

Please cite the Published Version

Mansur, Mumammad and Brearley, Francis Q (2023) Biomass and floristics of a secondary forest in West Kalimantan, Indonesia. Tropics, 32 (2). pp. 85-93. ISSN 0917-415X

DOI: https://doi.org/10.3759/tropics.MS22-09

Publisher: Japan Society of Tropical Ecology

BY

Version: Published Version

CC)

Downloaded from: https://e-space.mmu.ac.uk/633622/

Usage rights:

Creative Commons: Attribution 4.0

Additional Information: This is an open access article which originally appeared in Tropics, published by Japan Society of Tropical Ecology

Data Access Statement: Data will be uploaded to ForestPlots.net

Enquiries:

If you have questions about this document, contact openresearch@mmu.ac.uk. Please include the URL of the record in e-space. If you believe that your, or a third party's rights have been compromised through this document please see our Take Down policy (available from https://www.mmu.ac.uk/library/using-the-library/policies-and-guidelines)

FIELD NOTE

Biomass and floristics of a secondary forest in West Kalimantan, Indonesia

Mumammad Mansur¹ and Francis Q. Brearley^{2*}

¹ Research Center for Ecology and Ethnobiology, Indonesian National Research and Innovation Agency (BRIN), Cibinong Science Center, Jalan Raya Jakarta-Bogor Km 46, Cibinong 16911, Indonesia.

² Department of Natural Sciences, Manchester Metropolitan University, Chester Street, Manchester, M1 5GD, United Kingdom.

* Corresponding author: f.q.brearley@mmu.ac.uk

Received: February 27, 2023 Accepted: May 12, 2023 J-STAGE Advance published date: July 7, 2023

ABSTRACT To understand the biomass and floristics of secondary forests in Borneo better, we established a one-hectare plot on the lower slopes of Gunung Kelam in West Kalimantan, Indonesia. We recorded 683 stems (\geq 5 cm dbh) representing 50 species, 44 genera and 27 families; the five species with the greatest Importance Value were *Artocarpus elasticus* (IV = 81.5), *Vitex pinnata* (40.2), *Cryptocarya ferrea* (14.2), *Polyscias elliptica* (12.7) and *Gordonia excelsa* (10.7); stem dbh distributions differed among species indicating that succession was still occurring. The stand basal area was 29.0 m². We estimated biomass with eight different allometric equations. Four equations (Chave, Hashimoto, Kenzo and Manuri-DGH9) showed very close agreement at around 137 Mg ha⁻¹ suggesting they were all suitable for mid-aged secondary forest biomass estimation in this region. Despite tree diversity and biomass being lower than nearby primary forest, secondary forests will become increasingly prevalent in the future and this therefore necessitates their increased study and conservation.

Key words: biomass, diversity, Kalimantan, regeneration, secondary forest

INTRODUCTION

The dipterocarp-dominated forests of Borneo are among the world's most species-rich (Kier et al., 2005; Ashton, 2014) and productive (Banin et al., 2014; Taylor et al., 2019). Studies in the forests of Kalimantan (Indonesian Borneo) have shown a rich tree flora (Suzuki et al., 1997; Kohyama et al., 2003; Brearley et al., 2004; Cannon & Leighton, 2004; Wilkie et al., 2004; Kartawinata et al., 2008; Sheil et al., 2010) yet these forests are under threat from multiple disturbances (Gaveau et al., 2018; Alamgir et al., 2019). An increasing proportion of forests are now secondary in nature (Chazdon, 2014) so understanding the diversity, structure and functioning of tropical secondary forests is becoming more important as secondary forests will play a greater role in biodiversity conservation and ecosystem service provision in the future (Chazdon et al., 2009). Furthermore, given their increasing prevalence and rapid growth rates, secondary forests have the potential to act as effective carbon sinks, but the magnitude and time frame of this is not well understood (Chazdon et al., 2016). A number of studies have examined biomass accumulation (Ewel et al., 1983; Chai, 1997; Hashimoto et al., 2000; Ohtsuka, 2001; Lawrence, 2005; Jepsen, 2006; Kenzo et al., 2010; Tanaka et al., 2021) and/or species diversity and composition (Ewel et al., 1983; Prajadinata, 1996; Lawrence et

al., 2005; Wasli et al., 2011; Labrière et al., 2015; Karyati et al., 2018; Ulfah & Sulistyawati, 2018; Tanaka et al., 2021) in secondary forests of Borneo but they have largely focused on younger secondary forests (<20 years) with only a few studies on older forests (Okimori & Matius, 2000; Brearley et al., 2004; Wasli et al., 2011).

When determining forest biomass, allometric equations are required as it is rarely possible, nor desirable, to directly measure and enumerate all the trees present through direct harvesting. Secondary forest trees have faster growth rates and thus lighter wood and a contrasting architecture to primary forest trees. Equations developed for primary forests may, therefore, not be appropriate for secondary forest biomass estimation, so comparing allometric equations derived from primary and secondary forests, as well as those based on multiple sites (pantropical equations) is important for accurate biomass estimation in these forests (van Breugel et al., 2011).

Gunung (= Mount) Kelam in West Kalimantan, Indonesian Borneo, is a spectacular granite dome, one of the largest monolithic mountains in the world, best known botanically for *Nepenthes clipeata* (Mansur et al., 2021) although we have recorded at least 300 additional species in a preliminary study (Mansur et al., in revision). Gunung Kelam is protected as a 'Taman Wisata Alam' (Nature Tourism Park) and has forests covering its lower slopes – these forests were disturbed by fires brought about by El Niños in the 1980s and 1990s and are all now secondary. Our aims in this paper are to: i) describe the diversity and biomass of a plot within the secondary forest on the mountain, and ii) compare equations for estimating the secondary forest biomass.

MATERIALS AND METHODS

In January 2018 we established a one-hectare (100 m \times 100 m) sampling plot in the secondary forest at Gunung Kelam at 0°04′30.5″ North and 111°37′59.2″ East. The plot was based on a granite geology having steep topography and was laid out at *c*. 50 to 100 m altitude (Fig. 1). The plot was divided into 100 quadrats of 100 m² (10 m \times 10 m) and within each quadrat all trees with dbh (diameter at breast height; 1.3 m) \geq 5 cm were identified, their dbh was



Fig. 1. Internal view of secondary forest on the lower slopes of Gunung Kelam, Indonesian Borneo.

measured using a measuring tape, and tree heights were measured with a Senshin AT-15 measuring pole or estimated by comparing with the heights of selected trees that were used as a reference. Any trees with buttresses were measured 30 cm above the highest point; lianas were not measured. We collected herbarium specimens from each species within the plot and identified them at Herbarium Bogoriense (BO), Research Center for Ecology and Ethnobiology, National Research and Innovation Agency (BRIN), where they were deposited; only one single tree remained unidentified. We calculated species diversity metrics (Chao1, Fisher's α , Shannon-Wiener) using the equations in Colwell (2009) and the importance value index (IVI), which is the sum of relative density, relative frequency and relative dominance, according to Mueller-Dombois & Ellenberg (1974). To estimate the above-ground biomass of the forest, we compared four equations derived from secondary forests in South-east Asia: Hashimoto et al. (2004), Kenzo et al. (2009), Karyati et al. (2019) (we used their equation derived from 20-year-old secondary forest) and Ketterings et al. (2001) as well as two derived from South-east Asian primary forests: Yamakura et al. (1986) and Manuri et al. (2016) (we used their DGH9 equation). In addition, we also used the pan-tropical allometric equations of Brown (1997) for moist forests and Chave et al. (2014). Each equation uses a combination, or a subset, of tree diameter, height and wood density to calculate the biomass of each tree (Table 1) which was then summed to calculate total tree biomass in the one-hectare plot; we used the Global Wood Density Database of Zanne et al. (2009) when wood density was required (72 % at species level, 22 % at genus level, 4% at family level and 2% as the plot mean). Equations are henceforward generally referred to by their first author name only.

Table 1. Eight equations used to estimate tropical tree above-ground biomass (AGB) from tree diameter at breast height (dbh), height (H) and wood density (WD) applied to trees in a secondary forest at Gunung Kelam, Indonesian Borneo.

Equation name	Equation	No. trees	Location	Reference
Brown-moist	$AGB = exp(-2.134 + (2.53 \times ln(dbh)))$	170	Pantropical (5 study sites)	Brown (1997)
Chave	$AGB = 0.0673 \times (WD \times dbh^2 \times H)^{0.976}$	4004	Pantropical (58 study sites)	Chave et al. (2014)
Hashimoto	$AGB = \exp(2.44 \times \ln(dbh) - 2.51)$	191	Secondary forest (Kalimantan)	Hashimoto et al. (2004)
Karyati-20	$AGB = exp(2.3207 \times ln(dbh) - 1.89)$	30	Secondary forest (Kalimantan)	Karyati et al. (2019)
Kenzo	$AGB = 0.0829 \times dbh^{2.43}$	136	Secondary forest (Sarawak)	Kenzo et al. (2009)
Ketterings	$AGB = 0.11 \times WD \times dbh^{2.62}$	29	Secondary forest (Sumatra)	Ketterings et al. (2001)
Manuri-DGH9	$AGB = 0.071 \times (WD \times dbh^2 \times H)^{0.973}$	108	Primary forest (Kalimantan) (4 study sites)	Manuri et al. (2016)
Yamakura	$\begin{array}{l} AGB = (0.02903 \times (dbh^2 \times H)^{0.9813}) + \\ (0.1192 \times (0.02903 \ (dbh^2 \times H)^{0.9813})^{1.059}) + \\ (0.09146 \times ((0.02903 \times (dbh^2 \times H)^{0.9813}) + \\ (0.1192 \times (0.02903 \ (dbh^2 \times H)^{0.9813})^{1.059}))^{0.7266}) \end{array}$	191	Primary forest (Kalimantan)	Yamakura et al. (1986)

RESULTS

Vegetation Composition

Within the one-hectare plot there were 683 stems of 50 species, 44 genera and 27 families (575 stems, 43 species, 37 genera and 27 families for stems ≥ 10 cm dbh). The five dominant tree species (dbh \geq 5 cm) with the greatest Importance Values (IV) were Artocarpus elasticus (IV = 81.5), Vitex pinnata (IV = 40.2), Cryptocarya ferrea (IV = 14.2), Polyscias elliptica (IV = 12.7) and Gordonia excelsa (IV = 10.7) (Table 2). The abundances of all species found are listed in Table 2 along with their families and authorities. In terms of species richness, Fisher's α was 12.4 and the Shannon-Wiener diversity index was 2.90. The Chao1 estimate of species richness was 55.1 indicating that we found around 90 % of the species predicted to be present. There was only one species of dipterocarp in the plot (Anisoptera grossivenia) although two other species were found outside the plot (Shorea balangeran and S. parvifolia; Mansur et al., in revision). Two species were endemic to Kalimantan (Anisoptera grossivenia and Semecarpus glauca) (Sidiyasa, 2015) and four were on the IUCN Red List: Afzelia rhomboidea (VU), Artocarpus anisophyllus (VU), Dimocarpus longan subsp. malesianus (NT) and Palaquium hexandrum (NT).

Vegetation Structure

The trees in the plot had a total basal area of 29.0 m^2 $(28.5 \text{ m}^2 \text{ for trees} \ge 10 \text{ cm dbh})$; there was a general decline in the number of stems with increasing size classes (Fig. 2) although trees in the smallest size class for a given species were often less numerous than the next larger class. Three species with the largest dbhs were Gordonia excelsa (82.9 cm), Dacryodes rubiginosa (69.7 cm) and Palaquium hexandrum (67.1 cm). Among the ten most abundant species, some tree species had a fairly even distribution among dbh size classes. Many species had few stems in the smallest size class indicative of poor regeneration: Artocarpus elasticus (Fig. 2a), Vitex pinnata (Fig. 2b), Cryptocarya ferrea (Fig. 2c), Polyscias elliptica (Fig. 2d) and Cleistanthus oblongifolius (Fig. 2g), whist some other species were mostly of small dbh: Antidesma tetrandum (Fig. 2e) and Leucosyke capitellata (Fig. 2f), and others showed a fairly even distribution across size classes: Neo-uvaria acuminatissima (Fig. 2h) and Afzelia rhombodea (Fig. 2i). Only 2% of the trees were more than 20 m tall with the tallest tree (Dacryodes rubiginosa) reaching 26 m in height.

Forest Biomass

The eight equations to estimate the forest biomass gave contrasting results (Fig. 3). The Brown-moist equation estimated the greatest biomass (228 Mg ha⁻¹) and the Karyati-20 and Ketterings equations, both developed from trees in South-east Asian secondary forests, estimated forest biomass as 168 and 161 Mg ha⁻¹, respectively, with the South-east Asian primary forest equation of Yamakura estimating 159 Mg ha⁻¹. The other equations were either pan-tropical (Chave) or developed from other primary (Manuri-DGH9) or secondary forests in Borneo (Hashimoto, Kenzo) and all four gave remarkably similar estimates of between 135 and 141 Mg ha⁻¹ (Fig. 3).

DISCUSSION

As anticipated, the diversity and biomass of trees in this area of secondary forest in West Kalimantan (Indonesian Borneo) was lower than other similar primary forests (Slik et al., 2010), in fact, both the biomass and number of species were about one-third of those found at Serimbu which is the nearest extensively studied primary forest site (Kohyama et al., 2003). The species composition of the Gunung Kelam secondary forest plot shares a number of commonalities in species composition with of other secondary forests in Borneo and the broader region. It contained a similar set of key 'important' species to secondary forests of Sarawak where Artocarpus elasticus and Vitex pubescens were dominant species along with Macaranga gigantea (Nakagawa et al., 2013), and in East Kalimantan where a secondary forest plot was dominated by Vitex pinnata and Geunsia furfuracea (syn. Callicarpa pentandra) (Sukardjo, 1990). The low number of Macaranga trees (2% of the stems), in contrast to other secondary forests in the region (Riswan & Abdulhadi, 1992; Prajadinata, 1996; Lawrence et al., 2005; Nakagawa et al., 2013; Tanaka et al., 2021), is possibly due to the low nutrient status of the granitic substrate (Chua et al., 2013) or the older age of the forest. The high diversity of edible fruit trees (e.g. Artocarpus anisophyllus, A. elasticus, Durio zibenthinus, Dimocarpus longan, Nephelium lappaceum) is unusual for secondary forests and this might be due to the closeness of a campground where human vectors may be responsible for discarding fruit tree seeds into the secondary forest. This could be leading to an inadvertent 'forest garden' being produced (Salafsky, 1994; Suzuki et al., 1997; Mansur, 2007) in the future. The lack of dipterocarps, that dominate primary forests of Borneo (Brearley et al., 2016), indicates

Table 1. Stem number, basal area and importance value index (IVI) of all tree species in a secondary forest plot (1-ha) at Gunung Kelam, Indonesian Borneo.

Latin name	Family	Local name	Number of stems	Basal area $(m^2 ha^{-1})$	IVI
Afzelia rhomboidea (Blanco) S.Vidal	Leguminosae	Kayu gang	16	0.728	7.336
Agrostistachys borneensis Becc.	Euphorbiaceae	Lengkong	2	0.021	0.817
Alstonia scholaris (L.) R.Br.	Apocynaceae	Kayu pelai	10	0.717	5.970
Anisoptera grossivenia V.Sloot.	Dipterocarpaceae	Resak	3	0.197	1.571
Antidesma tetrandrum Blume	Phyllanthaceae	Remayan	32	0.298	10.45
Archidendron fagifolium (Miq.) I.C.Nielsen	Leguminosae	Jereng bukit	2	0.326	1.642
Ardisia laevigata Blume	Primulaceae	Sabang bubu	1	0.004	0.384
Artocarpus anisophyllus Mig.	Moraceae	Entawa	2	0.066	0.746
Artocarpus dadah Mia	Moraceae	Dadak	7	0.592	4 422
Artocarpus elasticus Reinw er Blume	Moraceae	Tekalong	184	10.85	81.51
Artocarpus gomezianus Wall ex Trécul	Moraceae	Cempedak	3	0.083	1 402
Reilschmiedia madana Blume	Lauraceae	Medang daun besar	7	0.096	2 484
Chisochaton natans Blume	Meliaceae	(Unknown)	1	0.012	0.412
Claistanthus oblongifolius (Poxh.) Müll Ara	Phyllentheces	(Ulikilowil) Paninana	22	0.012	10.22
Cleus dan dum villa sum Dhara	I amia ana a	Fapiliang	1	0.904	0.282
Clerodenarum villosum Blume	Lamiaceae	Empait	1	0.003	0.383
Cratoxylum cochinchinense (Lour.) Blume	Нурегісасеае	Mandieng	9	0.171	3.487
Cryptocarya ferrea Blume	Lauraceae	Medang	41	0.867	14.19
Dacryodes rubiginosa (A.W.Benn) H.J.Lam	Burseraceae	Kayu bunga	9	1.061	6.560
<i>Dillenia eximia</i> Miq.	Dilleniaceae	Simpur	6	0.035	2.128
Dimocarpus longan subsp. malesianus Leenh.	Sapindaceae	Lengkeng	2	0.149	1.257
Diospyros borneensis Hiern.	Ebenaceae	Kesepa/Merkuyung	2	0.101	1.093
Durio zibethinus L.	Malvaceae	Durian	10	0.214	4.459
Endospermum diadenum (Miq.) Airy Shaw	Moraceae	Rendong	5	0.271	2.795
Falcataria moluccana (Miq.) Barneby & J.W.Grimes	Leguminosae	Sepium	7	0.054	2.115
Ficus obscura Blume	Moraceae	Keruruh	7	0.079	2.426
Ficus variegata Blume	Moraceae	Kayu ara	15	0.610	7.688
Garcinia rigida Miq.	Clusiaceae	Kandis	4	0.228	2.276
Gomphia serrata (Gaertn.) Kanis	Ochnaceae	Bengkal	2	0.064	0.739
Gordonia excelsa (Blume) Blume	Theaceae	Kemidan	12	1.858	10.65
Leucosyke capitellata Wedd.	Urticaceae	Melangin	29	0.226	10.22
Macaranga triloba (Thunb.) Müll.Arg.	Euphorbiaceae	Purang	13	0.223	5.157
Magnolia liliifera (L.) Baill.	Magnoliaceae	Jambu batu	4	0.101	1.610
Mallotus mollissimus (Geiseler) Airy Shaw	Euphorbiaceae	Entali	1	0.003	0.382
Mangifera laurina Blume	Anacardiaceae	Mangga	1	0.005	0.389
Nauclea subdita (Korth.) Steud	Rubiaceae	Ketan	1	0.049	0.541
Neo-uvaria acuminatissima (Miq.) Airy Shaw	Annonaceae	Kumpang	23	0.863	10.18
Nenhelium lannaceum I	Sanindaceae	Rambutan	2	0.010	0 779
Palaguium havandrum (Griff) Baill	Sapotaceae	Tekam bukit	6	0.773	4 4 4 8
Polyseigs elliptica (Blume) Lowry & G M Plunkett	Araliaceae	Pekulai	3/	0.735	12 70
Psydrax sumatranus (Mia.) Mohyani	Pubiaceae	Ielumpit	1	0.016	0.427
Duranguig gourgeta Plumo	Thesesses	Mamara	12	0.010	4.710
	Theaceae	Mamere	12	0.398	4./10
	Burseraceae	(Unknown)	1	0.003	0.384
Semecarpus glauca Engl.	Anacardiaceae	Ketap hitam	2	0.030	1.074
Sterculia cordata Blume	Malvaceae	Gaus	5	0.240	2.690
Syzygium nervosum A.Cunn. ex DC	Myrtaceae	Bungkang	6	0.486	3.911
Syzygium claviflorum (Roxb.) Wall. ex A.M.Cowan & Cowan	Myrtaceae	Ubah	6	0.255	2.663
Turpinia sphaerocarpa Hassk	Staphyleaceae	Entili	6	0.644	4.453
Urophyllum arboreum (Reinw. ex Blume) Korth.	Rubiaceae	Tulang ular	2	0.007	0.769
Vitex pinnata L.	Lamiaceae	Leban	102	3.209	40.22
(Unidentified)	(Unidentified)	Maretepung	1	0.057	0.568



Diameter (cm)

Fig. 2. Diameter at breast (dbh) distributions of (a) all the stems and (b-j) the nine most abundant species in a secondary forest at Gunung Kelam, Indonesian Borneo. (b) Artocarpus elasticus, (c) Vitex pinnata, (d) Cryptocarya ferrea, (e) Polyscias elliptica, (f) Antidesma tetrandum, (g) Leucosyke capitellata, (h) Cleistanthus oblongifolius, (i) Neo-uvaria acuminatissima, and (j) Afzelia rhomboidea. Note the different vertical axis scale between panel (a) showing all stems and panels (b) to (j) showing single species.



Fig. 3. Above-ground biomass estimation of a secondary forest at Gunung Kelam, Indonesian Borneo, using eight different allometric equations that were either pan-tropical (black bars), or derived from South-east Asian secondary (white bars) or primary (grey bars) forests.

that the plot is still at a moderately early stage of succession. Additionally, dispersal limitation through the matrix habitat that has a high proportion of oil palm plantations will be difficult for these heavy-seeded and wind-dispersed species. Based on comparisons with other forests in the region, we estimate that this forest is 35 to 40 years old and

suggest that it is possibly recovering from burning in the 1982/83 El Niño (Wooster et al., 2012) although we cannot be certain on this. Whilst parts of the forest on Gunung Kelam also burnt during the 1997/98 El Niño, the location of the plot did not (Kayoman, 2005). Although fires have been set by humans for many thousands of years in Borneo, they are becoming increasingly frequent, severe and problematic leading to loss of biodiversity of a range of organisms (e.g. van Nieewstadt & Sheil, 2005). There were fewer stems in the 5-<10 cm dbh class than the next class above in size for a number of the abundant species. This suggests that current regeneration is poor, however, some of the species in the smaller size class are those that may take over as canopy dominants as succession proceeds, although others will remain as smaller understorey species. The current canopy is likely dominated by long-lived pioneers that are preventing establishment of shade-tolerant species. Additionally, the dense shrubby understorey may inhibit regeneration.

Above-ground biomass was lower than primary forests of Borneo at around only one-third of that of comparable forests (Slik et al., 2010). Poorter et al. (2016) found that mean biomass after 20 years of succession in South American forests was 122 Mg ha⁻¹ but there was an order of magnitude variation that was related, in part, to precipitation with wetter sites accumulating biomass more rapidly.

We used biomass equations specifically developed for secondary forests and it was interesting to note that two of the allometric equations that were derived from secondary forests in Borneo (Kenzo and Hashimoto) led to very similar biomass estimates but were also remarkably similar to the widely-used pan-tropical equation of Chave et al. (2014). While the Kenzo and Hashimoto equations are based on tree diameter alone, the Chave equation also includes tree height as well as wood density and therefore we would expect it to be better constrained with the inclusion of these parameters. The equation of Karyati-20, derived from a 20-year-old secondary forest in Kalimantan, was greater than the other secondary forest estimates, possibly because the mean wood density of trees (0.45 g cm^{-2}) included was greater than typical for secondary forests (e.g. 0.35 g cm^{-2} from Kenzo et al. (2009)). The equation of Ketterings produced greater biomass estimates than those noted already - although trees were harvested from a secondary forest, it appears to have been managed by local populations and the species composition was different. Among the equations including trees obtained from primary forest, those of Brown-moist and Yamakura provided the greatest biomass estimates, suggesting that location or forest-type specific equations would be more appropriate rather than those based on primary forest species with a large number of dipterocarps in the case of Yamakura. However, in contrast to that of Yamakura, the Manuri-DGH9 equation was very similar to that of Chave. Whilst derived from primary forest trees, it also included height and wood density indicating that some equations derived from primary forest trees could be appropriate for mid-aged secondary forests if well constrained. Further statistical comparison of these biomass estimates is not possible because we would need the raw data that was used to construct the allometric equations for error propagation and this data was not available in many cases.

In conclusion, we show here that this secondary forest plot at Gunung Kelam has a lower diversity and biomass than Bornean primary forests. In comparison with other secondary forests, successional dynamics may be influenced by the fragmented nature of the surrounding habitat and the infertile granitic substrate. The concurrence of four allometric equations for biomass estimation suggests their relevance for mid-aged secondary forests in this region.

ACKNOWLEDGEMENTS Thank you to: Simon Dowell, Philip Esseen, Mike Jordan, Hanna Khwaja, Johanna Rode-Margono, Scott Wilson and Stuart Young, staff of Chester Zoo who supported this research. We thank the Head of Research Center for Biology-LIPI and Head of Botany Division who entrusted us to do this research. We are grateful to the Natural Resources Conservation Center, Pontianak and Sintang, who granted the research permits and to the expedition team to Gunung Kelam, namely: Fauzi Rachmat, Supardi Jakalalana (RCB-LIPI) and Gustamansyah (PEH BKSDA-Sintang).

FUNDING

The research was funded by Chester Zoo, United Kingdom.

CONFLICTS OF INTEREST

The authors declare that they have no competing interests.

AVAILABILITY OF DATA

Data will be uploaded to ForestPlots.net

CODE AVAILABILITY

Not applicable

AUTHORS' CONTRIBUTIONS

MM and FQB have equal contributions to this work as the main contributors. MM designed the project and collected the data. MM and FQB performed the analyses and wrote the manuscript.

REFERENCE

- Alamgir, M, Campbell MJ, Sloan S, Suhardiman A, Supriatna J, Laurance WF. 2019. High-risk infrastructure projects pose imminent threats to forests in Indonesian Borneo. *Scientific Reports* 9: 140.
- Ashton PS. 2014. On the forests of tropical Asia: lest the memory fade. Kew Publishing, Royal Botanical Gardens, Kew, London, United Kingdom.
- Banin L, Lewis SL, López-Gónzalez G, Baker TR, Quesada CA, Chao K-J, Burslem DFRP, Nilus R, Abu Salim K, Keeling HC, Tan S, Davies SJ, Monteagudo Mendoza A, Vásquez R, Lloyd J, Neill DA, Pitman NCA, Phillips OL. 2014. Tropical

forest wood production: a cross-continental comparison. *Journal of Ecology* 102: 1025–1037.

- Brearley FQ, Prajadinata S, Kidd PS, Proctor J, Suriantata 2004. Structure and floristics of an old secondary rain forest in Central Kalimantan, Indonesia, and a comparison with adjacent primary forest. *Forest Ecology and Management* 195: 385–397.
- Brearley FQ, Banin LF, Saner P. 2016. The ecology of the Asian dipterocarps. *Plant Ecology and Diversity* 9: 429–436.
- Brown S. 1997. *Estimating biomass change of tropical forest: a primer*. FAO Forestry Paper 134. Food and Agriculture Organisation of the United Nations, Rome, Italy.
- Cannon CH, Leighton M. 2004. Tree-species distributions across five habitats in a Bornean rain forest. *Journal of Vegetation Science* 15: 257–266.
- Chai FYC. 1997. Above-ground biomass estimation of a secondary forest in Sarawak. *Journal of Tropical Forest Science* 9: 359– 368.
- Chave J, Réjou-Méchain M, Búrquez A, Chidumayo E, Colgan MS, Delitti WBC, Duque A, Eid T, Fearnside PM, Goodman RC, Henry M, Martínez-Yrízar A, Mugasha WA, Muller-Landau HC, Mencuccini M, Nelson BW, Ngomanda A, Nogueira EM, Ortiz-Malavassi E, Pélissier R, Ploton P, Ryan CM, Saldarriaga JG, Vieilledent G. 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology* 20: 3177–3190.
- Chazdon RL. 2014. Second growth: the promise of tropical forest regeneration in an age of deforestation. University of Chicago Press, USA.
- Chazdon RL, Peres CA, Dent DH, Sheil D, Lugo AE, Lamb D, Stork NE, Miller SE. 2009. The potential for species conservation in tropical secondary forests. *Conservation Biology* 23: 1406–1417.
- Chazdon RL, Broadbent EN, Rozendaal DMA, Bongers F, Almeyda Zambrano AM, Aide TM, Balvanera P, Becknell JM, Boukili V, Brancalion PHS, Craven D, Almeida-Cortez JS, Cabral GAL, de Jong BHJ, Denslow JS, Dent DH, DeWalt SJ, Dupuy JM, Durán SM, Espírito-Santo MM, Fandino MC, César RG, Hall JS, Hernández-Stefanoni JL, Jakovac CC, Junqueira AB, Kennard D, Letcher SG, Lohbeck M, Martínez-Ramos M, Massoca P, Meave JA, Mesquita R, Mora F, Muñoz R, Muscarella R, Nunes YRF, Ochoa-Gaona S, Orihuela-Belmonte E, Peña-Claros M, Pérez-García EA, Piotto D, Powers JS, Rodríguez-Velázquez J, Romero-Pérez IE, Ruíz J, Saldarriaga JG, Sanchez-Azofeifa A, Schwartz NB, Steininger MK, Swenson NG, Uriarte M, van Breugel M, van der Wal H, Veloso MDM, Vester HFM, Viera ICG, Bentos TV, Williamson GB, Poorter L. 2016. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. Science Advances 2: e1501639.
- Colwell RK. 2009. Biodiversity: concepts, patterns, and measurement. In: Levin SA (ed) *The Princeton guide to ecology*. Princeton University Press, New Jersey, USA. 257– 263.
- Chua SC, Ramage BS, Ngo KM, Potts MD, Lum SKY. 2013 Slow recovery of a secondary tropical forest in Southeast Asia.

Forest Ecology and Management 308: 153-160.

- Ewel JJ, Chai P, Lim MT. 1983. Biomass and floristics of three young second-growth forests in Sarawak. *The Malaysian Forester* 46: 347–364.
- Gaveau DLA, Locatelli B, Salim MA, Yaen H, Pacheco P, Sheil D. 2018. Rise and fall of forest loss and industrial plantations in Borneo (2000–2017). *Conservation Letters* 12: e12622.
- Hashimoto T, Kojima K, Tange T, Sasaki S. 2000. Changes in carbon storage in forest fallows in the tropical lowlands of Borneo. *Forest Ecology and Management* 126: 331–337.
- Hashimoto T, Tange T, Masumori M, Yagi H, Sasaki S, Kojima K. 2004. Allometric equations for pioneer tree species and estimation of the aboveground biomass of a tropical secondary forest in East Kalimantan. *Tropics* 14: 123–130.
- Jepsen MR. 2006. Above-ground carbon stocks in tropical fallows, Sarawak, Malaysia. *Forest Ecology and Management* 225: 287–295.
- Kartawinata K, Purwaningsih, Partomihardjo T, Yusuf R, Abdulhadi R, Riswan S. 2008. Floristics and structure of a lowland dipterocarp forest at Wanariset Samboja, East Kalimantan, Indonesia. *Reinwardtia* 12: 301–323.
- Karyati, Ipor IB, Jusoh I, Wasli ME. 2018 Tree stand floristic dynamics in secondary forests of different ages in Sarawak, Malaysia. *Biodiversitas* 19: 687–693.
- Karyati, Ipor IB, Jusoh I, Wasli ME. 2019. Allometric equations to estimate the above-ground biomass of trees in the tropical secondary forests of different ages. *Biodiversitas* 20, 2427– 2436.
- Kayoman L. 2005. Informasi kawasan konservasi Kalimantan Barat dan upaya konservasi lainnya. [Information on conservation areas in West Kalimantan and other conservation efforts]. Balai Konservasi Sumber Daya Alam Kalimantan Barat, Pontianak, Indonesia.
- Ketterings QM, Coe R, van Noordwijk M, Ambagau Y, Palm CA. 2001. Reducing uncertainly in the use of allometric biomass equations for predicting above ground trees biomass in mixed secondary forest. *Forest Ecology and Management* 146: 199– 209.
- Kier G, Mutke J, Dinerstein E, Ricketts TH, Küper W, Kreft H, Barthlott W. 2005. Global patterns of plant diversity and floristic knowledge. *Journal of Biogeography* 32: 1107–1116.
- Kenzo T, Ichie T, Hattori D, Itioka T, Handa C, Ohkubo T, Kendawang JJ, Nakamura M, Sakaguchi M, Takahashi N, Okamoto M, Tanaka-Oda A, Sakurai K, Ninomiya I. 2009. Development of allometric relationships for accurate estimation of above- and below-ground biomass in tropical secondary forests in Sarawak, Malaysia. *Journal of Tropical Ecology* 25: 371–386.
- Kenzo T, Ichie T, Hattori D, Kendawang JJ, Sakurai K, Ninomiya I. 2010. Changes in above- and belowground biomass in early successional tropical secondary forests after shifting cultivation in Sarawak, Malaysia. *Forest Ecology and Management* 260: 875–882.
- Kohyama T, Suzuki E, Partomihardjo T, Yamada T, Kubo T. 2003. Tree species differentiation in growth, recruitment and allometry in relation to maximum height in a Bornean mixed

dipterocarp forest. Journal of Ecology 91: 797-806.

- Labrière N, Laumonier Y, Locatelli B, Vieilledent G, Comptour M. 2015. Ecosystem services and biodiversity in a rapidly transforming landscape in northern Borneo. *PLoS One* 10: e0140423.
- Lawrence D, Suma V, Mogea JP. 2005. Change in species composition with repeated shifting cultivation: limited role of soil nutrients. *Ecological Applications* 15: 1952–1967.
- Mansur M. 2007. Penelitian ekologi jenis durian (*Durio* spp.) di desa Intuh Lingau, Kalimantan Timur [Ecological studies on durian species (*Durio* spp.) in the village of Intuh Lingau, East Kalimantan]. *Jurnal Teknologi Lingkungan* 8: 211–216.
- Mansur M, Brearley FQ, Rode-Margono EJ, Esseen PJ, Tarigan MRM. 2021. Ecology of *Nepenthes clipeata* on Gunung Kelam, Indonesian Borneo. *Plant Ecology and Diversity* 14: 195–204.
- Mansur M, Brearley FQ, Jakalalana S, Rachmat F, Gustamansyah. in revision. Preliminary plant inventory of Mount Kelam, West Kalimantan, Indonesia. *Edinburgh Journal of Botany*.
- Manuri S, Brack C, Noor'an F, Rusolono T, Anggraini SM, Dotzauer H, Kumara I. 2016. Improved allometric equations for tree aboveground biomass estimation in tropical dipterocarp forests of Kalimantan, Indonesia. *Forest Ecosystems* 3: 28.
- Mueller-Dombois D, Ellenberg H. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York, USA.
- Nakagawa M, Momose K, Kishimoto-Yamada K, Kamoi T, Tanaka HO, Kaga M, Yamashita S, Itioka T, Nagamasu H, Sakai S, Nakashizuka T. 2013. Tree community structure, dynamics, and diversity partitioning in a Bornean tropical forested landscape. *Biodiversity and Conservation* 22: 127–140.
- Ohtsuka T. 2001. Biomass changes in early tropical succession on a large-scale shifting cultivation area, northeast Borneo island. *Tropics* 10: 529–537.
- Okimori Y, Matius P. 2000. Tropical secondary forest and its succession following traditional slash-and-burn agriculture in Mencimai, East Kalimantan. In: Guhardja E, Fatawi M, Sutisna M, Mori T, Ohta S (eds) *Rainforest ecosystems of East Kalimantan: El Niño, drought, fire and human impacts*, Ecological Studies 140. Springer-Verlag, Tokyo, Japan. 185– 197.
- Poorter L, Bongers F, Aide TM, Almeyda Zambrano AM, Balvanera P, Becknell JM, Boukili V, Brancalion PHS, Broadbent EN, Chazdon RL, Craven D, de Almeida-Cortez JS, Cabral GAL, de Jong BHJ, Denslow JS, Dent DH, DeWalt SJ, Dupuy JM, Durán SM, Espírito-Santo MM, Fandino MC, César RG, Hall JS, Hernández-Stefanoni JL, Jakovac CC, Junqueira AB, Kennard D, Letcher SG, Licona J-C, Lohbeck M, Marín-Spiotta E, Martínez-Ramos M, Massoca P, Meave JA, Mesquita R, Mora F, Muñoz R, Muscarella R, Nunes YRF, Ochoa-Gaona S, de Oliveira AA, Orihuela-Belmonte E, Peña-Claros M, Pérez-García EA, Piotto D, Powers JS, Rodríguez-Velázquez J, Romero-Pérez IE, Ruíz J, Saldarriaga JG, Sanchez-Azofeifa A, Schwartz NB, Steininger MK, Swenson NG, Toledo M, Uriarte M, van Breugel M, van der Wal H, Veloso MDM, Vester HFM, Vicentini A, Vieira ICG,

Vizcarra Bentos T, Williamson GB, Rozendaal DMA. 2016. Biomass resilience of Neotropical secondary forests. *Nature* 530: 211–214.

- Prajadinata S. 1996. Studies on tree regrowth on shifting cultivation sites near Muara Joloi, Central Kalimantan, Indonesia. M.Sc. Thesis, University of Stirling, UK.
- Riswan S, Abdulhadi R. 1992. Succession after disturbance of lowland mixed dipterocarp forest by shifting agriculture in East Kalimantan, Indonesia. In: Goldhammer JG (ed) *Tropical forests in transition*. Birkhauser Verlag, Basel, Switzerland. 77–84.
- Salafsky N. 1994. Forest gardens in the Gunung Palung region of West Kalimantan, Indonesia: defining a locally-developed, market-oriented agroforestry system. *Agroforestry Systems* 28: 237–268.
- Sheil D, Kartawinata K, Samsoedin I, Priyadi H, Afriastini JJ. 2010. The lowland forest tree community in Malinau, Kalimantan (Indonesian Borneo): results from a one-hectare plot. *Plant Ecology and Diversity* 3: 59–66.
- Sidiyasa K. 2015. Jenis-jenis pohon endemik Kalimantan [Endemic tree species of Kalimantan]. Balai Penelitian Teknologi Konservasi Sumber Daya Alam, Balikpapan, Indonesia
- Slik JWF, Aiba S-I, Brearley FQ, Cannon, CH, Forshed O, Kitayama K, Nagamasu H, Nilus R, Payne J, Paoli G, Poulsen AD, Raes N, Sheil D, Sidiyasa K, Suzuki E, van Valkenburg JLCH. 2010. Wood specific gravity, stem density, basal area and aboveground biomass gradients and their environmental correlates in Borneo's tropical forests. *Global Ecology and Biogeography* 19: 50–60.
- Sukardjo S. 1990. The secondary forest of Tanah Grogot, East Kalimantan, Indonesia. In: Baas P, Kalkman K, Geesink R (eds) *The plant diversity of Malesia*. Kluwer Academic Publishers, Dordrecht, The Netherlands. 213–224.
- Suzuki E, Hotta M, Partomihardjo T, Sule A, Koike F, Noma N, Yamada T, Kaji M. 1997. Ecology of tengkawang forests under varying degrees of management in West Kalimantan. *Tropics* 7: 35–53.
- Tanaka K, Morikawa Y, Nagai Y, Satriadi T, Fauzi H, Aryadi M, Hiratsuka M. 2021. Biomass and tree diversity in a fragmented secondary forest in Tanah Laut, South Kalimantan province, Indonesia, *Tropics* 30: 31–39.
- Taylor PG, Cleveland CC, Soper F, Wieder WR, Dobrowski SZ, Doughty CE, Townsend AR. 2019. Greater stem growth, woody allocation, and aboveground biomass in Paleotropical forests than in Neotropical forests. *Ecology* 100: e02589.
- Ulfah S, Sulistyawati E. 2018. Perubahan struktur vegetasi pada sistem perladangan gilir balik masyarakat Dayak Pitap Kalimantan Selatan [Changes in vegetation structure in the Pitap Dayak community's shifting cultivation fallow system in South Kalimantan]. *Jurnal Bumi Lestari* 18: 63–74.
- van Breugel M, Ransijn J, Craven D, Bongers F, Hall JS. 2011. Estimating carbon stock in secondary forests: decisions and uncertainties associated with allometric biomass models. *Forest Ecology and Management* 262: 1648–1657.
- van Nieewstadt MGL. Sheil D. 2005. Drought, fire and tree survival in a Borneo rain forest, East Kalimantan, Indonesia.

Journal of Ecology 93: 191-201.

- Wasli ME, Tanaka S, Kendawang JJ, Abdu A, Lat J, Morooka Y, Mohd Long S, Sakurai K. 2011. Soils and vegetation condition of natural forests and secondary fallow forests within Batang Ai National Park boundary, Sarawak, Malaysia. *Kuroshio Science* 5: 67–76.
- Wilkie P, Argent G, Campbell E, Saridan A. 2004. The diversity of 15 ha of lowland mixed dipterocarp forest, Central Kalimantan. *Biodiversity and Conservation* 13: 695–708.
- Wooster MJ, Perry GLW, Zoumas A. 2012. Fire, drought and El

Niño relationships on Borneo during the pre-MODIS era (1980 –2000). *Biogeosciences* 9: 317–340.

- Yamakura T, Hagihara A, Sukardjo S, Ogawa H. 1986. Aboveground biomass of tropical rain forest stands in Indonesian Borneo Vegetatio 68: 71–82.
- Zanne AE, López-González G, Coomes DA, Ilic J, Jansen S, Lewis SL, Miller RB, Swenson NG, Wiemann MC, Chave J. 2009. Data from: Towards a worldwide wood economics spectrum, v5, Dryad, Dataset. https://doi.org/10.5061/dryad.234.