Ecological and biological characteristics and interactions of *Shorea balangeran* in peat swamp forest

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SUMMARY

Shorea balangeran (Korth.) Burck is widely distributed in Southeast Asian peat swamp forests although it is not endemic to this habitat type. This study examines the ecological and biological characteristics and interactions of *S. balangeran* in peat swamp forests, and in particular its interactions with co-occurring species and its capacity for adaptation to challenging environmental conditions. The study addresses key questions relating to the soil characteristics in areas where *S. balangeran* thrives, the nature of associations with commonly co-occurring species, and how the findings might inform peatland restoration strategies. Vegetation data, soil samples and species association records arising from field surveys conducted in a peat swamp forest in Central Kalimantan, Indonesia, were analysed. *S. balangeran* was found to be the second most dominant species in the area, and to show positive associations with other species such as *Gonystylus bancanus* and *Cratoxylum arborescens*, suggesting shared habitat preferences or environmental tolerances. *S. balangeran* was commonly found in moderately acidic soils with high organic matter and low nutrient content, indicating its adaptability to nutrient-poor conditions. These findings highlight ecological characteristics of *S. balangeran* that may commend it for use in peatland restoration programs. However, further research is needed to fully understand its role in ecosystem functioning and resilience.

KEY WORDS: adaptation, biodiversity, restoration, soil properties, tree species, tropical peatland

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INTRODUCTION

Peat swamp forests are among the planet's most distinctive and ecologically vital ecosystems, especially in tropical countries like Indonesia. These landscapes are pivotal for global climate regulation, hydrological balance and biodiversity conservation, offering refuge to a multitude of plant and animal species (Hirano *et al*. 2024). Despite their significance, large expanses of peat swamp forest have suffered degradation owing to persistent anthropogenic pressures (Turetsky *et al*. 2015). In Indonesia, one particularly important species inhabiting these ecosystems is *Shorea balangeran*, a member of the Dipterocarpaceae family. Notable for its resilience in the acidic, nutrient-depleted soils that are characteristic of peatlands, *S. balangeran* contributes substantially to forest structure and ecological function (Indriani *et al*. 2020). It is also the preferred species for reforestation initiatives in degraded peatlands (Smith *et al*. 2022), making it a focal point for restoration-oriented ecological research. Beyond its structural role, *S. balangeran* offers potential medicinal benefits, as phytochemical studies have identified various bioactive compounds such as alkaloids, saponins, tannins, phenolics, flavonoids, triterpenoids and glycosides present in its bark, foliage and twigs (Wardani & Susilo 2016).

Shorea balangeran is widely distributed within Indonesian peat swamp forests and is currently listed as Vulnerable by the IUCN (Robiansyah 2020). This species exhibits distinct morphological and physiological adaptations that allow it to survive in extreme environments characterised by thick layers of waterlogged peat, low pH and limited nutrient availability (Indriani *et al*. 2020). Its prominence in active revegetation programmes further highlights its ecological significance in the context of restoration efforts (Dharmawan *et al*. 2024).

The floristic composition of natural peat swamp forests is remarkably diverse and reflects complex interspecies relationships. Here, the harsh abiotic conditions influence not only species survival but also interspecific interactions. *S. balangeran* often coexists with genera such as *Eugenia* and *Ficus*, which play essential roles in sustaining ecological balance (Astiani 2016). *S. balangeran* also frequently associates with species capable of thriving under similar edaphic conditions, such as *Gonystylus bancanus* (ramin), *Dyera costulata* (jelutung), and various *Calophyllum* species. Collectively, these taxa support the structural and functional integrity of the peat swamp forest ecosystem (Astiani 2016). Therefore, analysing species associations within peat swamp forest ecosystems yields valuable insights into the ecological dynamics at play. Quantitative methods such as correlation analysis and multivariate techniques can be applied to discern patterns of co-occurrence and assess the influence of environmental variables on community assembly and structure (Seniczak *et al*. 2022, Aguadé-Gorgorió & Kéfi 2024). Such analyses are instrumental for crafting better-informed and more-effective conservation and land management strategies.

The present study aims to inform strategic interventions for the rehabilitation and sustainable management of degraded peat swamp forests, particularly in Central Kalimantan (Indonesia) where peatland conservation is a national priority. It investigates the distribution and growth performance of *S. balangeran* within the forest community of a tropical peat swamp forest environment, along with key soil properties including pH, nutrient content and water retention capacity. It further examines the ecological associations of *S. balangeran* with sympatric taxa such as *Gonystylus bancanus* and *Cratoxylum arborescens*, to identify instances of facilitation and competition. By elucidating species–environment and species–species interactions, this work contributes to the broader ecological understanding of peatland dynamics and enhances the scientific foundation for restoration policy and practice in Indonesia.

METHODS

Study location

The study was carried out in 2017 within the Tumbang Nusa Research Forest, located in Central Kalimantan, Indonesia (Figure 1). Geographically, the site lies between the co-ordinates 2° 18' 37" – 2° 22' 34" S and 114° 02' 48" – 114° 06' 46" E, approximately 30 km from the city of Palangka Raya. The terrain is predominantly flat with elevations ranging from 0 to 5 m above sea level and slopes between 0 % and 18 % (Kurniasari *et al*. 2021, Sakuntaladewi *et al*. 2024).

The regional climate is tropical, characterised by high temperatures that can reach up to 36 °C. A

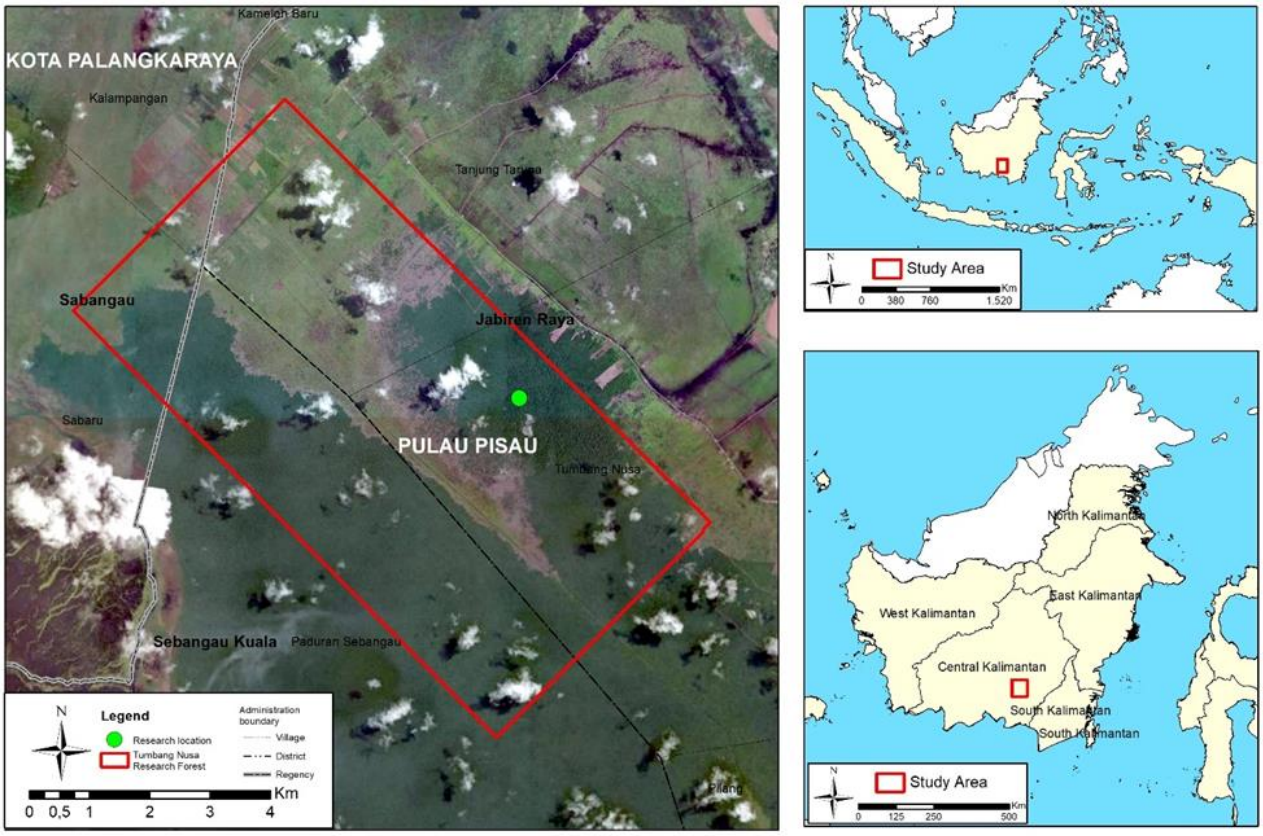

Figure 1. The research location in Tumbang Nusa, Central Kalimantan, Indonesia. Source: https://earth.google.com.

gradual increase in annual mean temperature has been observed, consistent with broader global climate change trends, leading to a greater incidence of hot days. Rainfall in the area is influenced by the Southeast Asian monsoon system, with annual precipitation ranging from 2,000 to 3,500 mm.

Recent years have seen a rise in the frequency and intensity of extreme rainfall events, heightening the risk of flooding, especially along the Kahayan River. Although the dry season typically spans June to August, climate variability has introduced significant shifts in the timing and duration of this period (Nugraheni & Zakaria 2023). As a result, the region remains highly susceptible to seasonal flooding, exacerbated by both heavy rainfall and tidal surges, with effects intensified by the ongoing climatic shifts in Southeast Asia (Yamamoto *et al*. 2021).

According to regulations of the Indonesian Ministry of Forestry, the Tumbang Nusa Research Forest is designated as a permanent production forest. It encompasses a mosaic of successional ecosystems comprising approximately 50 % secondary forest, 30 % forest dominated by *Combretocarpus rotundatus*, and 20 % open areas that have been colonised by fern-dominated vegetation (Mariaty & Santosa 2020).

Research procedure

Three one-hectare (100 m × 100 m) research plots, all orientated in a north-south direction, were established in the peat swamp forest. Each plot was divided into a 5 × 5 grid of 25 sub-plots (20 × 20 m) to ensure even spatial coverage (Figure 2). Vegetation data including tree species identity, stem diameter and abundance were recorded from all 25 sub-plots within each plot to provide a comprehensive representation of the plant community structure.

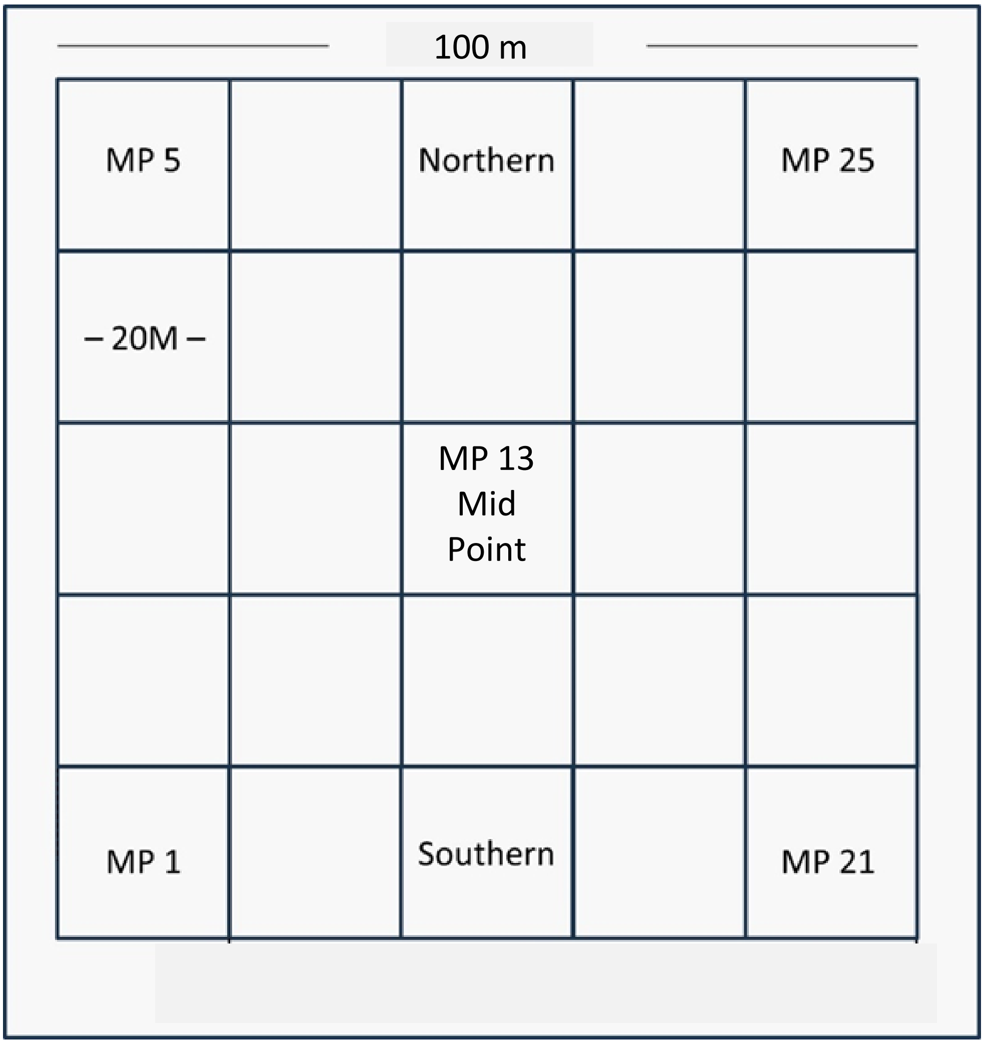

Figure 2. Schematic layout of an example (1-hectare) research plot, divided into 25 (20 × 20 m) sub-plots (MP 1–MP 25). This illustration represents the standard design used in all three plots.

Within each sub-plot, all trees with diameter at breast height (DBH) ≥ 10 cm were inventoried. These individuals were classified as 'mother trees', based on the assumption that they represented reproductively mature and structurally dominant components of the forest canopy. Species were identified in the field with support from local botanical experts and standard field guides, using vegetative and reproductive morphological characteristics including leaves, stems, flowers and fruits.

For measurements of habitat factors (not reported here), measurement points were established systematically at the centres of all sub-plots and numbered sequentially along a linear track starting at the south-west corner of the plot (MP1), moving alternately north and south through the rows of sub-plots and ending at the north-east corner of the plot (MP 25). This design facilitated spatially coherent data collection within each research plot.

Soil samples were collected at MP 1, MP 5, the mid point (MP 13), MP 21 and MP 25 (Figure 2). At these five locations within each of the three plots, single soil samples were collected from depth intervals 0–20 cm, 20–40 cm and 40–60 cm. The five samples from each depth per plot were mixed to create a composite sample representing the whole plot.

Soil analyses were conducted at the Soil Science Laboratory, Faculty of Agriculture, Mulawarman University. Bulk density (BD), porosity, and water holding capacity (WHC) were assessed using gravimetric methods. For WHC determination, fresh peat samples were saturated with water for 24 hours, allowed to drain under gravity for two hours, weighed, and then oven-dried at 105 °C for 48 hours. WHC (%) was calculated using the equation:

$$\text{WHC} = \frac{(\text{saturated weight} - \text{dry weight})}{\text{dry weight}} \times 100 \qquad [1]$$

In addition to physical measurements, chemical analyses were carried out to determine pH (in H_2O and KCl), cation exchange capacity (CEC; Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}), exchangeable Al^{3+} and H^{+}, total nitrogen (Ntot), organic carbon (Corg) and concentrations of available phosphorus (P_2O_5) and potassium (K_2O), using standard procedures described by Ahad *et al*. (2015) and Comber *et al*. (2023).

Data analysis included calculation of the Importance Value Index (IVI), assessment of the spatial distribution and species associations of *S. balangeran*, and mapping using Quantum Geographic Information Systems (QGIS) version 2.18.

The IVI for each species was derived by summing relative density (RD), relative frequency (RF) and relative dominance (RDo), based on the following formulae (Malahayati *et al*. 2023):

$$\text{RD} = \frac{\text{number of individuals of the species}}{\text{total individuals}} \qquad [2]$$

$$\text{RF} = \frac{\text{frequency of the species}}{\text{total frequencies}} \qquad [3]$$

$$\text{RDo} = \frac{\text{basal area of the species}}{\text{total basal area}} \qquad [4]$$

$$\text{IVI} = \text{RD} + \text{RF} + \text{RDo} \qquad [5]$$

To examine species associations within each plot, we employed chi-square (χ^2) contingency table analysis as proposed by Mueller-Dombois & Ellenberg (1974). The strength and direction of species co-occurrence were further evaluated using Cole's coefficient (C), calculated as:

$$\text{C} = \frac{(ad-bc)}{\sqrt{\{(a+b)(c+d)(a+c)(b+d)\}}} \qquad [6]$$

where: a = number of subplots containing both species A and B; b = subplots with A but not B; c = subplots with B but not A; d = subplots with neither species (Cole 1949); thus:

$$N = a + b + c + d \qquad [7]$$

where N is the total number of subplots.

To evaluate the relationship between soil properties and the strength of association between *S. balangeran* and other species, a Spearman rank correlation analysis was conducted. The Spearman correlation was selected because its non-parametric nature makes it suitable for non-normally distributed data and small sample sizes. Physical and chemical soil properties (BD, porosity, WHC, pH, cation exchange rates, Corg, Ntot, C/N, P_2O_5, K_2O) were averaged across the three soil sampling depths and all sub-plots for each of the three research plots. The chi-square (χ^2) values from the interspecies analysis that indicated significant associations were used as a measure of the strength of species association. The dataset was compiled by mapping the chi-square values onto the averaged soil properties per plot. The analysis was performed using SPSS version 26.0 (IBM Corporation, Armonk NY, USA), with a two-tailed significance test at α = 0.05. Correlation coefficients (ρ) and p-values were reported.

RESULTS

Soil physical and chemical characteristics

Overall, the physical properties of the soil across the study plots exhibited a consistent trend of increasing BD with increasing depth below the ground surface, as shown in Table 1. The BD of the peat soil was remarkably low, ranging from 0.16 to 0.17 g cm^{-3}. Soil porosity was extremely high, between 93.37 % and 94.12 %. WHC also increased with depth, rising from 518.07 % at 0–20 cm to approximately 589.84 % at 40–60 cm.

As presented in Table 2, the soil was strongly acidic, with pH values ranging from 4.1 to 4.5. CEC tended to increase with depth, varying between 5.48 and 7.09 meq $100g^{-1}$. Organic carbon content (Corg) was very high (34.62–36.54 %). C/N was also substantial (29–32), indicating a slow rate of organic matter decomposition. The concentrations of the macronutrients P_2O_5 and K_2O were generally higher in the upper layers and decreased with increasing depth.

Species composition and distribution

In total, 1,453 individual trees were recorded across the three study plots (Figure 3), representing 30 species. Amongst these species, *S. balangeran* was the most abundant *Shorea* species with 140 individuals (9.64 %). There were 116 specimens (7.98 %) of *Shorea teysmanniana* and only 14 (0.96 %) of *Shorea platyclados*. Collectively, the 27 species belonging to other genera dominated the tree community, comprising 81.42 % of the total individuals (Table 3).

Table 1. Physical characteristics of peat soil in Tumbang Nusa Research Forest. Values per depth interval are means ± SD of three composite samples (one per plot). BD: bulk density; WHC: water holding capacity.

Depth (cm)	BD (g cm^{-3})	Porosity (%)	WHC (%)
0–20	0.16 ± 0.01	94.12 ± 0.52	518.07 ± 38.21
20–40	0.17 ± 0.01	93.48 ± 0.46	592.73 ± 41.15
40–60	0.17 ± 0.00	93.37 ± 0.38	589.84 ± 45.60
Overall mean ± SD	0.17 ± 0.006	93.66 ± 0.41	566.88 + 42.30

Table 2. Chemical properties of peat soil in Tumbang Nusa Research Forest. Values per depth interval are means and standard deviations (SD; in parentheses) of three composite samples (one per plot). CEC: cation exchange capacity; C/N: Corg/Ntot.

Depth (cm)	pH (1:25)		Cation exchange rate (meq $100g^{-1}$)							Organic content (%)		C/N	Mineral (mg kg^{-1})	
	H_2O	KCl	Ca^{2+}	Mg^{2+}	Na^{+}	K^{+}	CEC	Al^{3+}	H^{+}	Ntot	Corg		P_2O_5	K_2O
0–20	4.1 (0.2)	2.2 (0.1)	0.65 (0.12)	0.42 (0.08)	0.29 (0.05)	0.48 (0.09)	5.48 (0.75)	2.92 (0.44)	1.08 (0.21)	1.27 (0.18)	36.54 (2.81)	29 (3)	105.17 (18.42)	228.10 (32.15)
20–40	4.5 (0.3)	2.0 (0.2)	0.68 (0.15)	0.41 (0.07)	0.22 (0.04)	0.20 (0.05)	6.34 (0.51)	2.75 (0.51)	2.08 (0.33)	1.20 (0.16)	34.62 (3.10)	29 (2)	97.88 (15.33)	124.16 (28.17)
40–60	4.4 (0.2)	1.7 (0.1)	0.22 (0.06)	0.38 (0.09)	0.17 (0.03)	0.06 (0.02)	7.09 (0.91)	4.08 (0.67)	2.17 (0.29)	1.14 (0.20)	36.54 (2.95)	32 (4)	56.59 (12.10)	62.18 (19.44)
Overall mean	4.3 (0.3)	1.9 (0.2)	0.52 (0.24)	0.40 (0.08)	0.23 (0.06)	0.25 (0.19)	6.30 (0.92)	3.25 (0.72)	1.78 (0.58)	1.20 (0.18)	35.90 (0.58)	30 (3)	86.55 (26.61)	138.15 (74.10)

The IVI values (Table 4) indicated that *Cratoxylum arborescens* was the dominant species (IVI = 0.681), followed by *Gonystylus bancanus* (IVI = 0.593) and *Combretocarpus rotundatus* (IVI = 0.417). *S. balangeran* had an IVI of 0.282, suggesting it plays a notable ecological role, even though it is not a dominant species within the community.

Species association and co-occurrence

The association analysis between *S. balangeran* and other species is summarised in Table 5. The chi-square values revealed highly significant positive associations with *Gonystylus bancanus* and *Syzigium* sp., and eleven negative associations (four highly significant, seven significant) with other species.

Spearman correlation analysis

The results of the correlation analysis for the 12 species that were significantly associated with *S. balangeran* are presented in Table 6. Significant correlations were found for BD (ρ = -0.62, p = 0.03), porosity (ρ = 0.58, p = 0.04), pH H_2O (ρ = -0.55, p = 0.05), Corg (ρ = 0.60, p = 0.03) and Al^{3+} (ρ = -0.59, p = 0.04). Other soil properties (WHC, CEC, Ntot, C/N, P_2O_5, K_2O) exhibited no significant correlations ($p > 0.05$).

(a) (b) (c)

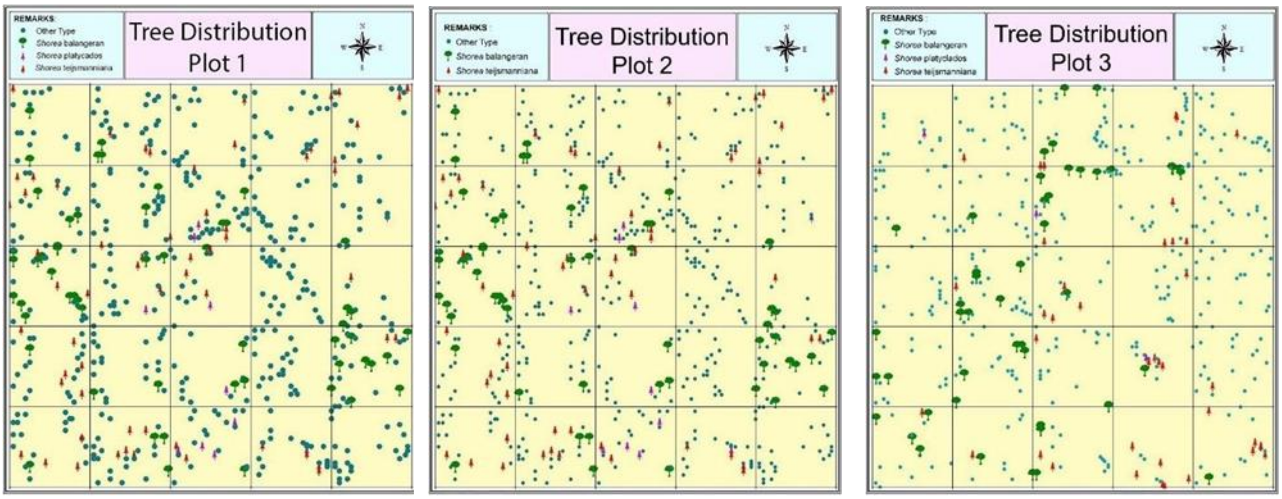

Figure 3. Spatial distributions of tree species in (a) Plot 1, (b) Plot 2 and (c) Plot 3.

Table 3. Occurrence of *Shorea* and other tree species in each research plot.

No.	Latin Name	Plot 1	Plot 2	Plot 3	N	%
1	*Shorea balangeran*	55	39	46	140	9.64
2	*Shorea platyclados*	11	0	3	14	0.96
3	*Shorea teysmanniana*	62	13	41	116	7.98
4	Other species	429	399	355	1183	81.42
	Total	557	451	445	1453	100.00

Table 4. Derivation of Importance Value Index (IVI) for all tree species recorded within the three research plots in Tumbang Nusa Research Forest. N = Number of individuals; F = Frequency - number of the 20 m × 20 m sub-plots where the species was present (maximum 75); G = Basal area (m^2); RD = Relative Density; RF = Relative Frequency; RDo = Relative Dominance; IVI = Importance Value Index (see Equations 2–5); (unknown) = species for which only a local name was assigned (i.e., Latin name unknown).

No.	Latin name	N	F	G	RD	RF	RDo	IVI
1	*Cratoxylum arborescens*	415	70	8.701	0.286	0.146	0.250	0.681
2	*Gonystylus bancanus*	324	69	7.875	0.223	0.144	0.226	0.593
3	*Combretocarpus rotundatus*	183	57	6.008	0.126	0.119	0.172	0.417
4	***Shorea balangeran***	**140**	**46**	**3.131**	**0.096**	**0.096**	**0.090**	**0.282**
5	*Shorea teysmanniana*	116	44	3.211	0.080	0.092	0.092	0.264
6	*Litsea cubeba*	66	38	1.716	0.045	0.079	0.049	0.174
7	*Horsfieldia* sp.	54	29	1.044	0.037	0.060	0.030	0.128
8	*Campnosperma auriculata*	34	29	0.616	0.023	0.060	0.018	0.101
9	*Calophyllum kunstleri*	26	20	0.616	0.018	0.024	0.018	0.077
10	*Diospyros* sp.	20	15	0.392	0.014	0.031	0.011	0.056
11	*Tetramerista glabra*	16	11	0.289	0.011	0.023	0.008	0.042
12	*Shorea platyclados*	14	10	0.300	0.010	0.021	0.009	0.039
13	*Syzigium* sp.	7	7	0.118	0.005	0.015	0.003	0.023
14	*Carallia brachiata*	6	6	0.133	0.004	0.013	0.004	0.020
15	*Myristica iners*	4	4	0.068	0.003	0.008	0.002	0.013
16	*Stemonurus scorpiodes*	4	3	0.067	0.003	0.006	0.002	0.011
17	*Dyera polyphylla*	3	3	0.048	0.002	0.006	0.001	0.010
18	*Garcinia celabica*	3	3	0.048	0.002	0.006	0.001	0.010
19	*Palaquium cochleari*	3	2	0.105	0.002	0.004	0.003	0.009
20	*Mezzetia parvifolia*	3	2	0.090	0.002	0.004	0.003	0.009
21	*Nephelium* sp.	2	2	0.041	0.001	0.004	0.001	0.007
22	*Eugenia* sp.	2	2	0.027	0.001	0.004	0.001	0.006
23	Martibo (unknown)	1	1	0.041	0.001	0.002	0.001	0.004
24	*Litsea* sp.	1	1	0.038	0.001	0.002	0.001	0.004
25	Pampaning (unknown)	1	1	0.028	0.001	0.002	0.001	0.004
26	Lilin (unknown)	1	1	0.027	0.001	0.002	0.001	0.004
27	*Syzygium zeylanicum*	1	1	0.019	0.001	0.002	0.001	0.003
28	*Sapindaceae* sp.	1	1	0.018	0.001	0.002	0.001	0.003
29	Lamiju (unknown)	1	1	0.012	0.001	0.002	0.000	0.003
30	*Artocarpus elasticus*	1	1	0.011	0.001	0.002	0.000	0.003
	Totals:	1453	480					

Table 5. Associations of *S. balangeran* with other tree species as indicated by the chi-square analysis and Cole's coefficient (C; Equation 6). Critical chi-square value (χ^2 table) = 3.841 (α = 0.05, df = 1). The strength of association is interpreted as follows: Very real (highly significant): $\chi^2 \geq 6.635$; Real (significant): $\chi^2 \geq 3.841$.

Plot	Tree species	χ^2	Association	C
1	*Gonystylus bancanus*	6.67	Very real	- 0.06
	Lamiju (unknown)	6.67	Very real	- 0.06
	Litsea sp.	6.67	Very real	- 0.06
	Pampaning (unknown)	6.67	Very real	- 0.06
	Sapindaceae sp.	6.67	Very real	- 0.06
2	*Calophyllum kunstleri*	6.51	Real	- 0.19
	Cratoxylum arborescens	3.84	Real	- 0.15
	Syzygium zeylanicum	5.25	Real	- 0.06
	Carallia brachiata	4.48	Real	- 0.14
	Martibo (unknown)	3.84	Real	- 0.15
	Myristica iners	5.25	Real	- 0.06
3	Martibo (unknown)	4.20	Real	- 0.17
	Syzigium sp.	7.31	Very real	- 0.18

Table 6. Spearman correlation coefficients (and p-values) relating the strengths of significant *S. balangeran* species associations (metric: χ^2 values from Table 5) and soil properties averaged across each of the three research plots. * = significant at $p \leq 0.05$; ns = not significant ($p > 0.05$); N = 13 (the number of significant species associations).

Soil property	Spearman coefficient (ρ)	p-value	Significance
BD	-0.62	0.03	*
Porosity	0.58	0.04	*
WHC	0.12	0.65	ns
pH H_2O	-0.55	0.05	*
CEC	0.08	0.78	ns
Corg	0.60	0.03	*
Ntot	0.15	0.59	ns
C/N	0.20	0.48	ns
P_2O_5	-0.10	0.72	ns
K_2O	-0.14	0.63	ns
Al^{3+}	-0.59	0.04	*

DISCUSSION

The peat soils at the study site exhibited distinctive physical properties, characterised by exceptionally low BD (0.16–0.17 g cm^{-3}) and extremely high porosity (93.37–94.12 %), as presented in Table 1. These characteristics enhance both water and air retention, which are crucial for the survival of species such as *S. balangeran* in waterlogged environments (Basri *et al*. 2021, Crnobrna *et al*. 2022). WHC was remarkably high, ranging from 518.07 % at the surface to 592.73 % at depth 20–40 cm. These values reflect the soil's high organic matter content and its highly porous structure. Such extreme porosity (WHC > 500 %) allows peat soils to retain large volumes of water. This extraordinary WHC is primarily attributed to the soil's low BD and the high absorbency of organic material which enables peat to hold several times its dry weight of water (Parra-Gómez *et al*. 2023). While high WHC can be advantageous under dry conditions, in saturated peat it may inhibit gas exchange and root respiration, potentially limiting plant growth (Link *et al*. 2023).

The peat also exhibited high acidity, with pH values ranging from 4.1 to 4.5 (Table 2), posing a considerable challenge for plant development. The acidic conditions, largely driven by elevated concentrations of Al^{3+} and H^{+} ions (Table 3) often result in toxicity to plants. Soluble aluminum ions (Al^{3+}) can impair root system functions, restrict root elongation and reduce the efficiency of nutrient uptake, particularly phosphorus (P), potassium (K), and calcium (Ca) (Li *et al*. 2022). However, applications of organic acids, phytohormones and biochar have been shown to alleviate aluminum toxicity by modulating gene expression and enhancing antioxidant defences (Ahmad *et al*. 2024, Ur Rahman *et al*. 2024). The ability of *S. balangeran* to persist under such harsh conditions suggests that it possesses inherent tolerance mechanisms, possibly involving ion exclusion or internal detoxification strategies.

The peat soils were also marked by high C/N values of 29–32 (Table 2), indicative of slow organic matter decomposition and limited nutrient availability typical of ombrotrophic peat systems (Wilson *et al*. 2022, Nachtigall *et al*. 2023). Although the total organic carbon content (34.62–36.54 %) was remarkably high, the low concentrations of P_2O_5 (105.17 mg kg^{-1}) and K_2O (228.10 mg kg^{-1}) in the deeper peat layers revealed nutrient limitations crucial to plant growth. This finding supports the understanding that plant productivity in peatlands is more strongly constrained by nutrient availability than by total organic carbon. The spatial distribution of these nutrients highlights their greater availability in the surface layer, underscoring the importance of soil depth in assessing nutrient dynamics within peat ecosystems (Becher *et al*. 2018). Nutrient leaching, slow decomposition and the inherent chemical properties of peat soils may account for the observed decline in P_2O_5 and K_2O concentrations with depth (Becher *et al*. 2020, Husen *et al*. 2014).

The tree community at the study site comprised 30 species, with *Cratoxylum arborescens*, *Gonystylus bancanus* and *Combretocarpus rotundatus* identified as the most-dominant species on the basis of IVI (Table 4). *S. balangeran* was the second most abundant species with 140 individuals (9.64 %) (Table 3), although it exhibited an IVI of only 0.282. Its consistent presence across all plots suggests a broad ecological tolerance to the characteristic conditions of tropical peatlands, including high acidity and prolonged inundation. This ecological resilience is supported by morphological and physiological adaptations such as pneumatophores and a shallow root system capable of efficient oxygen and water uptake under saturated conditions (Indriani *et al*. 2020). With a survival rate of up to 97 % in peatland environments, *S. balangeran* is a leading candidate for peatland restoration using native species (Dharmawan *et al*. 2024).

Regarding the association of *S. balangeran* with other tree species, every statistically significant relationship revealed by the chi-square (χ^2) test results and Cole's coefficient (C) was negative (Table 5). Cole's coefficient suggests that paired species will tend not to co-occur. This indicates possible spatial avoidance or competition, as well as the possibility of different habitat requirements, which may contribute to the lack of coexistence within the same microhabitats (Brazeau & Schamp 2019, Blanchet *et al*. 2020).

The five species *Gonystylus bancanus*, Lamiju (unknown), *Litsea* sp., Pampaning (unknown) and *Sapindaceae* sp. had strong (very real) negative associations with *S. balangeran* ($\chi^2 \geq 6.635$). This suggests that *S. balangeran* segregates ecologically into distinct habitats which are perhaps more waterlogged or even nutrient poor; a finding that reinforces the idea of habitat filtering, where only species with particular tolerances can survive extreme environmental conditions (Dharmawan *et al*. 2024, Collins *et al*. 2025).

The six species *Calophyllum kunstleri*, *Cratoxylum arborescens*, *Syzygium zeylanicum*, *Carallia brachiata*, Martibo (unknown) and *Myristica iners* had significant (real) negative associations with *S. balangeran* ($\chi^2 \geq 3.841$). The negative association is so consistent that it begs the question of whether ecological niche separation is at play, which suggests that *S. balangeran* has different environmental requirements compared to most other species in the community of the peat swamp forest. This is consistent with the finding that the distribution of tree species in Southeast Asian peat swamp forests is primarily driven by the depth of the peat, water level and the nutrients. Thus, only species with overlapping physiological tolerances are able to co-occur within a given habitat (Astiani *et al*. 2021, Osaki *et al*. 2023).

The differences in the soil characteristics and floristic assemblages of peat swamp and kerangas forests further explain the habitat separation among species (Collins *et al*. 2025). The negative association patterns are filters of habitat, leaving species with high tolerance to extreme conditions, prolonged flooding and low nutrients to persist and co-exist with *S. balangeran* (Indriani *et al*. 2020, Irwin & Schluter 2022). For this reason, *S. balangeran* is able to withstand more stressful conditions compared to other species in the community, which makes it a stabilising and resilient species within peat swamp forest communities.

Spearman's correlation analysis revealed that several soil properties were significantly correlated with the strength of associations between *S. balangeran* and other species in the peatland ecosystem of Tumbang Nusa Research Forest. A moderate negative correlation with BD ($\rho = -0.62$, $p = 0.03$) and a positive correlation with porosity ($\rho = 0.58$, $p = 0.04$) suggest that *S. balangeran* tends to form stronger associations in less compact, more porous peat soils. These conditions probably enhance root aeration and water availability, which are critical for tree growth in waterlogged peat environments. These findings are consistent with those of Astiani *et al*. (2021), who noted that peat soil structure influences tree species distribution in tropical wetlands.

A negative correlation with soil pH H_2O ($\rho = -0.55$, $p = 0.05$) indicates that more acidic soil conditions favour the association of *S. balangeran* with other species such as *Gonystylus bancanus* and *Syzygium* sp. (Table 5). The acidic nature of peat soil, with an average pH ranging from 4.1 to 4.5 (Table 2), is a characteristic feature of this ecosystem that enables adaptive species like *S. balangeran* to compete effectively. A positive correlation with organic carbon ($\rho = 0.60$, $p = 0.03$) confirms that high organic matter content (34.62–36.54 %; Table 2) supports species interactions, possibly by enhancing nutrient retention in nutrient-poor soils. Conversely, a negative correlation with Al^{3+} ($\rho = -0.59$, $p = 0.04$) suggests that high aluminum levels may inhibit associations, perhaps due to toxicity affecting companion species.

The absence of significant correlations for water-holding capacity, CEC, Ntot, C/N, P_2O_5 and K_2O (Table 6) indicates that these factors have limited influence on *S. balangeran* associations. This may be attributed to low variation in these characteristics across plots or the dominance of soil physical properties in shaping species interactions in peat ecosystems. Previous research by Mustamo *et al*. (2016) similarly found that soil physical properties, such as porosity, are stronger determinants than mineral nutrients in peatland ecosystems.

These findings underscore the critical importance of maintaining the structure of peat soil (low BD, high porosity) and chemical conditions (low pH, high organic carbon content) to support tree communities, as well as the keystone species *S. balangeran*, in peatland ecosystems. Positive associations with species such as *Gonystylus bancanus* and *Syzygium* sp. suggest facilitative interactions, which could be leveraged in peatland restoration strategies. However, elevated Al^{3+} concentrations, particularly at 40–60 cm depth (Table 2), may constrain restoration success if not properly managed.

Integrating soil characterisation with species association patterns offers a holistic understanding of the ecological niche occupied by *S. balangeran* in peat swamp ecosystems. This species not only demonstrates resilience to extreme site conditions but also plays a pivotal role in shaping community structure through specific interactions with other species. Therefore, in the context of peatland restoration, selecting *S. balangeran* alongside ecologically compatible species such as *Gonystylus bancanus* may enhance the long-term success and stability of restoration efforts.

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AUTHOR CONTRIBUTIONS

NS initiated the research, conducted field data collection, developed the sampling protocol, and performed data analysis. All authors contributed to the interpretation of findings and to writing.

REFERENCES

Aguadé-Gorgorió, G., Kéfi, S. (2024) Alternative cliques of coexisting species in complex ecosystems. *Journal of Physics: Complexity*, 5(2), 25022. https://doi.org/10.1088/2632-072X/ad506a

Ahad, T., Kanth, T.A., Nahi, S. (2015) Soil bulk density as related to texture, organic matter content and porosity in Kandi soils of district Kupwara (Kashmir valley), India. *International Journal of Scientific Research*, 4(1), 198–200.

Ahmad, S., Sehrish, A.K., Alomrani, S.O., Zhang, L., Waseem, M., Noureen, S., Ullah, I., Tabassam, R., Abbas, G., Ali, S. (2024) Combined application of biochar and metal-tolerant bacteria alleviates cadmium toxicity by modulating the antioxidant defense mechanism and physicochemical attributes in rice (*Oryza sativa* L.) grown in cadmium-contaminated soil. *Plant Stress*, 11, 100348. https://doi.org/10.1016/j.stress.2024.100348

Astiani, D. (2016) Tropical peatland tree-species diversity altered by forest degradation. *Biodiversitas*, 17(1), 102–109. https://doi.org/10.13057/biodiv/d170115

Astiani, D., Ekamawanti, H.A., Ekyastuti, W., Widiastuti, T., Tavita, G.E., Suntoro, M.A. (2021) Tree species distribution in tropical peatland forest along peat depth gradients: Baseline notes for peatland restoration. *Biodiversitas*, 22(7), 2571–2578. https://doi.org/10.13057/biodiv/d220704

Basri, K., Zainorabidin, A., Mohamad, H.M., Musta, B. (2021) Determining the peat soil dynamic properties using geophysical methods. *Magazine of Civil Engineering*, 105(5), 10508. https://doi.org/10.34910/MCE.105.8

Becher, M., Pakuła, K., Pielech, J., Trzcińska, E. (2018) Phosphorus resources and fractions in peat-muck soils. *Environmental Protection and Natural Resources*, 29(3), 1–6. https://doi.org/10.2478/oszn-2018-0012

Becher, M., Pakuła, K., Jaremko, D. (2020) Phosphorus accumulation in the dehydrated peat soils of the Liwiec river valley. *Journal of Ecological Engineering*, 21(5), 213–220. https://doi.org/10.12911/22998993/122673

Blanchet, F.G., Cazelles, K., Gravel, D. (2020) Co-occurrence is not evidence of ecological interactions. *Ecology Letters*, 23(7), 1050–1063. https://doi.org/10.1111/ele.13525

Brazeau, H.A., Schamp, B.S. (2019) Examining the link between competition and negative co-occurrence patterns. *Oikos*, 128(9), 1358–1366. https://doi.org/10.1111/oik.0605

Cole, L.C. (1949) The measurement of interspecific association. *Ecology*, 30(4), 411–424. https://doi.org/10.2307/1932444

Collins, C., Cobb, A.R., Sukri, R.S., Eri, J., Wardle, D.A. (2025) Floristic and soil properties of co-occurring peat and kerangas forests in Brunei Darussalam. *Journal of Tropical Ecology*, 41, e13. https://doi.org/10.1017/S0266467425000112

Comber, S., Lunt, P., Taylor, M., Underwood, N., Crocker, R., Schindler, R. (2023) Restoration management of phosphorus pollution on lowland fen peatlands: A data evidence review from the Somerset Levels and Moors. Agricultural Water Management, 287, 108419. https://doi.org/10.1016/j.agwat.2023.108419

Crnobrna, B., Llanqui, I.B., Cardenas, A.D., Panduro Pisco, G. (2022) Relationships between organic matter and bulk density in Amazonian peatland soils. *Sustainability*, 14(19), 12070. https://doi.org/10.3390/su141912070

Dharmawan, I.W.S., Lisnawati, Y., Siahaan, H., Premono, B.T., Iqbal, M., Junaedi, A., Sakuntaladewi, N., Bastoni, Fauzi, R., Ramawati, Nugroho, A.W., Undaharta, N.K.E., Achmadi, A.S., Setyawati, T., Siregar, C.A., Pratiwi, Suhartana, S., Soenarno, Dulsalam, Sukmana, A. (2024) Use of an adaptive-vegetation model to restore degraded tropical peat swamp forest to support climate resilience. *Land*, 13(9), 1377. https://doi.org/10.3390/land13091377

Hirano, T., Ohkubo, S., Itoh, M., Tsuzuki, H., Sakabe, A., Takahashi, H., Kusin, K., Osaki, M. (2024) Large variation in carbon dioxide emissions from tropical peat swamp forests due to disturbances. *Communications Earth and Environment*, 5(1), 221. https://doi.org/10.1038/s43247-024-01387-7

Husen, E., Salma, S., Agus, F. (2014) Peat emission control by groundwater management and soil amendments: Evidence from laboratory experiments. *Mitigation and Adaptation Strategies for Global Change*, 19(6), 821–829. https://doi.org/10.1007/s11027-013-9526-3

Indriani, F., Siregar, U.J., Matra, D.D., Siregar, I.Z. (2020) De novo transcriptome datasets of *Shorea balangeran* leaves and basal stem in waterlogged and dry soil. *Data in Brief*, 28, 104998. https://doi.org/10.1016/j.dib.2019.104998

Irwin, D., Schluter, D. (2022) Hybridization and the coexistence of species. *The American Naturalist*, 200(3), E93–E109. https://doi.org/10.1086/720365

Kurniasari, F., Kurniawan, S., Nopriani, L.S., Rachmanadi, D. (2021) Analisis sifat kimia gambut pasca kebakaran dengan berbagai upaya pemulihan hutan di Kawasan Hutan Dengan Tujuan Khusus (KHDTK) Tumbang Nusa, Kalimantan Tengah (Analysis of the chemical properties of post-fire peat with various forest restoration efforts in the Special Purpose Forest Area (KHDTK) Tumbang Nusa, Central Kalimantan. *Jurnal Tanah Dan Sumberdaya Lahan*, 8(1), 221–230 (in Indonesian). https://doi.org/10.21776/ub.jtsl.2021.008.1.25

Li, W., Ullah, S., Xu, Y., Bai, T., Ye, S., Jiang, W., Yang, M. (2022) Effects of elevated aluminum concentration and distribution on root damage, cell wall polysaccharides, and nutrient uptake in different tolerant *Eucalyptus* clones. *International Journal of Molecular Sciences*, 23(21), 13438. https://doi.org/10.3390/ijms232113438

Link, N.T., McLaughlin, D.L., Stewart, R.D., Strahm, B.D., Varner, J.M., Word, C.S., Wurster, F.C. (2023) Hydrologic-based modelling of burn depth potentials in degraded peat soils. *Hydrological Processes*, 37(1), e14808. https://doi.org/10.1002/hyp.14808

Malahayati, Arlita, T., Dewiyanti, I. (2023) Indeks nilai penting dan keanekaragaman jenis vegetasi mangrove di Pesisir Utara Aceh Besar (Index of importance value and diversity of mangrove vegetation species on the north coast of Aceh Besar. *Jurnal Ilmiah Mahasiswa Pertanian*, 8(1), 522–531 (in Indonesian).

Mariaty, M., Santosa, P.B. (2020) Studi tingkat keanekaragaman hayati lahan bekas terbakar di Taman Nasional Sebangau & Kawasan Hutan Dengan Tujuan Khusus (KHDTK) Tumbang Nusa (Biodiversity level study of burned land in Sebangau National Park & Tumbang Nusa Special Purpose Forest Area (KHDTK)). *Daun: Jurnal Ilmiah Pertanian Dan Kehutanan*, 6(2), 129–139 (in Indonesian). https://doi.org/10.33084/daun.v6i2.1259

Mueller-Dombois, D., Ellenberg, H. (1974) *Aims and Methods of Vegetation Ecology*. John Wiley & Sons Inc, New York, 547 pp.

Mustamo, P., Hyvärinen, M., Ronkanen, A.K., Kløve, B. (2016) Physical properties of peat soils under different land use options. *Soil Use and Management*, 32(3), 400–410. https://doi.org/10.1111/sum.12272

Nachtigall, S., Mohr, K., Giani, L. (2023) Water, soil and vegetation under the influence of high atmospheric nitrogen deposition in a cutover and rewetted raised bog in Northwest Germany. *Mires and Peat*, 29, 07. https://doi.org/10.19189/MaP.2022.OMB.Sc.1805613

Nugraheni, M., Zakaria, A. (2023) Analisis Pengaruh Fenomena Iklim El-Nino dan La-Nina terhadap Curah Hujan di Kalimantan Tengah (Analysis of the influence of El-Nino and La-Nina climate phenomena on rainfall in Central Kalimantan). *Jurnal Teknik Sumber Daya Air*, 3(2), 117–128 (in Indonesian). https://doi.org/10.56860/jtsda.v3i2.83

Osaki, M., Kato, T., Turjaman, M., Asep, Y.A., Tsuji, N. (2023) Triharmony/trilemma of nutrients assets in tropical peatland. *Research Outreach*, February 10, 2023, www.researchoutreach.org. https://doi.org/10.32907/RO-134-3989821456

Parra-Gómez, L.J., Muraro, S., Jommi, C. (2023) An insight into drying-wetting cycles of peat. *E3S Web of Conferences*, 382, 01005. https://doi.org/10.1051/e3sconf/202338201005

Robiansyah (2020) Red Balau: *Shorea balangeran* (Plantae - Magnoliopsida). *The IUCN Red List of Threatened Species 2020: e.T33103A68072336.* (Vol. 8235). www.iucnredlist.org

Sakuntaladewi, N., Mendham, D.S., Subarudi, Rochmayanto, Y., Jalilov, S.M., Djaenudin, D., Effendi, R., Astana, S., Wibowo, A. (2024) Vulnerability of communities living on peatlands to climate change and peatland degradation: A case study in Tumbang Nusa Village, Central Kalimantan, Indonesia. *Mires and Peat*, 30, 05. https://doi.org/10.19189/MaP.2023.OMB.Sc.2118578

Seniczak, A., Seniczak, S., Iturrondobeitia, J.C., Gwiazdowicz, D.J., Waldon-Rudzionek, B., Flatberg, K.I., Bolger, T. (2022) Mites (Oribatida and Mesostigmata) and vegetation as complementary bioindicators in peatlands. *Science of the Total Environment*, 851, 158335. https://doi.org/10.1016/j.scitotenv.2022.158335

Smith, S.W., Rahman, N.E.B., Harrison, M.E., Shiodera, S. and 39 others (2022) Tree species that 'live slow, die older' enhance tropical peat swamp restoration: Evidence from a systematic review. *Journal of Applied Ecology*, 59(8), 1950–1966. https://doi.org/10.1111/1365-2664.14232

Turetsky, M.R., Benscoter, B., Page, S., Rein, G., van der Werf, G.R., Watts, A. (2015) Global vulnerability of peatlands to fire and carbon loss. *Nature Geoscience*, 8, 11–14. https://doi.org/10.1038/ngeo2325

Ur Rahman, S., Han, J.C., Ahmad, M., Ashraf, M.N., Khaliq, M.A., Yousaf, M., Wang, Y., Yasin, G., Nawaz, M.F., Khan, K.A., Du, Z. (2024) Aluminum phytotoxicity in acidic environments: A comprehensive review of plant tolerance and adaptation strategies. *Ecotoxicology and Environmental Safety*, 269, 115791. https://doi.org/10.1016/j.ecoenv.2023.115791

Wardani, M., Susilo, A. (2016) Deskripsi tempat tumbuh, keragaman morfologi dan kandungan senyawa fitokimia *Shorea balangeran* Burck di hutan Bangka Belitung (Description of habitat, morphological diversity and phytochemical compound content of *Shorea balangeran* Burck in Bangka Belitung Forest) *Buletin Plasma Nutfah*, 22(2), 81–92 (in Indonesian). https://doi.org/10.21082/blpn.v22n2.2016.p81-92

Wilson, R.M., Hough, M.A., Verbeke, B.A., Hodgkins, S.B., Tyson, G., Sullivan, M.B., Brodie, E., Riley, W.J., Woodcroft, B., McCalley, C., Dominguez, S.C., Crill, P.M., Varner, R.K., Frolking, S., Cooper, W.T., Chanton, J.P., Saleska, S.D., Rich, V.I., Tfaily, M.M. (2022) Plant organic matter inputs exert a strong control on soil organic matter decomposition in a thawing permafrost peatland. *Science of the Total Environment*, 820, 152757. https://doi.org/10.1016/j.scitotenv.2021.152757

Yamamoto, K., Sayama, T., Apip (2021) Impact of climate change on flood inundation in a tropical river basin in Indonesia. *Progress in Earth and Planetary Science*, 8, 5. https://doi.org/10.1186/s40645-020-00386-4

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