compared to the other two habitats, indicating dominance of certain species. These results strengthen our cluster analysis and categorisation of habitats into three main habitat types in the mosaic.

Structural differences

Multinomial logistic regression indicated significant trends between the three main habitat types (Figure 6). For a one-unit increase in DBH, the odds of a tree in a low pole and mixed swamp decrease by 4.1%. That is, larger girth trees are significantly more

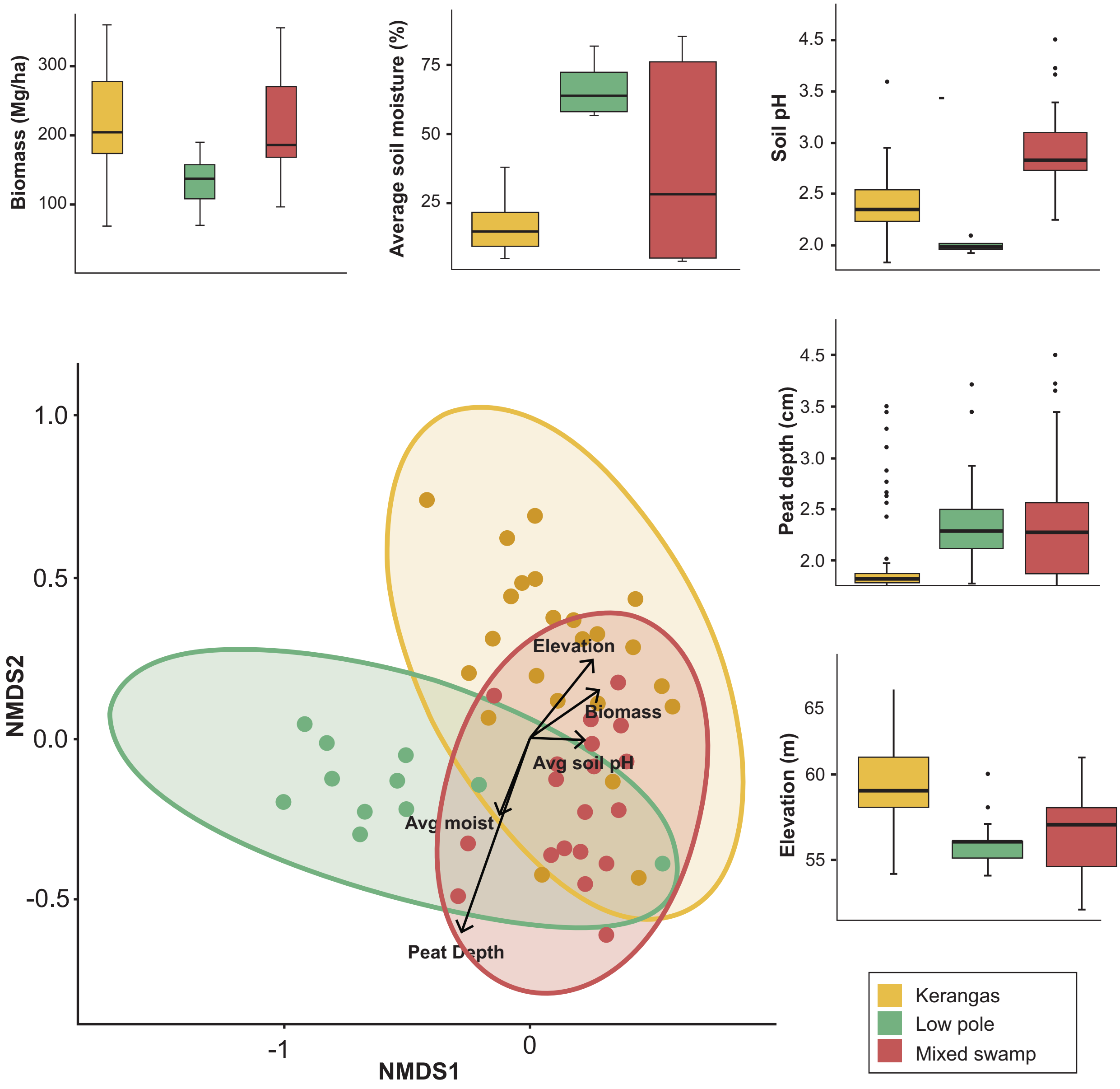

Figure 4. A. Nonmetric multidimensional scaling (NMDS) of tree species in each habitat type. The vectors (arrows) indicate the habitat predictors influencing tree species diversity. The length and angle of the vectors indicate the strength and direction of effect on the three habitat types. Box plots indicating the mean, standard deviation, and outliers for biomass, soil moisture, soil pH, peat depth, and elevation across each habitat type.

likely to be in kerangas, followed by mixed swamp, and less likely to be in low pole habitat (DBH: Kerangas > mixed swamp > low pole).

With respect to tree height, the odds of taller trees in low pole decrease by 4.4% compared to those in kerangas. However, comparing mixed swamp to kerangas, taller trees are 2.1% more likely to be present in mixed swamp as compared to kerangas (tree height: Mixed swamp > kerangas > low pole).

Discussion

Our updated estimate of kerangas forest coverage in Kalimantan, of ~ 16,586 km^2, is significantly lower than previous estimates of 24,750 km^2 (MacKinnon 1996). This suggests a reduction in kerangas forest cover over the past two decades, though historical inconsistencies in differentiating kerangas from other forest types—such as lowland dipterocarp or peat-swamp forests—may explain the higher estimates in the past. Nevertheless, the extensive distribution of kerangas forests within Kalimantan highlights their potential importance for biodiversity conservation.

Through our analysis of remote sensing and tree plot data, we identified a complex and extensive habitat mosaic within Central Kalimantan's lowland heath forests, whereby flooding is mediated by major rivers and topography, resulting in a mosaic of low pole swamp and kerangas forests, interspersed with mixed swamps. Rather than being seen as a homogeneous forest ecosystem, these heath forests are in fact highly transitional, comprising a mix of plant communities on peat and sandy soils.

Our findings suggest that the kerangas-dominated landscape consists of multiple habitats influenced by variations in soil, water, and topography. The mixed swamp habitats share species with habitats in proximity, reflecting a pattern similar to Amazonian

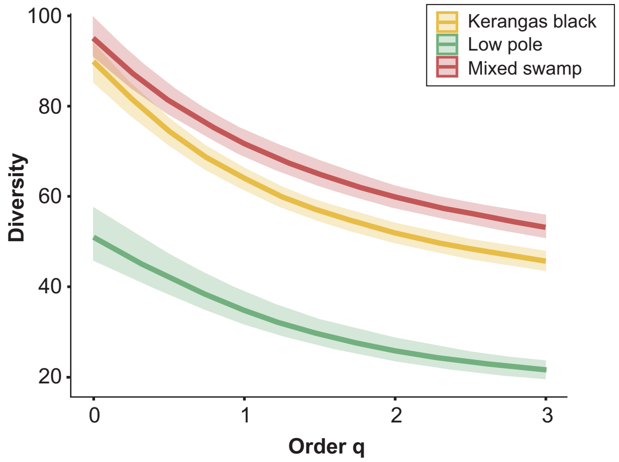

Figure 5. Diversity of three different habitat assemblages as a function of the diversity order (q), where q1, q2, and q3 represent Hill numbers, shaded areas denote 84% CI. The table presents the values of diversity and evenness of each habitat type.

freshwater swamps, where many species inhabit neighbouring well-drained areas (Draper *et al.* 2018, 2019; Pitman *et al.* 2014). The observed habitat infidelity suggests a neutrality in species distribution, with minimal dispersal limitations and relatively uniform conditions across adjacent habitats (Cannon and Leighton 2004).

In Borneo's heath forests, large-scale variations in floral composition are often determined by topography, particularly in relation to hill leaching gradients (Austin *et al.* 1972). Topographic variables such as elevation and slope affect tree species diversity (Miyamoto *et al.* 2003; Sellan *et al.* 2019). This is particularly important for kerangas forests in the lowlands, where sandy soils exacerbate moisture variability due to poor water retention (O'Brien and Escudero 2022). In Rungan-Kahayan, kerangas forests dominate the higher elevations, implying drier soils due to low water retention and increased runoff. However, contrary to findings in heath forests in Malaysian Borneo (Jucker *et al.* 2018), peat depth was found to be more influential than topography in lowland Central Kalimantan. This difference may be attributed to the higher elevations typical of heath forest formation in Malaysian Borneo, where elevations may range from 50 to 150 m.a.s.l. (Jucker *et al.* 2018), which are more representative of hill kerangas

Tree densities in the Rungan-Kahayan kerangas forests were slightly higher than other Bornean heath forests, with 746 stems/ha compared to 602 stems/ha in East Kalimantan (Riswan 1982) and 708 stems/ha in Sarawak (Proctor *et al.* 1983). While the floristic composition varies across different heath forests, families like Myrtaceae, Clusiaceae, and Rubiaceae are common (Davies and Becker 1996; Ikbal *et al.* 2023), with Myrtaceae present across all Rungan-Kahayan habitat types. Dipterocarps, though less prevalent in heath forests generally, dominate the canopy in Rungan-Kahayan alongside species from Calophyllaceae. Other species typical of waterlogged peat forests, like *Gonystylus bancanus* and *Xanthophyllum falvescens*, were largely absent, while species from hill kerangas and dipterocarp forests, such as *Santiria laevigata* and *Garcinia beccarii*, are present. Certain species adapted to low-pH soils, like *Dryobalanops rappa* and *Kayea calophylloides*, were restricted to kerangas habitats (Newbery and Proctor 1984).

Although the elevation gradient in our study site was minimal compared to hill kerangas sites in Borneo (Ikbal *et al.* 2023), the variation in canopy height and biomass between kerangas and mixed swamp habitats reflects different strategies for biomass accumulation. Kerangas forests, with their variable height profiles and larger tree girths, contrast with the taller but smaller-girthed trees in mixed swamps. This is atypical and is contrasting with other studies that have evaluated stand structure (Nishimura and Suzuki 2001). This difference could potentially be driven by adaptations to nutrient availability and water conditions, where trees in kerangas are slow growing, heavy wood trees (Ashton, 2014), which invest in larger girths to store energy and enhance nutrient uptake, while swamp species grow taller due to abundant nutrients and hydrological stability (Zhang *et al.* 2016) relative to kerangas. Additional factors, such as the need for structural support in drier habitats (Peguero-Pina *et al.* 2020) and competition for light in dense swamps (Nishimura and Suzuki 2001), also influence these morphological differences.

Soil acidity is a key factor in shaping the structure of heath forests (De Graaf *et al.* 2009; Proctor 1999). The kerangas in our study area had lower pH values compared to other sites, which range from 3.8 to 4.1 (Jaafar *et al.* 2016; Sellan *et al.* 2019; Vernimmen *et al.* 2013). Acidic, well-drained soils with low organic content support distinct tree families, for example, drought-tolerant Dipterocarpaceae species dominant in hill kerangas (Wong and Kamariah, 1999). This is consistent with our findings of abundant dipterocarps in Rungan-Kahayan kerangas habitats.

In contrast, the higher peat depth and lower pH in the low pole explain the similarities in tree species composition to kerangas habitats. Genera like *Calophyllum*, *Shorea*, and *Syzygium* had lower

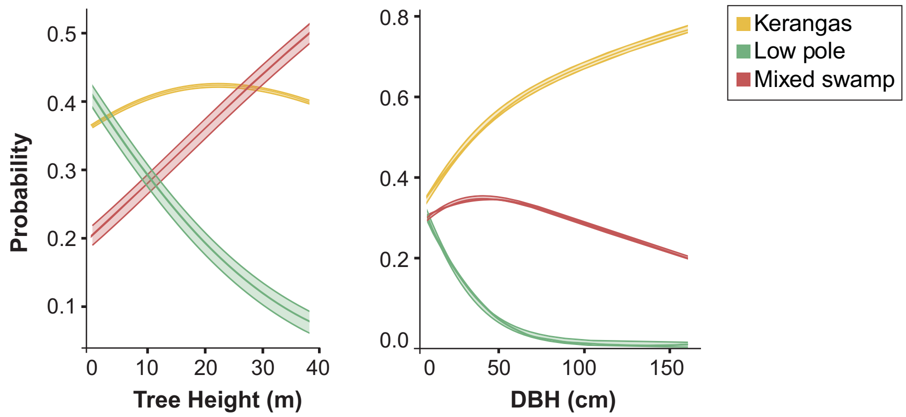

Figure 6. Predicted probabilities plotted against DBH, tree height, and peat depth for three habitat types.

canopy heights and girths in low pole, with DBH not significantly different across habitats for trees ≥ 10 cm DBH, in line with other studies in Borneo (Paoli 2004; Sukri *et al.* 2012). Furthermore, the abundance of tropical conifers such as *Agathis borneensis* and *Gymnostoma nobile*, particularly in kerangas and low pole habitats, has nitrogen-fixing actinomycetes in their root nodules, and the presence of carnivorous plants (*Nepenthes* spp.) indicates adaptations to low-nitrogen and nutrient-deficient soils (Wong *et al.* 2015).

Hydrology plays a major role in forest composition especially in wet habitats (Rodríguez-González *et al.* 2010). Waterlogged forests, forming on shallow organic soils, are rare in Borneo and resemble heath forests in their acidity but have lower nutrients and organic matter (Jaafar *et al.* 2016). The low pole habitat in our study site aligns with descriptions of '*kerapahs*', a type of heath forest found in Borneo (Din *et al.* 2015; Nafiah *et al.* 2022); though our site lacked an abundance of typical kerapah species like *Dacrydium*, these species have been reported in adjacent forest areas in the region (Maimunah *et al.* 2021, 2022). Instead, genera like *Calophyllum* and *Combretocarpus* dominated, suggesting that these low pole forests may be younger peat formations (Anderson 1981). The peat depth observed in our study supports this, as young peat formations, like those in the Kutai lakes (Hope *et al.* 2005), often feature *Pandanus* species and carnivorous plants, which were common in the low pole habitat in our study. Based on these observations, we hypothesise that the low-canopy pole swamp forests in our study may represent a variant of kerapahs, a wet heath forest type in Borneo, rather than it being a variation of peat swamp forests. Further studies are necessary to confirm this hypothesis.

Conservation of lowland kerangas

Heath forests are of considerable ecological interest, characterised by strong biotic and abiotic interactions despite appearing homogeneous and stable (Fagúndez 2013). High spatial heterogeneity is a major feature of kerangas, making these forests challenging to define, map, study, and manage. Kerangas cover about 3% of Kalimantan's total forest area, with most (~ 73%) outside formally protected areas, leaving them highly susceptible to conversion, primarily for oil palm and artisanal small-scale gold mining in Central Kalimantan. The protected areas with the greatest extent of kerangas are Tanjung Puting National Park (5.26%) and Bukit Sapat Hawung Nature Reserve (2.24% of the total Kerangas cover in Kalimantan).

In the Rungan-Kahayan landscape, ~ 70% of the forests lack formal protection. However, since 2016, the social forestry schemes introduced by the Ministry of Environment and Forestry of Indonesia have granted several villages management rights over fragmented forest blocks, providing short-term protection to many kerangas-dominated areas. The establishment of MBERF, forests, further aids in conservation for a relatively large kerangas-dominated forest block in the landscape. Social forestry schemes in the region offer a promising approach to conserving kerangas forests by supporting community-managed non-timber forest products (NTFPs), while preventing other extractive activities. However, ensuring long-term sustainability requires further research and detailed assessment into the socio-economic benefits from NTFPs, community dependence, and access to forest resources. Despite these efforts, only ~ 3% of the kerangas habitat is currently protected under these schemes in the Rungan-Kahayan landscape, leaving the majority at risk of rapid degradation.

These protected areas are fragmented and surrounded by extractive activities driven by limited livelihood alternatives and market access (Anirudh 2025). Such activities, though restricted outside community-managed forest areas, increase edge effects (Piessens *et al.* 2006) and vulnerability to fires (Tuah *et al.* 2020) and invasive species (Loke *et al.* 2023). Additionally, pollutants from gold mining, like mercury, pose further risks to the region's sensitive biodiversity by increasing water acidity and affecting connected ecosystems (Elvince *et al.* 2008).

Heath forests are particularly vulnerable to fire and drought. Their sandy, porous soils and relatively more open canopy allow light penetration, thereby increasing the likelihood of ignition (Ikbal *et al.* 2023; Tuah *et al.* 2020). In northern Borneo, burning of kerangas has facilitated the invasion of fire-adapted *Acacia* species, further enhancing fire susceptibility (Jambul *et al.* 2020). Re-establishing kerangas forests requires eradicating invasive *Acacia* and restoring canopy cover to promote the growth of typical heath-tolerant species (Ibrahim *et al.* 2023). The kerangas-dominated forest mosaic in our study landscape has begun to show evidence of *Acacia* invasion especially in ex-gold mining sites and areas affected by widespread fires in the region. Restoration plays a crucial role in the conservation of kerangas forests. However, the recovery of Borneo's kerangas forests can be a slow process, especially in areas where surface peat layers have been lost (Jambul *et al.* 2020; Suhaili *et al.* 2015). This loss significantly affects the feasibility and effectiveness of restoration efforts, requiring dedicated, long-term research to develop sustainable restoration strategies.

In addition to harbouring unique species characteristic to the heath forest habitat (Maimunah *et al.* 2019), our study area supports two critically endangered, four endangered, seven near-threatened, and ten vulnerable tree species as listed under the IUCN Red List and nine Bornean endemics (see Supplementary Material Table 6). While many of these species are not exclusively associated with heath forests, the mosaic nature of such landscapes in Kalimantan facilitates their occurrence through transition zones between distinct habitat types, leading to species overlaps, as demonstrated by our ordination analysis. Our observations emphasise kerangas forests as priority areas for conservation, considering their important role in sustaining high biodiversity across diverse, interconnected habitats.

From a bioprospecting perspective, kerangas provide valuable timber resources, including species of *Shorea* that are abundant. They are also rich in lianas, plants, and trees species with medicinal value, providing traditional cures for illnesses ranging from common colds to cancer (Oktavia *et al.* 2022). These forests also contribute to local food security through edible ferns, wild fruits, honey, fungi, heart of palm, and tubers (Weihreter 2014). Hence, the lack of formal protection of these habitats may further have implications on human well-being due to compromised ecosystem services.

Considering the paucity of research in lowland kerangas and consequently limited knowledge regarding the impacts of both anthropogenic threats and conservation interventions, our findings provide a baseline by attempting to disentangle the mosaic structure of the lowland kerangas and demonstrating that it is indeed a unique habitat type in the landscape. We suggest that more research targeted towards lowland kerangas is required by building on this baseline. This is important for the development of more scientifically informed lowland heath forest conservation strategies and for increased recognition of such forest types within policy for the protection of heath forests in Indonesia and beyond.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0266467425100084.

Data availability statement. Plot data from our study has been previously submitted to the collaboration network coordinated by Prof. Ferry Slik and was used to produce a published article (DOI: 10.1111/geb.13878).

Data supporting our findings will be made available on global databases (GBIF and forestplots.net) and will be available on request to the corresponding authors.

Acknowledgements. We thank the National Research and Innovation Agency of Indonesia for permits and Universitas Muhammadiyah Palangkaraya for permitting research. We appreciate the support from the provincial and regional government departments in Central Kalimantan. Our gratitude extends to the local community and students for their involvement in data collection.

Author contributions. *Study design*: MEH, BJWB, BRC, FJvV, SMC, WME, SM, NSB, AF, SJH

Data collection and compilation: BJWB, BRC, SM, KPM, A, EE, NSB, S, NN, SMC, MEH, WME, NBA

Data analysis: NBA, BRC, FJvV, DJIS, NJD

Writing: NBA

Review: NBA, MJS, NJD, FJvV, WME, AR, MEH

Financial support. NBA's work was supported by the Leverhulme Trust UK under the Tropical Defaunation Hub, DICE, University of Kent, and Borneo Nature Foundation International, UK. FJvV and MEH's contributions were supported by UKRI through the Global Challenges Research Fund (grant number NE/T010401/1).

Competing interests. The authors declare none.

Ethical standards. This research complied with Indonesian National and local legal and ethical standards and regulations. Data collection was conducted under research permits issued by the National Research and Innovation Agency of the Republic of Indonesia to several authors of this study. For a detailed acknowledgement and list of research permits, please refer to Supplementary Text 2.

The research did not involve the transportation or analysis of any samples (e.g. soil/plant matter) and hence did not require any material transfer agreement and/or other special permits to this effect. No harm was caused to flora or fauna during data collection processes.

References

Adeleye MA, Haberle SG, Harris S, Hopf FV-L, Connor S and Stevenson J (2021) Holocene heathland development in temperate oceanic Southern Hemisphere: key drivers in a global context. *Journal of Biogeography* **48**, 1048–1062. https://doi.org/10.1111/jbi.14057.

Adeney JM, Christensen NL, Vicentini A and Cohn-Haft M (2016) White-sand ecosystems in Amazonia. *Biotropica* **48**, 7–23. https://doi.org/10.1111/btp.12293.

Anderson AB (1981) White-sand vegetation of Brazilian Amazonia. *Biotropica* **13**, 199–210. https://doi.org/10.2307/2388125.

Anirudh NB (2025) *Exploring Biodiversity and Ecological Impacts: A Case Study of the Rungan-Kahayan Landscape in Central Kalimantan.* Depok, Indonesia: Universitas Indonesia .

Ashton P (2014) *On the Forests of Tropical Asia Lest the Memory Fade.* London: Kew Publishing.

Austin MP, Ashton PS and Greig-Smith P (1972) The application of quantitative methods to vegetation survey: iii. a re-examination of rain forest data from Brunei. *Journal of Ecology* **60**, 305–324. https://doi.org/10.2307/2258348.

Brown MJM, Walker BE, Black N, Govaerts RHA, Ondo I, Turner R and Nic Lughadha E (2023) R WCVP: a companion R package for the world checklist of vascular plants. *New Phytologist* **240**, 1355–1365. https://doi.org/10.1111/nph.18919.

Brunig EF (1974) *Ecological Studies in the Kerangas Forests of Sarawak and Brunei.* Borneo Literature Bureau for Sarawak Forest Department xiv+, **237**.

Cannon CH and Leighton M (2004) Tree species distributions across five habitats in a Bornean rain forest. *Journal of Vegetation Science* **15**, 257–266. https://doi.org/10.1111/j.1654-1103.2004.tb02260.x.

Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK and Ellison AM (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs* **84**, 45–67. https://doi.org/10.1890/13-0133.1.

Clarke KR and Green RH (1988) Statistical design and analysis for a 'biological effects' study. *Marine Ecology Progress Series* **46**, 213–226.

Congedo L (2021) Semi-automatic classification Plugin: a Python tool for the download and processing of remote sensing images in QGIS. *Journal of Open Source Software* **6**, 3172. https://doi.org/10.21105/joss.03172.

Coomes DA and Grubb PJ (1996) Amazonian caatinga and related communities at La Esmeralda, Venezuela: forest structure, physiognomy and floristics, and control by soil factors. *Vegetatio* **122**, 167–191.

Davies CE, Moss D and Hill MO (2004) Eunis habitat classification revised 2004. European Environment Agency European Topic Centre on Nature Protection and Biodiversity, United Kingdom.

Davies SJ and Becker P (1996) Floristic composition and stand structure of mixed dipterocarp and heath forests in Brunei Darussalam. *Journal of Tropical Forest Science* **8**, 542–569.

De Graaf MCC, Bobbink R, Smits NAC, Van Diggelen R and Roelofs JGM (2009) Biodiversity, vegetation gradients and key biogeochemical processes in the heathland landscape. *Biological Conservation* **142**, 2191–2201. https://doi.org/10.1016/j.biocon.2009.04.020.

Din H, Metali F and Sukri RS (2015) Tree diversity and community composition of the tutong white sands, Brunei Darussalam: a rare tropical heath forest ecosystem. *International Journal of Ecology* **2015**, e807876. https://doi.org/10.1155/2015/807876.

Dinerstein E, Olson D, Joshi A, Vynne C, Burgess ND, Wikramanayake E, Hahn N, Palminteri S, Hedao P, Noss R, Hansen M, Locke H, Ellis EC, Jones B, Barber CV, Hayes R, Kormos C, Martin V, Crist E, Sechrest W, Price L, Baillie JEM, Weeden D, Suckling K, Davis C, Sizer N, Moore R, Thau D, Birch T, Potapov P, Turubanova S, Tyukavina A, De Souza N, Pintea L, Brito JC, Llewellyn OA, Miller AG, Patzelt A, Ghazanfar SA, Timberlake J, Klöser H, Shennan-Farpón Y, Kindt R, Lillesø J-PB, Van Breugel P, Graudal L, Voge M, Al-Shammari KF and Saleem M (2017) An ecoregion-based approach to protecting half the terrestrial realm. *BioScience* **67**, 534–545. https://doi.org/10.1093/biosci/bix014.

Draper FC, Asner GP, Honorio Coronado EN, Baker TR, García-Villacorta R, Pitman NCA, Fine PVA, Phillips OL, Zárate Gómez R, Amasifuén Guerra CA, Flores Arévalo M, Vásquez Martínez R, Brienen RJW, Monteagudo-Mendoza A, Torres Montenegro LA, Valderrama Sandoval E, Roucoux KH, Ramírez Arévalo FR, Mesones Acuy Í, Del Aguila Pasquel J, Tagle Casapia X, Flores Llampazo G, Corrales Medina M, Reyna Huaymacari J and Baraloto C (2019) Dominant tree species drive beta diversity patterns in western Amazonia. *Ecology* **100**, e02636. https://doi.org/10.1002/ecy.2636.

Draper FC, Honorio Coronado EN, Roucoux KH, Lawson IT, A. Pitman NC, A. Fine PV, Phillips OL, Torres Montenegro LA, Valderrama Sandoval E, Mesones I, García-Villacorta R, Arévalo FRR and Baker TR (2018) Peatland forests are the least diverse tree communities documented in Amazonia, but contribute to high regional beta-diversity. *Ecography* **41**, 1256–1269. https://doi.org/10.1111/ecog.03126.

Elvince R, Inoue T, Tsushima K, Takayanagi RArdianor,, Darung U, Gumiri S, Dohong S, Nagafuchi O, Kawakami T and Yamada T (2008) Assessment of mercury contamination in the Kahayan River, Central Kalimantan, Indonesia. *Journal of Water and Environment Technology* **6**, 103–112. https://doi.org/10.2965/jwet.2008.103.

Fagúndez J (2013) Heathlands confronting global change: drivers of biodiversity loss from past to future scenarios. *Annals of Botany* **111**, 151–172. https://doi.org/10.1093/aob/mcs257.

Fine PVA and Baraloto C (2016) habitat endemism in white-sand forests: insights into the mechanisms of lineage diversification and community assembly of the Neotropical Flora. *Biotropica* **48**, 24–33. https://doi.org/10.1111/btp.12301.

Garnica-Díaz C, Berazaín Iturralde R, Cabrera B, Calderón-Morales E, Felipe FL, García R, Hechavarría JLG, Guimarães AF, Medina E, Paul ALD, Rajakaruna N, Restrepo C, Siebert SJ, Van Den Berg E, Van Der Ent A, Velasquez G and M. Hulshof C (2023) Global plant ecology of tropical ultramafic ecosystems. *The Botanical Review* **89**, 115–157. https://doi.org/10.1007/s12229-022-09278-2.

Gaston KJ and Blackburn TM (2000) *Pattern and Process in Macroecology*. Oxford, OX; Malden, MA, USA: Blackwell Science.

Gaveau DLA, Sloan S, Molidena E, Yaen H, Sheil D, Abram NK, Ancrenaz M, Nasi R, Quinones M, Wielaard N and Meijaard E (2014) Four Decades of forest persistence, clearance and logging on Borneo. *PLoS ONE* **9**, e101654. https://doi.org/10.1371/journal.pone.0101654.

Geekiyanage N, Goodale UM, Cao K and Kitajima K (2019) Plant ecology of tropical and subtropical karst ecosystems. *Biotropica* **51**, 626–640. https://doi.org/10.1111/btp.12696.

Giesen W, Wijedasa LS and Page SE (2018) Unique Southeast Asian peat swamp forest habitats have relatively few distinctive plant species. *Mires and Peat*, 1–13. https://doi.org/10.19189/MaP.2017.OMB.287.

Hope G, Chokkalingam U and Anwar S (2005) The stratigraphy and fire history of the Kutai Peatlands, Kalimantan, Indonesia. *Quaternary Research* **64**, 407–417. https://doi.org/10.1016/j.yqres.2005.08.009.

Hsieh TC, Ma KH and Chao A (2016) INEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution* **7**, 1451–1456. https://doi.org/10.1111/2041-210X.12613.

Hulshof CM and Spasojevic MJ (2020) The edaphic control of plant diversity. *Global Ecology and Biogeography* **29**, 1634–1650. https://doi.org/10.1111/geb.13151.

Ibrahim MH, Sukri RS, Tennakoon KU, Rosli NN and Metali F (2023) Changes in soil physicochemical and water properties in response to exotic acacia invasion in a Bornean coastal heath forest. *Journal of Soil Science and Plant Nutrition* **23**, 3393–3406. https://doi.org/10.1007/s42729-023-01257-9.

Ikbal IM, Din HHM, Tuah WH, Md Jaafar S, Ahmad N and Sukmaria Sukri R (2023) Review: diversity, structure, and community composition of Bornean heath forest with a focus on Brunei Darussalam. *Biodiversitas Journal of Biological Diversity* **24**, 2814–2829. https://doi.org/10.13057/biodiv/d240535.

Jaafar SM, Sukri RS and ProcheÅŸ Å (2016) An investigation of soil physico-chemical variables across different lowland forest ecosystems of Brunei Darussalam. *Malaysian Journal of Science* **35**, 151–168. https://doi.org/10.22452/mjs.vol35no2.6.

Jambul R, Limin A, Ali AN and Slik F (2020) Invasive *Acacia mangium* dominance as an indicator for heath forest disturbance. *Environmental and Sustainability Indicators* **8**, 100059. https://doi.org/10.1016/j.indic.2020.100059.

Jensen JR (2005) *Introductory Digital Image Processing: A Remote Sensing Perspective*, 3rd Edn. Upper Saddle River, NJ: Pearson/Prentice Hall.

Jucker T, Bongalov B, Burslem DFRP, Nilus R, Dalponte M, Lewis SL, Phillips OL, Qie L and Coomes DA (2018) Topography shapes the structure, composition and function of tropical forest landscapes. *Ecology Letters* **21**, 989–1000. https://doi.org/10.1111/ele.12964.

Kartawinata K (1980) *A Note on a 'Kerangas' (Heath) forest at Sebulu East Kalimantan (Indonesia)*. Bogor, Indonesia: Herbarium Bogoriense.

Keith D, Lindenmayer D, Lowe A, Russell-Smith J, Barrett S, Enright N, Fox B, Guerin G, Paton D, Tozer M and Yates C (2014) *Heathlands*. In *Biodiversity and Environmental Change Monitoring, Challenges and Direction*. CSIRO Publishing, pp. 213–281.

Köhler B, Gigon A, Edwards PJ, Krüsi B, Langenauer R, Lüscher A and Ryser P (2005) Changes in the species composition and conservation value of limestone grasslands in Northern Switzerland after 22 years of contrasting managements. *Perspectives in Plant Ecology, Evolution and Systematics* **7**, 51–67. https://doi.org/10.1016/j.ppees.2004.11.003.

Langner A, Achard F, Vancutsem C, Pekel J-F, Simonetti D, Grassi G, Kitayama K and Nakayama M (2015) Assessment of above-ground biomass of Borneo forests through a new data-fusion approach combining two pan-tropical biomass maps. *Land* **4**, 656–669. https://doi.org/10.3390/land4030656.

Loke TY, Margrove JA, Ahmad B, Jikim GE, Endawie AC, Hatta SM, Andrew AP and Maycock CR (2023) The invasion of alien species Miconia crenata (Vahl) Michelang in disturbed and undisturbed lowland mixed dipterocarp and Kerangas forests in Sabah, Malaysia. Taiwania 68, 178–188. https://doi.org/10.6165/tai.2023.68.255.

Loke TY, Margrove JA, Ahmad B, Jikim GE, Endawie AC, Hatta SMHD, Andrew AP and Maycock CR (2023) The invasion of alien species Miconia crenata (Vahl) Michelang in disturbed/undisturbed lowland mixed dipterocarp and Kerangas forests in Sabah, Malaysia. *Taiwania* **68**, 178–188. https://doi.org/10.6165/tai.2023.68.255.

MacGregor-Fors I and Payton ME (2013) Contrasting diversity values: statistical inferences based on overlapping confidence intervals. *PLoS ONE* **8**, e56794. https://doi.org/10.1371/journal.pone.0056794.

MacKinnon K (1996) *The Ecology of Kalimantan*. Periplus Editions, Hong Kong.

Maimunah S, Capilla BRArmadiyanto, and Harrison ME (2019) Tree diversity and forest composition of a Bornean heath forest, Indonesia. *IOP Conference Series: Earth and Environmental Science* **270**, 012028. https://doi.org/10.1088/1755-1315/270/1/012028.

Maimunah S, Kessler PJA, Indrioko S and Naiem M (2022) Natural distribution of the genus Dacrydium Lamb. (Podocarpaceae) in Central Kalimantan, Indonesia. *Biodiversitas Journal of Biological Diversity* **23**. https://doi.org/10.13057/biodiv/d230605.

Maimunah S, Kessler PJA, Indrioko S, Naiem M and Samek JH (2021) Study of species associations in native habitats of the genus Dacrydium Lamb. (Podocarpaceae) in Central Kalimantan, Indonesia. *IOP Conference Series: Earth and Environmental Science* **886**, 012050. https://doi.org/10.1088/1755-1315/886/1/012050.

McWethy DB, Haberle SG, Hopf F and Bowman DMJS (2017) Aboriginal impacts on fire and vegetation on a Tasmanian island. *Journal of Biogeography* **44**, 1319–1330. https://doi.org/10.1111/jbi.12935.

Miyamoto K, Suzuki E, Kohyama T, Seino T, Mirmanto E and Simbolon H (2003) Habitat differentiation among tree species with small-scale variation of humus depth and topography in a tropical heath forest of central Kalimantan, Indonesia. *Journal of Tropical Ecology* **19**, 43–54. https://doi.org/10.1017/S0266467403003067.

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA and Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858.

Nafiah NS, Sukri RS, Ya'akub MYSM, Jaafar SM and Metali F (2022) Contrasting patterns of woody seedlings diversity, abundance and community composition in Bornean heath and peat swamp forests. *Mires and Peat* **28**, 1–18. https://doi.org/10.19189/MaP.2021.MEH.StA.2160.

Newbery DM and Proctor J (1984) Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. | Journal of Ecology | EBSCOhost. *Journal of Ecology* **72**, 475–493. https://doi.org/10.2307/2260060.

Nishimura TB and Suzuki E (2001) Allometric differentiation among tropical tree seedlings in heath and peat-swamp forests. *Journal of Tropical Ecology* **17**, 667–681.

O'Brien MJ and Escudero A (2022) Topography in tropical forests enhances growth and survival differences within and among species via water availability and biotic interactions. *Functional Ecology* **36**, 686–698. https://doi.org/10.1111/1365-2435.13977.

Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Solymos P, Stevens MHH, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista HBA, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill MO, Lahti L, McGlinn D, Ouellette MH, Ribeiro Cunha E, Smith T, Stier A, Ter Braak CJF and Weedon J (2024) *Vegan: Community Ecology Package*. R package version 2.6-8. Available at: https://CRAN.R-project.org/package=vegan

Oktavia D, Pratiwi SD, Munawaroh S, Hikmat A and Hilwan I (2022) The potential of medicinal plants from heath forest: Local knowledge from Kelubi Village, Belitung Island, Indonesia. *Biodiversitas Journal of Biological Diversity* **23**. https://doi.org/10.13057/biodiv/d230731.

Page SE, Rieley JO, Shotyk W and Weiss D (1999) Interdependence of peat and vegetation in a tropical peat swamp forest. *Philosophical Transactions of the Royal Society B: Biological Sciences* **354**, 1885–1897.

Paoli G (2004) *Causes and ecosystem consequences of tree species turnover along soil nutrient gradients in lowland rain forest of Indonesian Borneo* (Ph.D.). University of Michigan, United States – Michigan. https://www.proquest.com/docview/305180263/abstract/7565D4CFD0F347F3PQ/1

Peguero-Pina JJ, Vilagrosa A, Alonso-Forn D, Ferrio JP, Sancho-Knapik D and Gil-Pelegrín E (2020) Living in drylands: functional adaptations of trees and shrubs to cope with high temperatures and water scarcity. *Forests* **11**, 1028. https://doi.org/10.3390/f11101028.

Piessens K, Honnay O, Devlaeminck R and Hermy M (2006) Biotic and abiotic edge effects in highly fragmented heathlands adjacent to cropland and forest. *Agriculture, Ecosystems & Environment* **114**, 335–342. https://doi.org/10.1016/j.agee.2005.11.016.

Pitman NCA, Andino JEG, Aulestia M, Cerón CE, Neill DA, Palacios W, Rivas-Torres G, Silman MR and Terborgh JW (2014) Distribution and abundance of tree species in swamp forests of Amazonian Ecuador. *Ecography* **37**, 902–915. https://doi.org/10.1111/ecog.00774.

Proctor J (1999) Heath forests and acid soils. *Botanical Journal of Scotland* **51**, 1–14. https://doi.org/10.1080/03746609908684920.

Proctor J, Anderson JM, Chai P and Vallack HW (1983) Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak: i. forest environment, structure and floristics. *Journal of Ecology* **71**, 237–260. https://doi.org/10.2307/2259975.

Réjou-Méchain M, Tanguy A, Piponiot C, Chave J and Hérault B (2017) Biomass: An R package for estimating above-ground biomass and its uncertainty in tropical forests. *Methods in Ecology and Evolution* **8**(9), 1163–1167. https://doi.org/10.1111/2041-210X.12753

Riswan S (1982) Ecological studies on primary, secondary and experimentally cleared mixed dipterocarp forest and berangas forest in East Kalimantan, Indonesia (Ph.D.). University of Aberdeen (United Kingdom), Scotland. https://www.proquest.com/docview/301342241/abstract/D90F126C9F724EB4PQ/1

Riswan S and Kartawinata K (1991) Species strategy in early stage of secondary succession associated with soil properties status in a lowland mixed Dipterocarp forest and Kerangas forest in East Kalimantan. *Tropics* **1**, 13–34. https://doi.org/10.3759/tropics.1.13.

Rodríguez-González PM, Stella JC, Campelo F, Ferreira MT and Albuquerque A (2010) Subsidy or stress? Tree structure and growth in wetland forests along a hydrological gradient in Southern Europe. *Forest Ecology and Management* **259**, 2015–2025. https://doi.org/10.1016/j.foreco.2010.02.012.

Rwanga SS and Ndambuki JM (2017) Accuracy assessment of land use/land cover classification using remote sensing and GIS. *International Journal of Geosciences* **08**, 611–622. https://doi.org/10.4236/ijg.2017.84033.

Sari IL, Weston CJ, Newnham GJ and Volkova L (2023) Land cover modelling for tropical forest vulnerability prediction in Kalimantan, Indonesia. *Remote Sensing Applications: Society and Environment* **32**, 101003. https://doi.org/10.1016/j.rsase.2023.101003.

Saxon E and Sheppard S (2010) Land Systems of Indonesia and New Guinea, The Regional Physical Planning Programme for Transmigration (RePPProT). Data Basin. Available at https://databasin.org/datasets/eb74fe29b6fb49d0a6831498b0121c99/ (accessed 18 January 2024)

Sellan G, Thompson J, Majalap N and Brearley FQ (2019) Soil characteristics influence species composition and forest structure differentially among tree size classes in a Bornean heath forest. *Plant and Soil* **438**, 173–185. https://doi.org/10.1007/s11104-019-04000-5.

Sprecht RL and Womersley JS (1980) Heathlands and related shrublands of Malesia (with particular reference to Borneo and New Guinea). *Elsevier* **22**, 321–338.

Stibig H-J, Achard F, Carboni S, Raši R and Miettinen J (2014) Change in tropical forest cover of Southeast Asia from 1990 to 2010. *Biogeosciences* **11**, 247–258. https://doi.org/10.5194/bg-11-247-2014.

Suhaili ALR, Tennakoon K and Sukri RS (2015) Soil seed bank of an exotic Acacia sp. plantation and an adjacent tropical heath forest in Brunei Darussalam. *Biotropia* **22**, 140–150.

Sukri RS, Wahab RA, Salim KA and Burslem DFRP (2012) Habitat associations and community structure of dipterocarps in response to environment and soil conditions in Brunei Darussalam, Northwest Borneo. *Biotropica* **44**, 595–605. https://doi.org/10.1111/j.1744-7429.2011.00837.x.

Thorp M, Thomas M, Martin T and Whalley B (1990) Late Pleistocene sedimentation and landform development in western Kalimantan (Indonesian Borneo). *Geologie En Mijnbouw* **69**, 133–150.

Trethowan LA, Brambach F, Cámara-Leret R, Laumonier Y, Sheil D, Ferry Slik JW, Webb CO, Murdjoko A, Bastian ML, Kartawinata K, Mansor A, Mansur M, Mirmanto E, Nurtjahya E, Permana A, Rozak AH, Wilkie P, Rahmad Z, Arifiani D, Putu Gede P. Damayanto I, Puglisi C, Asmarayani R, Benu NMH, Bramley GLC, Dharma W, Heatubun CD, Hidayat A, Kuswandi R, Mathews S,, MegawatiRustiami H, Santika Y, Santoso W, Setiawan E, Triono T, Wambrauw K, Wanma JF, Hery Yanto A, Siregar M, Sadili A, Dewi Atikah T, Kintamani E, Tjoa A, Culmsee H, Girmansyah D, Gunawan H, Pitopang R, Utteridge TMA, Morley R, Schrader J and Brearley FQ (2024) From earthquakes to island area: multi-scale effects upon local diversity. *Ecography* **2024**. https://doi.org/10.1111/ecog.07038.

Tuah W, Tennakoon K, Jaafar S and Sukri R (2020) Post-fire impacts on tree diversity in coastal heath forests of Brunei Darussalam. *Scientia Bruneiana* **19**. https://doi.org/10.46537/scibru.v19i1.109.

Turner MG, Gardner RH and Golley FB (2015) *Landscape Ecology in Theory and Practice: Pattern and Process*, 2nd Edn. New York: Springer.

Venables WN and Ripley BD (2002) Modern Applied Statistics with S. 4th edn. Springer, New York. ISBN 0-387-95457-0. Available at: https://www.stats.ox.ac.uk/pub/MASS4/

Vernimmen RRE, Bruijnzeel LA, Proctor J, Verhoef HA and Klomp NS (2013) Does water stress, nutrient limitation, or H-toxicity explain the differential stature among Heath Forest types in Central Kalimantan, Indonesia? *Biogeochemistry* **113**, 385–408. https://doi.org/10.1007/s10533-012-9766-4.

Weihreter E (2014) *Traditional knowledge, perceptions and forest conditions in a Dayak Mentebah community, West Kalimantan, Indonesia*. Bogor: Center for International Forestry Research (CIFOR).

Wong KM and Kamariah AS (1999) Forests and trees of Brunei Darussalam. Universiti Brunei Darussalam in association with Forestry Dept., Ministry of Industry and Primary Resources. Available at https://cir.nii.ac.jp/crid/1130282271052619648 (accessed 24 May 2024).

Wong KM, Low YW, Muhammad Ariffin AK and Joffre AA (2015) Novitates Bruneienses, 4. New records in the Araliaceae, Araucariaceae, Arecaceae, Fagaceae, Musaceae and Thymelaeaceae. *Gardens' Bulletin Singapore* **67**, 275. https://doi.org/10.3850/S238258121500023X.

Zhang C, Li X, Chen L, Xie G, Liu C and Pei S (2016) Effects of topographical and edaphic factors on tree community structure and diversity of subtropical mountain forests in the lower Lancang river basin. *Forests* **7**, 222. https://doi.org/10.3390/f7100222.