The orangutan habitat in Sebangau National Park, Indonesia: Twenty years of forest regrowth

Adventus Panda[1], Tjut Sugandawaty Djohan[2]

[1] Department of Biological Science, University of Palangka Raya, Central Kalimantan, Indonesia
[2] Ecology and Conservation Laboratory, Universitas Gadjah Mada, Yogyakarta, Indonesia

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SUMMARY

Forest logging operations have negatively affected the populations of orangutans and other wildlife species in Sebangau National Park, Indonesia. Understanding these changes is critical for effective conservation efforts. While techniques for mapping vegetation at landscape scale have advanced significantly, detailed assessments of forest profiles and orangutan habitats at local scale are lacking. To address this gap, data were collected from four forest zones with distinct tree composition, located in two different areas: the Natural Laboratory Peat Swamp Forest (NLPSF) and Punggualas (PA). Sixteen 20 m × 20 m plots were used to collect data on vegetation, soil and water quality, and to construct tree species profiles using the Oldeman method. Physico-chemical factors were measured on-site and laboratory analyses of soil samples were carried out. Canonical correspondence analysis was employed to examine site – species relationships in three dimensions. The analysis revealed that forest regrowth is in progress at both the NLPSF and PA, with significant potential for replacement of the previously logged trees by saplings. Continuous habitat restoration is essential to foster the natural regeneration of tree seedlings that will contribute to future forest recovery. The study also identified spatial heterogeneity in the NLPSF and PA forest habitats, reflecting the disturbed forest structure and the responses of trees to altered patterns of light intensity and water table depth. Nonetheless, the combination of tree species at both locations provided abundant dietary resources for orangutans. Ongoing efforts to enhance recovery of the Sebangau forest ecosystem, involving community participation, have further supported orangutan habitat conservation.

KEY WORDS: heterogeneity, *Pongo pygmaeus*, tropical peat swamp forest, vegetation, vertical structure

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INTRODUCTION

Habitat loss has been widely recognised as a critical factor influencing biodiversity dynamics, and the importance of understanding how habitat changes influence wildlife behaviour has been emphasised by numerous authors (Fagan *et al*. 1999, Hanski 2011, Hardus *et al*. 2012, Loken *et al*. 2013, Ashbury *et al*. 2015, Hoverman & Searle 2016). In this study we record ecosystem characteristics and elucidate the effects on biota of modifications to habitat structure at Sebangau Forest as a representative example of lowland tropical peat swamp forest, which is a vital ecosystem on the island of Borneo. This forest supports a diverse biological community including 215 tree and 92 non-tree plant, 73 ant, 66 butterfly, 297 spider, 41 dragonfly/damselfly, 55 fish, 11 amphibian, 46 reptile, 172 bird and 65 mammal taxa (Husson *et al*. 2018). However, between 1970 and 2000, Sebangau Forest was disturbed by (legal) logging concession activities. Additionally, most of the forest was affected by illegal logging until early 2005, when the Indonesian government took law enforcement action through the Presidential Instruction INPRES No. 4/2005 regarding the eradication of illegal logging. Both the logging concessions and illegal logging have contributed to habitat loss and fragmentation within the Sebangau peat swamp forest ecosystem, which has severely affected orangutan populations.

Forest structure can significantly influence wildlife behaviour and trophic dynamics. Therefore, understanding how the forest's structure has changed over the last three decades, and the consequences for wildlife behaviour, is crucial for conservation efforts. A previous vegetation study at Sebangau revealed distinct differences in forest structure and tree species composition along the sequence of forest subtypes (riverine, mixed-swamp, low-pole, tall interior) encountered when moving from the river's edge towards the interior (Page *et al*. 1999). Further classification of habitat types within these forest subtypes accounted for orangutan movement range, highlighting canopy connectivity categories such as tall-connected, medium-incomplete connectivity and low mixed secondary (Morrogh-Bernard *et al*. 2014). The agent-based simulation model BORNEO (arBOReal aNimal movEment mOdel) was applied in the NLPSF to further illustrate effects on orangutan movement in detail (Widyastuti *et al*. 2022). By considering tree spacing and canopy structure, these authors effectively elucidated both terrestrial and arboreal movements of orangutan within the Sebangau forest ecosystem.

The interplay between ecological and epidemiological factors underscores the need to consider disease dynamics within the context of changing forest structures in the Sebangau ecosystem (Harrison *et al*. 2020). Instances where forest fragmentation has altered intra- and inter-species interactions are well documented (Murcia 1995, Fagan *et al*. 1999, Fahrig 2003, Foley *et al*. 2005), and disturbed forest habitats in Africa often create optimal conditions for inter-species transmission of pathogenic agents in primates (Mbora & Meikle 2004, Mbora & Munene 2006, Gillespie *et al.* 2008, Mbora & McPeek 2009). Through exposure to external factors and edge effects, orangutans are increasingly susceptible to transmission of intestinal parasites from humans and other species, and vice versa (Kuze *et al*. 2010, Labes *et al*. 2010, Nurcahyo *et al*. 2017). Recent studies have revealed that such parasitic transmission has indeed occurred in Sebangau orangutans (Hilser 2011, Gwynn *et al*. 2024, Panda *et al*. 2025).

Similarly, structural changes in the Sebangau forest, including alterations to vegetation density, canopy cover and fragmentation, have altered the availability of suitable habitats for orangutans. These changes may have resulted in reduced habitat connectivity and even the displacement of orangutan populations (Buchholtz *et al*. 2020, Schmera *et al*. 2020, Garsetiasih *et al*. 2022). Many studies have utilised remote sensing, drone and other un-manned vehicle technology to create vegetation maps and assess burnt areas and habitat connectivity at the landscape scale (Gaveau *et al*. 2014, Estoque *et al*. 2021, Sloan *et al*. 2022, Arasumani *et al*. 2023, Lippmann *et al*. 2023, Steenvoorden & Limpens 2023). For the Sebangau ecosystem, however, detailed assessments of forest profiles, particularly regarding forest layer stratification and canopy interconnectivity after 20 years of regrowth, are still needed. This study examined the growth-form composition and availability of orangutan diet trees across forest subtypes within two study areas. Additionally, we assessed vertical forest structure and physico-chemical properties of peat in the context of potential effects on orangutan distribution.

METHODS

Study sites

The research on forest profiles was conducted at two peat swamp forest sites in Central Kalimantan Province, Indonesia, namely the Natural Laboratory Peat Swamp Forest (NLPSF) and Punggualas (PA) Forest (Figure 1). The NLPSF is located in the north-eastern part of Sebangau National Park and is managed by the Centre for International Co-operation in Sustainable Management of Tropical Peatland (CIMTROP) UPR. It was formerly a logging concession operated by PT Setia Alam Jaya and since 1998 has been designated as a research centre encompassing an area of 50,000 hectares. It lies adjacent to Kereng Bangkirai, the only village located nearby. In contrast, the PA Forest is situated in the western part of Sebangau National Park, at the Katingan River adjacent to Karuing and Jahanjang Villages. Like the NLPSF, it was previously a logging concession (managed by PT. Nusantara Plywood). Currently, the PA Forest serves as a focal point for tourism, offering opportunities to observe wildlife species including orangutans.

Historically, logging practices have altered the structure and composition of the forest communities. In the lower-riverine zone of the NLPSF forest ecosystem, commercial tree species such as *Calophyllum hosei, Shorea belangeran* and *Diospyros areolata* are prevalent. On the other hand, the lower-riverine zone of the PA forest consists mainly of non-commercial species like *Lophopetalum* sp., *Gardenia* cf. *pterocalyx* and *Ardisia* cf. *sanguinolenta*. In 2004–2005, illegal logging primarily targeted the lower-riverine zone along the Katingan River, particularly in Rasau and PA riverine. Logging operations focused on particular species including *Dyera polyphylla*, *Mezzetia leptopoda*, *Parartocarpus venenosus* and *Xylopia fusca* as well as the genera *Palaquium, Callophylum* and *Diospyros* (Husson & Morrogh-Bernard 2004).

Both of the study areas have experienced forest fires. The PA forest burned once in 2001–2002 (M. Porkab, GIS Specialist for WWF-ID, personal communication); whereas the NLPSF has experienced recurrent fires, in 2001–2002, 2005, 2009, 2013 and 2015 (Erb *et al.* 2018, Santika *et al.* 2020).

Field data collection and sampling

At both study sites, four distinct forest zones were delineated. The lower-riverine zone was closest to the Sebangau River (at NLPSF) or the Katingan River (at PA), whereas the upper-interior zone was farthest from the river in each case. In terms of distance from

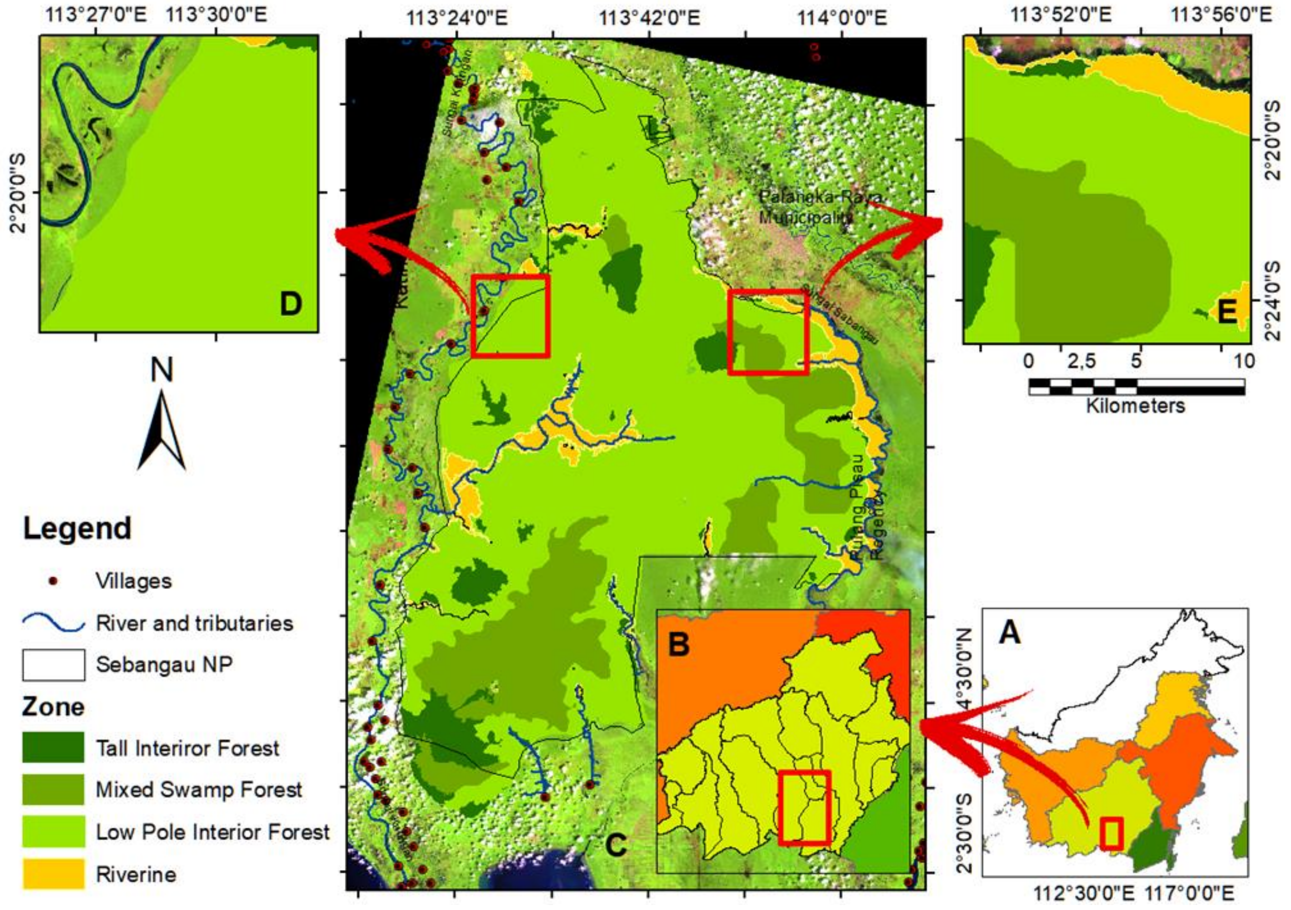

Figure 1. Maps of the study areas at NLPSF and PA study sites in Sebangau Forest. A: Kalimantan Island; B: Central Kalimantan Province; C: Sebangau Forest, showing the boundary of Sebangau National Park; C: PA forest; E: NLPSF forest.

the river, the four zones were arranged as follows: lower-riverine zone (0.5–1.5 km), middle zone (1.6–3.4 km), lower-interior zone (3.5–6 km), and upper-interior zone (6.1–8 km) (Figures 1C–E and 2a).

Vegetation data were collected using belt transects, which were 0.1 km wide and 8 km long (Figure 2). Within each forest zone along the belt transect, two randomly placed 20 m × 20 m quadrat plots were established (note that plots were not spaced evenly along the transects). Each plot was divided into four quadrants (Figure 2b), and all tree plants (seedlings, saplings and trees) per quadrant were identified and recorded. Species with other growth forms (e.g., shrubs, herbs, herbaceous and woody lianas) were recorded within 1 m × 1 m and 5 m × 5 m subdivisions of one quadrant of the plot as schematised in Figure 2c. Trees were categorised on the basis of individual measurements of diameter at breast height (DBH) as: seedlings (height < 1.5 m, DBH < 3 cm), saplings (DBH 3–19.9 cm) and trees (DBH ≥ 20 cm). For each tree species, the following data were collected: density, basal area, first branch height, total height and total canopy cover (Oldeman 1972, Hallé *et al.* 1978). In both study areas a local botanist was present to identify the species. Scientific names were assigned according to checklists of Sebangau flora (Husson *et al.* 2018) and Punggualas flora (Panda *et al.* 2013, 2023).

Other data collected on-site at each plot (five locations; see Figure 2d) were: water table depth (below ground level) using a piezometer made from 6.4 cm PVC pipe (Panda *et al*. 2011); air temperature and relative humidity (RH) using a TH-22® data logger; light intensity using a WT81® light meter; and peat soil pH using a Soil Tester Takemura® DM15. For broader context, precipitation, temperature and water table data for 2004–2019 (see Figure 3) were provided by Dr Kitso Kusin of CIMTROP UPR.

Peat samples were collected from 20 cm depth at the same five sampling points (Figure 2d), into a 5 cm PVC tube mounted on a modified peat auger. The five

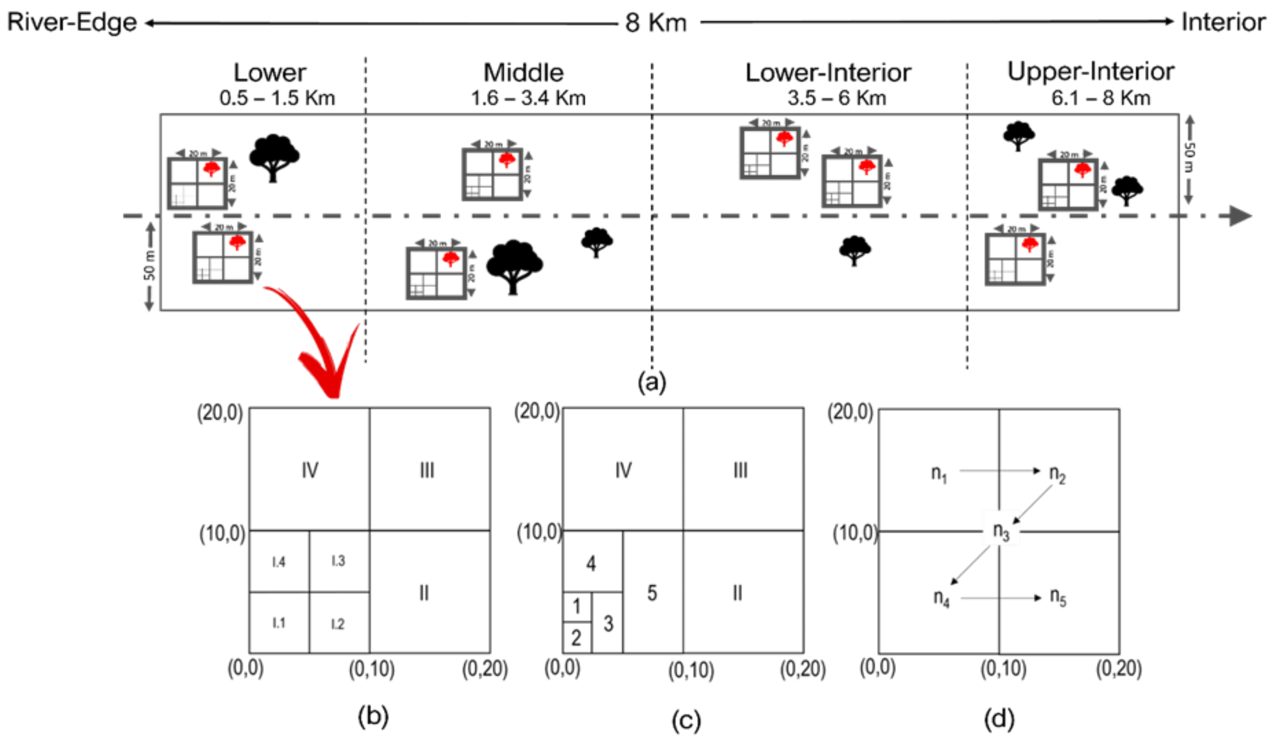

Figure 2. Field data collection and sampling workflow: (a) belt transect (8 km) through four zones; (b and c) the sequence of plant-data collection in each quadrant of a plot; (d) the arrangement of points (n_1–n_5) for light intensity and other measurements plus collection of composite ($\Sigma[n_1, n_2 ... n_5]$) soil samples. Labels around the plot edges in (b), (c) and (d) refer to the co-ordinate system used to guide surveyors. Not to scale.

peat samples from each vegetation plot were mixed to form one composite sample per plot.

Laboratory analyses

The peat samples were analysed at the Analytical Laboratory, University of Palangka Raya, for total N (Kjedahl method), P_2O_5 (Bray I method), total C-org (Spectro-UV method), and pyrite (H_2O_2). The analytical procedures followed Burt (2004) and Hikmatullah & Sukarman (2015).

Data analysis

The vegetation data were used to develop habitat profile drawings. All of the species counts were used to calculate Sorenson's Index of Similarity (Chao *et al.* 2006, Legendre & De Cáceres 2013, Schmera *et al.* 2020) between the NLPSF and PA forest habitats. A dendrogram was also constructed using hierarchical cluster analysis (Ward.D2 algorithm; Ward 1963), to quantify the extent of similarity.

Canonical correspondence analysis (CCA) was employed to create three-dimensional plots, facilitating multivariate analysis. Finally, CCA and degree of similarity calculations, including graphical visualisation, were performed using R-Studio 4.4.1 (R Core Team 2024).

RESULTS

Forest composition and structure

The growth forms of all plant species recorded across all zones of the NLPSF and PA forests encompassed nine categories: trees, tree saplings, tree seedlings, herbs, epiphytes, shrubs, herbaceous lianas, woody lianas and ferns. At NLPSF, all nine growth forms were present in the lower-interior zone, whereas ferns and epiphytes were absent from the lower-riverine and middle zones, respectively (Figure 4). In contrast, the PA forest zones exhibited variable absence of 2–4 growth forms including shrubs, herbs, epiphytes and ferns. The most abundant and species-rich growth form across almost all forest subtypes in both NLPSF and PA was tree seedlings.

Canopy gaps allow sunlight to penetrate to the forest floor, influencing plant growth and diversity. In the NLPSF forest, gap sizes ranged from 8 m^2 to 22.14 m^2. Conversely, from the lower-riverine zone to the interior of the PA forest, canopy gap sizes ranged from 19 m^2 to 131.25 m^2. A second notable feature at PA was the absence of herbs, epiphytes and shrubs from the lower-riverine zone (Figure 4).

The number of forest-floor plant species differed between the NLPSF and PA habitats, with 46 species

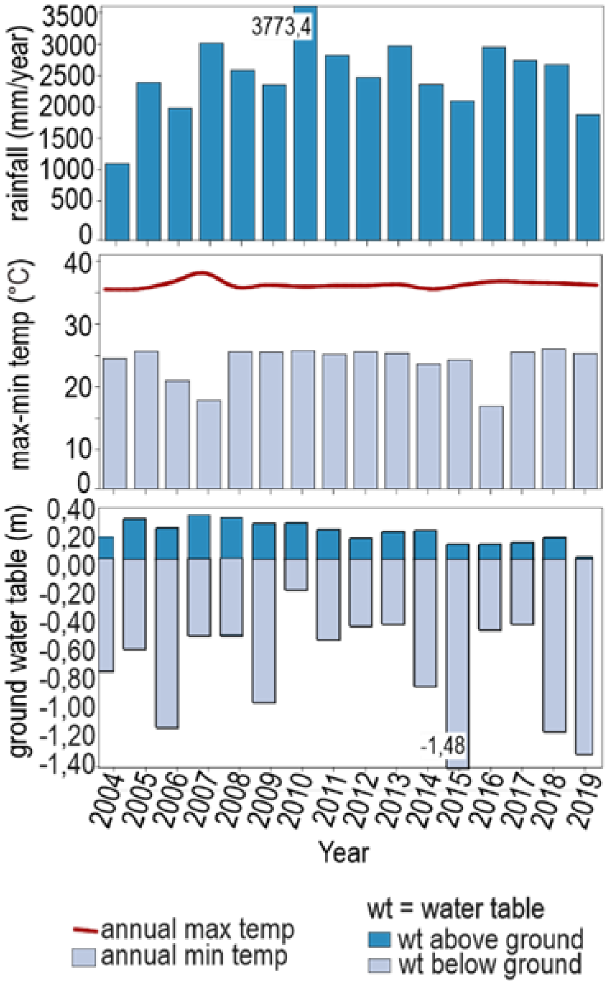

Figure 3. Annual precipitation (mm), and maximum and minimum values of temperature (°C) and water table level (m) for the period 2004–2019, recorded at NLPSF Meteorology Station (Dr Kitso Kusin, personal communication 2020).

recorded at NLPSF and 67 species at PA. In the NLPSF, the number of forest-floor species decreased progressively from the lower-riverine zone through the middle and lower-interior zones to the upper-interior zone, which returned counts of 36, 40, 33 and 24, respectively. Conversely, in the PA forest habitat, the number of forest-floor species increased from the lower-riverine zone to the upper-interior zone, with species counts of 6, 10, 34 and 31, respectively (Figures A1–A4 in the Appendix).

Vertically, the forest profiles in the two study sites comprised five layers, namely tree, tree-sapling, tree-seedling, understorey and floor vegetation. The tree canopy shapes in the NLPSF forest were predominantly oval to circular. In contrast, the PA forest featured tree canopies that were primarily rhomboid, with circular shapes being rare (Figures A5–A8). Additionally, the canopy gap sizes in the PA forest habitat increased from 19 m^2 to 131.25 m^2 from the lower-riverine to the upper-interior zone.

Physico-chemical factors

The data from the NLPSF Meteorology Station (Figure 3) show the large range of water table levels (relative to ground level) recorded at Sebangau, from a maximum around + 30 cm during some wet seasons to approximately -148 cm in the most intensely dry seasons of the El-Niño cycle. Results from the belt transects showed that the mean water table level varied from 0.21 m in the lower-riverine zone to 0.3 m in the interior of the NLPSF forest, whereas it changed from 0.18 m to 0.43 m across the same zonal range in the PA forest (Figure 5). The intensity of light reaching the forest floor was closely related to the canopy profiles across the habitat zones. In the lower-riverine zones of both the NLPSF and the PA forest habitats, light intensity was recorded as 690.25 Lux. In the NLPSF habitat, the light intensity decreased to 529.25 Lux in the middle zone, then increased to 581 Lux in the lower-interior zone and fell to 513.5 Lux in the upper-interior zone. Conversely, the PA forest habitat exhibited a pattern of monotonically decreasing light intensity across these zones, with values of 597.9, 541.3 and 525.95 Lux, respectively (Figure 5). Peat soil pH in the NLPSF forest ranged from 4 in the lower-riverine zone to 4.3 in the upper-interior zone; while the PA forest habitat exhibited a pH range of 3.8 to 4.5 across the same zones. The total nitrogen (N-tot) content of the peat exhibited varied across the forest habitats. At NLPSF, it decreased from 1.2 % in the lower-interior zone to 0.5 % in the upper-interior zone. The PA forest habitat showed a wider range, from 0.3 % to 1.9 % across the four zones. Organic carbon content varied across the zones from lower-riverine to upper-interior at both NLPSF and PA. At the NLPSF site, organic carbon (C-org) showed minimal variation, ranging from 56.57 % to 56.89 %. In contrast, soil in the PA forest exhibited a broader variation of C-org values, ranging from 50.14 % to 56.73 %. The P-available (P_2O_5) content also varied between zones at both study sites. In the NLPSF forest habitat, the sequence of P-available values from the lower-riverine zone to the upper-upper interior zone was 114.15, 133.07, 96.54, 87.79 ppm. In the PA forest habitat, the corresponding values were 108.57, 72.49, 80.35 and 181.87 ppm (Figure 5).

Statistical analyses

The forest communities at NLPSF and PA responded differently to the physico-chemical properties of their respective habitats, as demonstrated by tri-plot canonical correspondence analysis (CCA). In the

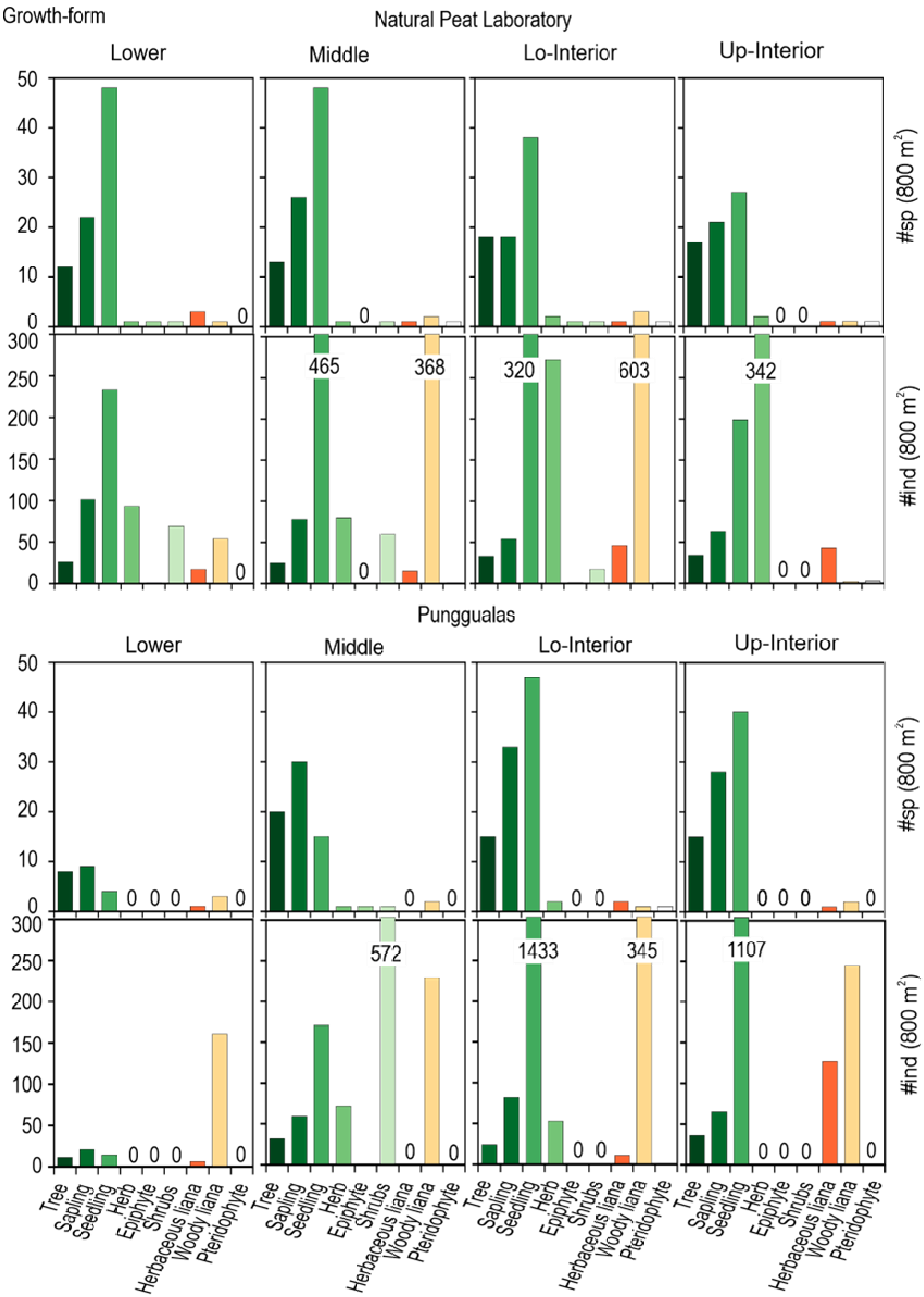

Figure 4. Total counts (per 800 m^2) of species and individual plants belonging to all of the plant growth-form groups that were distinguished in each forest zone at NLPSF (top) and PA (bottom); #sp: number of species; #ind: number of individuals.

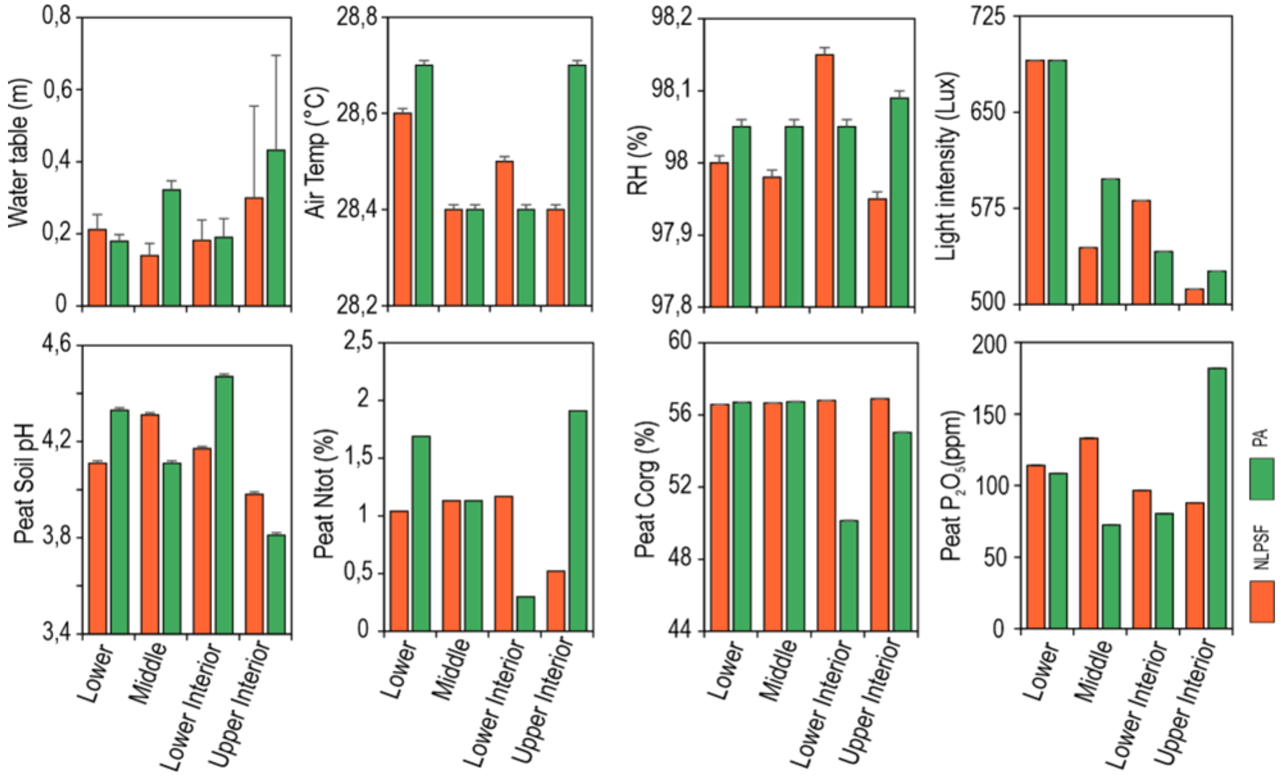

Figure 5. Physico-chemical factors: water table level relative to ground level (m), air temperature (°C), relative humidity (RH; %), light intensity (Lux), peat soil pH, peat N-tot (%), peat C-org (%), and peat P_2O_5 (ppm). The values plotted are averages of ten measurements (two plots) per zone, at NLPSF (orange) and PA (green).

NLPSF forest habitat, the total inertia variance was 1.125 and the eigenvalues were CCA1: 0.4338 and CCA2: 0.2633. On the other hand, the PA forest showed a total inertia variance of 2.303 and eigenvalues CCA1: 0.7937 and CCA2: 0.3813.

The CCA analysis (Figure 6) revealed spatial heterogeneity in both the NLPSF and the PA forest habitats. The inertia and weighted variance values indicated variations in species growth forms along the physico-chemical gradient (CCA1) and between spatial zones (CCA2) at both sites. In the CCA triplot for the NLPSF forest habitat the lower-riverine zone (Plot 1 and Plot 2) appeared isolated, with species distribution influenced primarily by light intensity, N-tot and P_2O_5 content. On the other hand, the zones from middle to upper-interior formed a distinct cluster, with species distribution influenced by gradients in peat soil pH, relative humidity and water level. Similarly, in the PA forest habitat, the lower-riverine zone (Plot 1 and Plot 2) appeared separate in the CCA triplot, with species distribution influenced by soil pH and light intensity. The plots in the other three zones again formed a clustered group, with species distribution influenced by a combination of water table level, relative humidity and P_2O_5 content.

The CCA results correspond well with the outcome of the Sorenson's Index of Similarity (SI) analysis (Figure 7). The degree of similarity between the NLPSF and PA forest habitats, as revealed by the SI, varies between 10 % and 40 %. Furthermore, the dendrogram constructed using the Ward.D2 algorithm (Figure 8) confirms the heterogeneity of tree species composition between NLPSF (Plots 1–8) and PA (Plots 9–16).

DISCUSSION

Physico-chemical factors

The variations in N-tot that we observed align with the findings of Page *et al*. (1999), who reported N-tot values ranging from 1 % to 1.8 % in the middle zone and 0.8 % to 1.4 % in the upper- and lower-interior zones. Nitrogen sources in peat ecosystems include atmospheric nitrogen deposition, nitrogen deposits in peat pore-water, and absorption mechanisms facilitated by mycorrhizal complexes (Vesala *et al.* 2021). However, this study did not measure nitrogen deposition or mycorrhizal absorption mechanisms. Atmospheric nitrogen deposition is suspected to be

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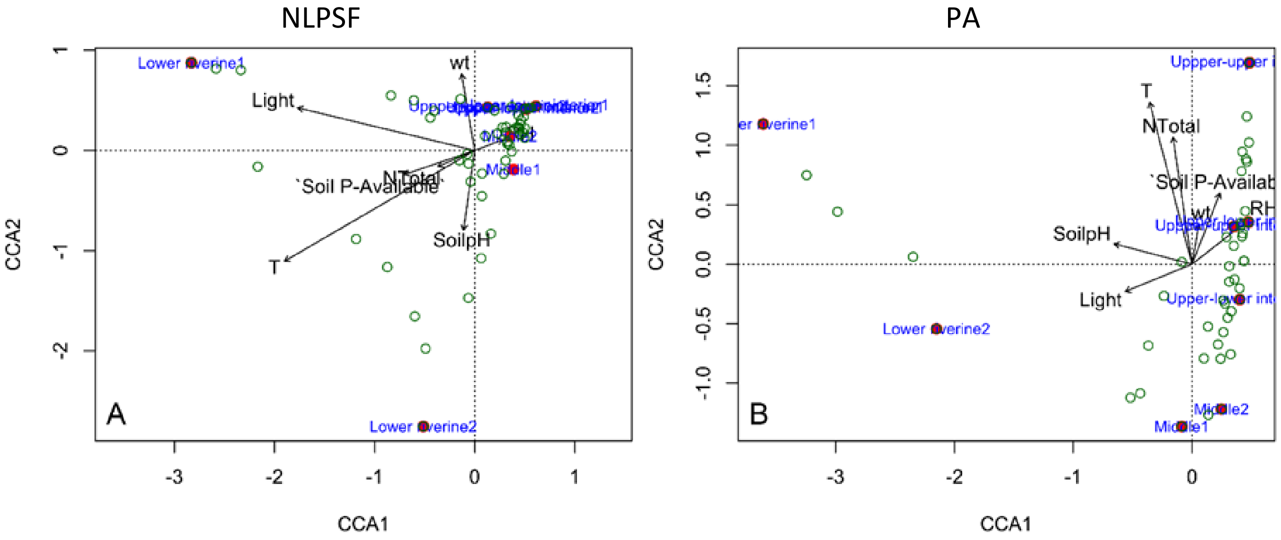

Figure 6. Site – species canonical correspondence analysis (CCA) for NLPSF (A) and PA (B).

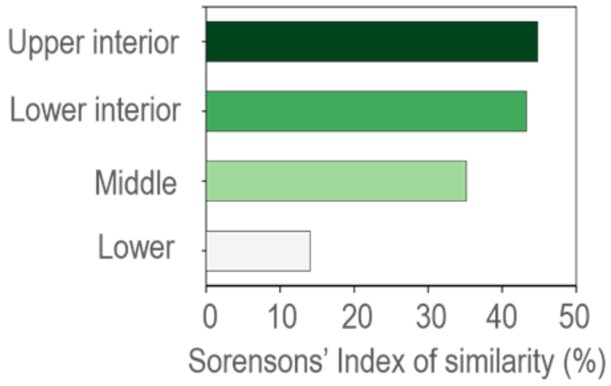

Figure 7. Sorenson's Index of Similarity, comparing the species composition of each forest zone between NLPSF and PA.

the primary nitrogen source in these ecosystems. Nitrogen fixation is carried out predominantly by members of the Fabaceae (Leguminosae) family. Nitrogen-fixing species found in the forest habitats of NLPSF and PA include *Koompasia malaccensis*, *Adenanthera pavonina* and *Leucamphalos callicarpus*. *K. malaccensis* was not observed in the study plots, but *A. pavonina* was present as seedlings and saplings (Figures A2 and A3). Interestingly, the N-content is inversely proportional to the tannin levels in these ecosystems. Higher nitrogen levels correspond to lower tannin levels and vice versa (Ong *et al.* 2015).

Peat pH in both NLPSF and PA generally falls within the range 3.5–4.2 (Page *et al.* 2006, Yule & Gomez 2009, Page & Baird 2016). These low pH values are linked to the accumulation of organic plant parts such as tree trunks, dead tree roots and leaf litter, that release phenol and tannin compounds into the surrounding puddles as they decompose. In addition, the characteristics of peat water and prevailing anaerobic conditions play a critical role in determining the extent of organic matter decomposition.

Peat chemical properties including N-tot, C-org and P_2O_5 contents are interconnected within the organic material cycle of the peatland ecosystem. In this study we observed variations in these factors between the different forest habitat zones at NLPSF and PA. Nonetheless, P_2O_5 values in the upper of 0–3 m of peat predominantly fell within the range 67–256 ppm. Page *et al.* (1999) reported previously that P_2O_5 content in NLPSF peat decreased from 256 ppm at the surface to 67 ppm at 8.0–8.4 m depth before rising to 311 ppm at 9.6–9.8 m, while Okolo *et al.* (2023) found that P_2O_5 content generally decreased with increasing peat decomposition.

Water level and the anoxic environment act as rate-limiting factors for the decomposition of organic matter from stems and branches in tropical peatland ecosystems, whereas leaves can decompose shortly after falling onto the non-waterlogged surface of the root mat. The amount of organic carbon influences the peat's capacity to immobilise nitrogen by retaining it in peat pore-water rather than releasing it into the atmosphere as gas. This underscores the role of peatland ecosystems as significant carbon pools. However, fluctuations in water table depth, light intensity, N content, organic carbon and P_2O_5 are met with adaptive responses in growth form by species occurring in the NLPSF and PA forest habitats.

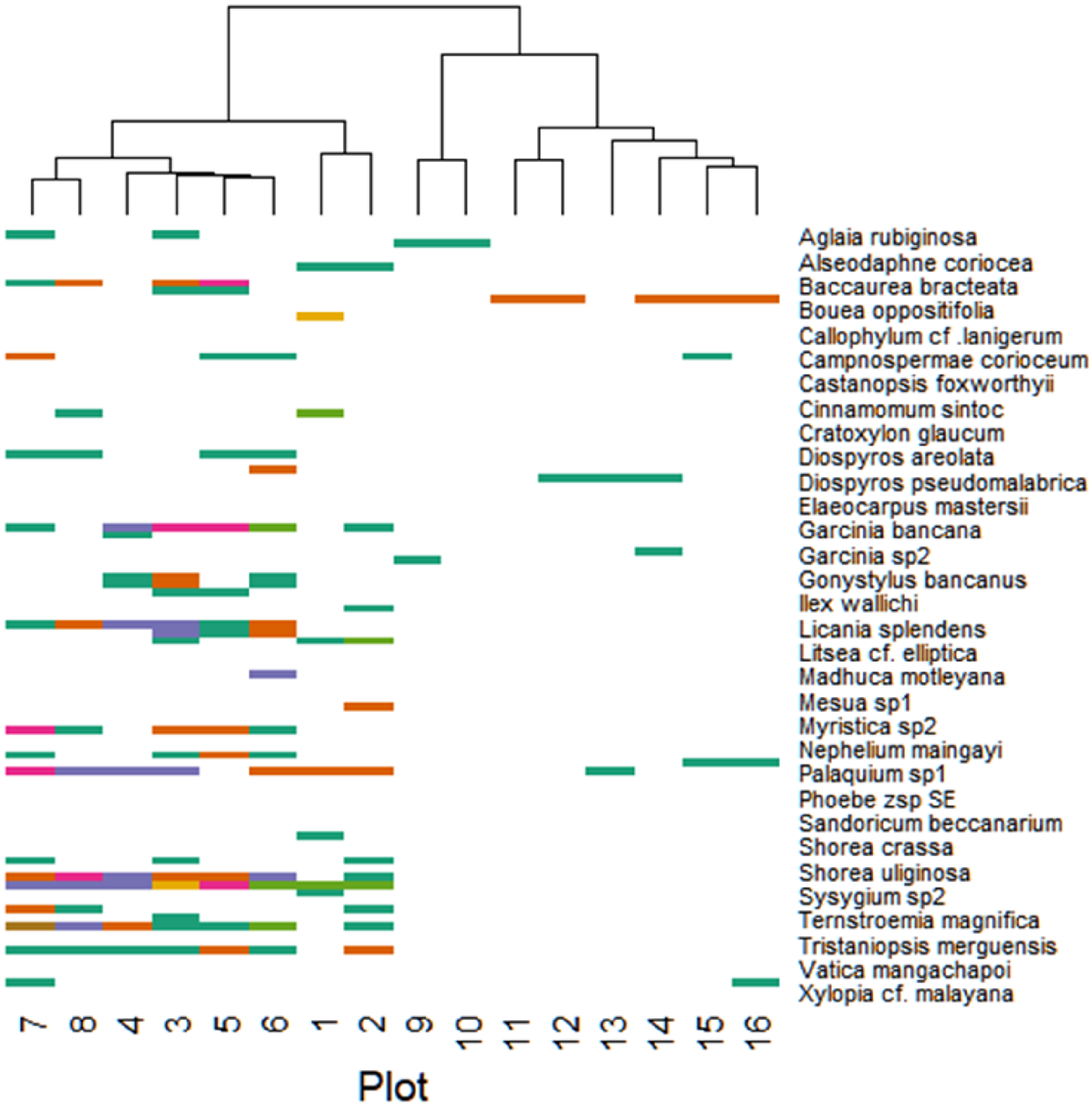

Figure 8. Dendrogram showing the degree of similarity amongst the species lists per plot, based on the Ward.D2 algorithm; Plots 1–8 are in the NLPSF study area and Plots 9–16 are at PA.

Effects of disturbance on forest structure and growth forms

Healthy tropical peat swamp forest is characterised by consistently high water table and permanently waterlogged soil conditions. Research at Mawas (adjacent to Sebangau) revealed a linear relationship between tree canopy top height and peat depth, with canopy height declining from 34 to 23 m across the peat dome. The linear relationship was not changed by logging although mean canopy height was significantly reduced (Wedeux & Coomes 2015). The decline in canopy height from edge to centre of the peat dome correlates with flooding duration and the characteristics of the species comprising the forest community (Mirmanto 2009). For instance, the endemic tree species *Shorea belangeran* (Posa *et al.* 2011) is highly flood-tolerant. Its growth strategy is suited to central peat-dome conditions, where biomass growth is relatively slow but the density of trees is greater than at more-peripheral locations.

The habitat conditions recorded in our study reflect disturbance caused by past logging activities. These activities often included the construction of railway systems to transport the logs through and out of the concession areas. However, not all concessionaires installed permanent railtracks because the required track lengths varied from year to year, depending on distance to the felling block.

To address this, temporary railways were often constructed from non-commercial timber. Logging operations also involved digging transport canals, which were cost-effective and whose dimensions (length and width) could be customised. Once the logs had been brought to a canal, they were transported on wooden rafts. Thus, although commercial timber was targeted for felling, non-commercial timber was also utilised for infrastructure. This not only resulted in wide canopy gaps, but also triggered adaptations of growth form in the trees that remained in the various forest zones which can be regarded as survival strategies, linked especially to the characteristics and degree of waterlogging of the peat. At Sebangau, the peat in the lower-riverine zone, in particular, has yet to fully recover its pre-logging water storage capacity.

Factors influencing the growth of individual trees include species characteristics and environmental adaptations. Shade-intolerant species like *Shorea belangeran*, along with fire-resistant species such as *Combretocarpus rotundatus* and *Cratoxylon arborescens*, have shown resilience in these disturbed habitats (Astiani 2016). More generally, the growth forms and individual counts of species within the forest community reflect the habitat conditions. Thus it is likely that variations in growth form are a response to, or an interaction with, physico-chemical changes resulting from logging activities. In turn, the shape and size of the canopy determines the intensity of light that reaches the forest floor. This is apparent in our data from both the NLPSF and PA forest habitats, where the variation in light intensity between zones is influenced by the vertical structure of the forest profile, canopy layer, canopy cover and the presence or absence of gap areas (Figure 5).

Forest regeneration

Currently, the forest communities at Sebangau are experiencing succession, with abundant potential for saplings to replace missing trees at both NLPSF and PA. A previous study in this peat swamp forest reported seed-bank densities of 16–74 seeds per square metre and a maximum of eleven tree species (Graham & Page 2018). However, seeds transported by animals during their migrations within core areas are unlikely to germinate unless they fall in puddle-free zones, drift after flooding, or encounter shallow water table conditions (Blackham *et al.* 2013). Thus, importantly, the presence of tree seedlings and saplings at Sebangau is a key indicator that missing trees can be replaced successfully in the future.

The position of the water table relative to ground level affects the growth of seedlings. We associate the total absence of herbs, epiphytes and shrubs from the lower-riverine zone at PA with surface flooding and, more generally, with the large range of water level fluctuations observed at Sebangau (Figure 3). Building on this idea, we distinguish three ‘forest condition’ types in terms of water level extremes, to indicate the likely presence or absence of specific plant growth forms (Figure 9), as follows:

a. Type 1: This forest type is characterised by mounds formed by intertwined tree roots, hummocks, puddles and waterlogged areas typical of peat swamp forest ecosystems. Tree species with numerous growth forms, saplings and seedlings are present, with counts per 800 m^2 of 16–48 species. Sunlight penetrates to the forest floor, allowing germination of seeds from the seed bank stored in the soil. However, the seeds remain dormant if conditions are unfavourable for their growth. Tree seedlings typically colonise near the parent trees, thus flagging the availability of a viable seed bank.

b. Type 2: The presence of water on the forest floor, including that which is absorbed by tree seedlings, is a primary factor in the observed patterns of vegetation growth. The surface flooding that occurs in the riverine environment has been found to have a detrimental effect on the growth of seedling shrubs, herbs and epiphytes; although in certain reaches of the Sebangau River and its tributaries, the herb *Hanguana malayana* has been observed to grow on the water surface and colonise, while shrubs such as *Pandanus helicopus* have been documented to relocate from their initial growing positions during floods. In the middle- and upper-interior zones, seedlings are at a disadvantage in the competitive environment due to their K-strategy, which contrasts with the strategy exhibited by herbs and shrubs, which are classified as r-strategy species. In environments characterised by high density-independent (D.I.) mortality or r-strategy, populations exhibit a strategic prioritisation of reproduction over survival in conditions of high population density. Conversely, populations exhibiting density-dependent (D.D.) regulation, often referred to as K-strategists, prioritise non-reproductive endeavours, which can curtail their reproductive success in environments characterised by high D.I. mortality (Gadgil & Solbrig 1972, Pianka 1972, Bohn *et al*. 2014). Orangutans are adversely affected because prospective forage and nesting trees fail to grow in the lower-riverine and middle zones, where plant communities are dominated by shrubs and herbs.

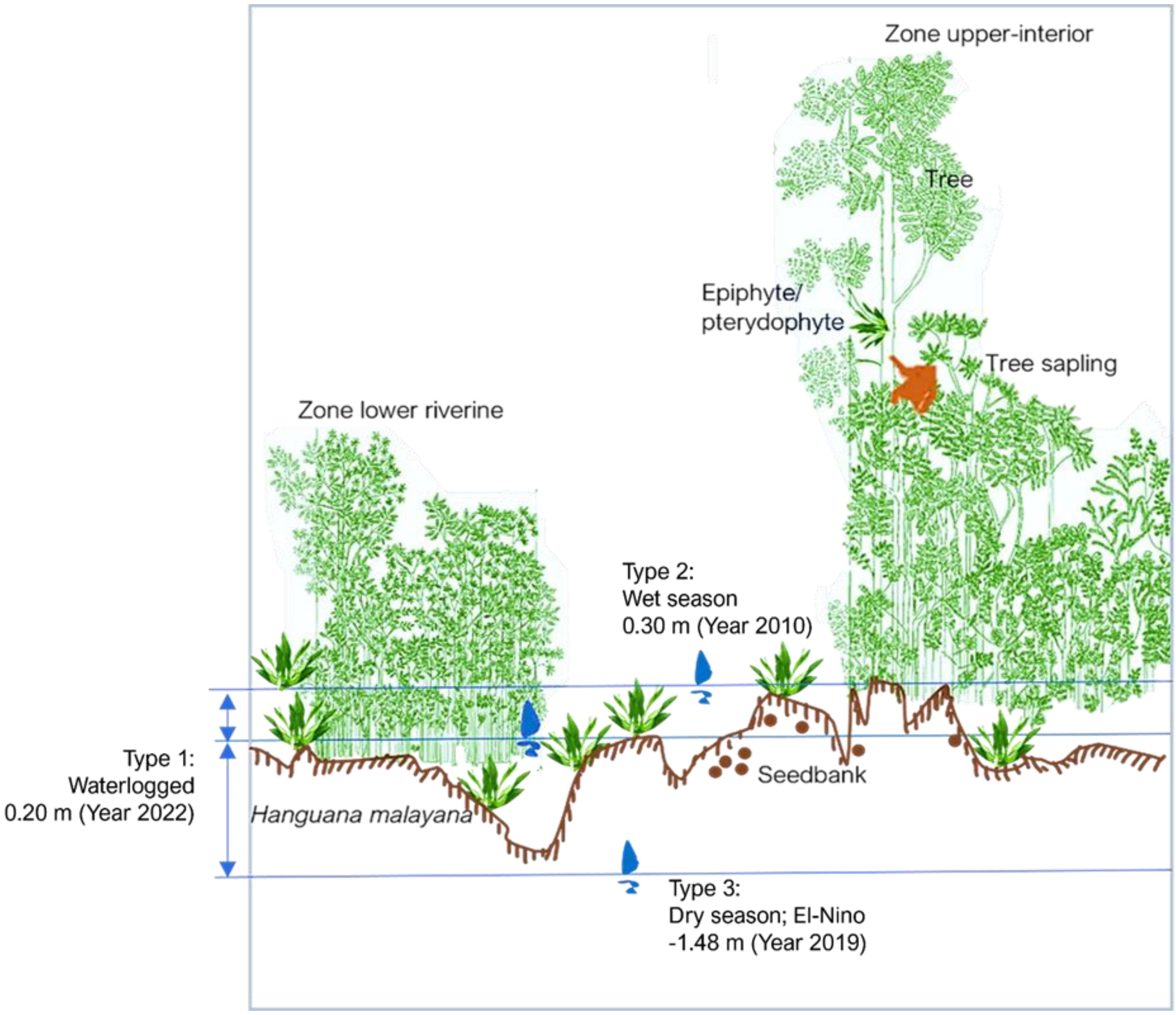

Figure 9 Interpretation of water level extremes recorded during the period 2010–2022 in terms of their significance for plant communities in the three peat swamp forest condition types (not drawn to scale). Type 1: waterlogged; Type 2: flooding; Type 3: over-drained.

c. Type 3: This type develops in over-drained situations with water table conditions such as those shown in Figure 3 for the dry seasons of 2006, 2015 and 2019. This reflects the interannual climate variation, with fires being most intense during dry years induced by El Niño episodes (Santika *et al.* 2020). Viable seed banks are present in some areas, but lowering of the water table leads to prolonged dormancy with no signs of germination. Furthermore, during fire events, smoke potentially reduces light intensity and even negatively affects photosynthetic rates (Harrison *et al.* 2009). The presence of this forest type underlines the urgent need for water management measures such as channel blocking to prevent and mitigate water loss from the peat. If old logging channels are unblocked, the situation will worsen.

Light intensity also contributes to the growth of seedlings. In fact, the responses of tree saplings to nutrient limitations and light reaching the forest floor through canopy gaps are critical for their survival in degraded forest habitats. This means the distributions of individual tree species in previously damaged forests reflect the adaptive responses of their saplings to the environmental conditions. One key factor in this regard is the forest canopy profile and its projection. This finding highlights the effects of past disturbance to canopy cover resulting from logging activities, not only on regeneration but also on the growth of seedlings, saplings and trees. In turn, the interaction of water level, light reaching the forest floor and the abundance of trees, saplings and seedlings is likely to determine the presence or absence of herbs and shrubs in each forest zone.

Implications for orangutan conservation

Our findings from this study indicate that the species composition of plant communities at the study sites provides a substantial food supply for orangutans. At both NLPSF and PA, the tree species that returned the highest count of saplings was *Syzygium havilandii*, which contributed 258 individuals per 800 m^2 or 17.2 % of the total number of saplings. Cross-referencing to the 2012–2019 phenological data from PA reveals that the fruiting period of *Syzygium* (wild guava) species is relatively consistent throughout the year except during the dry months of August and September (Ari Meididit, Kal-Teng Orangutan Forum, personal communication 2023). This reproductive consistency is associated with two distinct (synchronous and asynchronous) reproductive strategies (Morrogh-Bernard 2009). Species with synchronous reproductive cycles, such as *Calophyllum hosei*, *Stemonurus* cf. *scorpioides* and *Syzygium havilandii*, tend to produce flowers and fruits simultaneously. In contrast, species with asynchronous cycles, including *Diospryros areolata*, *Palaquium ridleyii* and *Tetractomia tetrandra*, do not produce flowers and fruits concurrently.

The species *Freycinetia angustifolia* was present in every habitat zone of NLPSF and PA except for the upper-interior zone at NLPSF, and delivered the highest recorded individual-species count of 731 individuals per 800 m^2. *Pandanus helicopus* is generally abundant in the lower-riverine zone, but our sampling results show that this species can also be found in the middle, lower-interior and upper-interior zones of NLPSF and PA. The data for forest-floor vegetation further highlighted liana vine species that are consumed by orangutans, including *Freycinetia angustifolia*, *Schefflera* sp. and *Ziziphus* cf. *angustifolia* (Russon *et al*. 2009, Panda *et al*. 2023). The lowest number of forest-floor plant species was recorded for the lower-riverine zone at PA, where only six species were observed.

The density of lianas, some members of the Pandanaceae family and tree seedlings is influenced by the shape of the canopy as well as water table depth. However, the presence of canopy gaps does not necessarily indicate improved habitat conditions, particularly in relation to the movement of orangutans between zones, since orangutans typically avoid areas with canopy gaps. Thus, a change in orangutan movement patterns might be interpreted as a probable response to changes in forest structure caused by logging (and potentially fire). The changes in forest structure may well have contributed to the recently observed alterations in orangutan behavioural patterns, which include an increase in the proportion of terrestrial locomotion relative to arboreal movement (Loken *et al.* 2013, Ancrenaz *et al.* 2014, Ashbury *et al.* 2015). This may be disadvantageous for a variety of reasons including an increased food requirement because terrestrial locomotion expends more energy (Vogel *et al.* 2017, Widyastuti *et al.* 2022).

On the basis of our observations of forest structure and recent changes in orangutan behaviour we conclude that, to promote the recovery of orangutan habitats, it is crucial to ensure that tree seedlings and saplings continue to have opportunities to grow so they can eventually replace the lost mature trees. In this context it is clear that continued attention to rewetting of the Sebangau peatland is required, since this can be expected to play a substantial role in the further enhancement of orangutan habitat.

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AUTHOR CONTRIBUTIONS

AP and TSD contributed to the design of the research; AP collected and analysed the data, and drew the forest profiles; AP and TSD wrote the manuscript; AP was responsible for communications with journal editors and reviewers.

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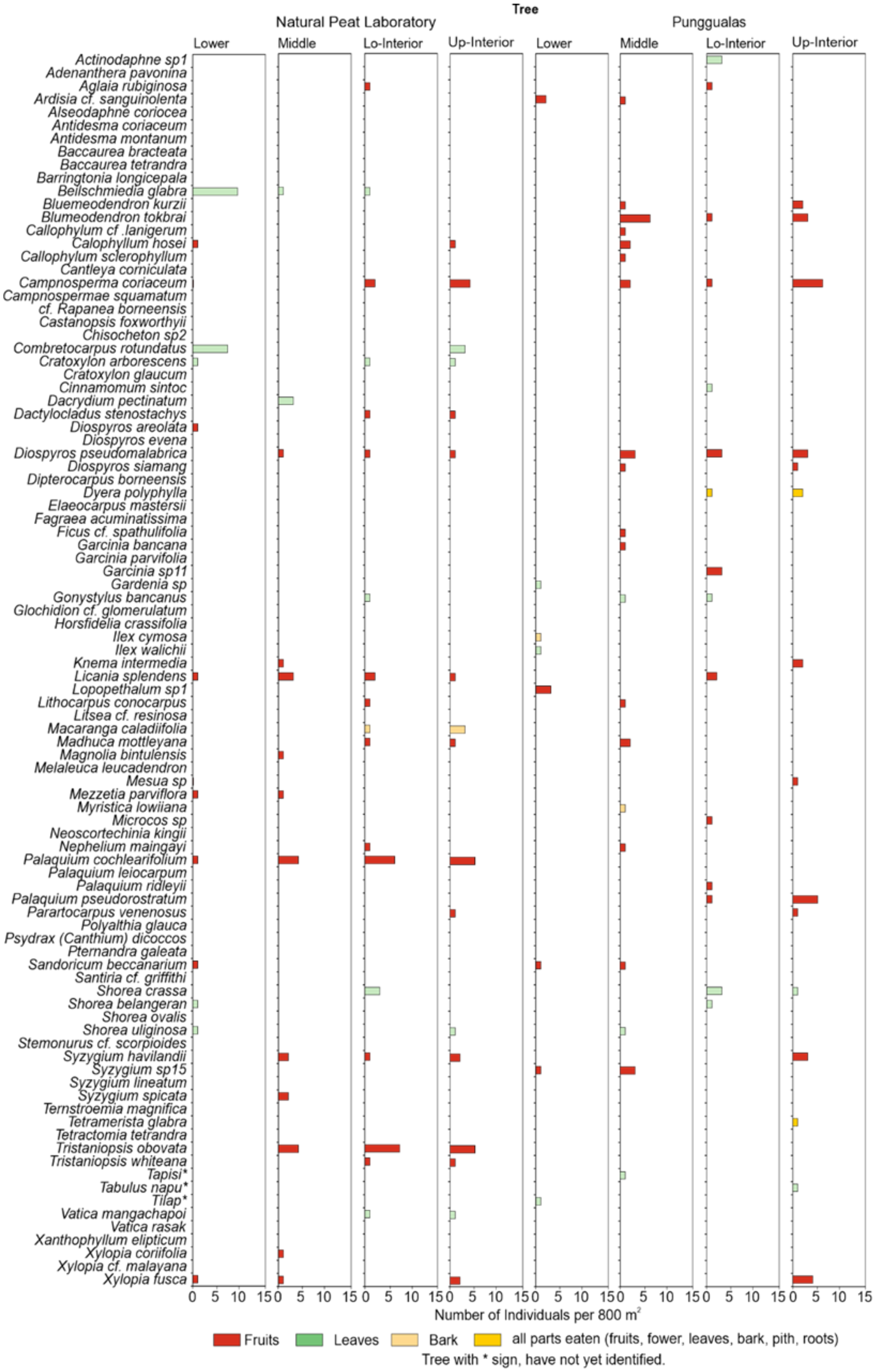
Author for correspondence: Dr Adventus Panda, Department of Biological Science, Faculty of Mathematics and Natural Science, University of Palangka Raya (UPR), Central Kalimantan Indonesia 73111A
Tel: +62 823 5984 0003; E-mail: apanda@mipa.upr.ac.id

Appendix



Tree with * sign, have not yet identified.

Figure A1. Trees: species and individual counts (per 800 m^2) in each forest zone at NLPSF and PA, September–October 2022. Coloured bars indicate plant parts that are used as food by orangutans (Panda *et al*. 2023, Russon *et al*. 2009).

Figure A2. Tree saplings: species and individual counts (per 800 m^2) in each forest zone at NLPSF and PA, September–October 2022. Coloured bars indicate plant parts that are used as food by orangutans (Panda *et al*. 2023, Russon *et al*. 2009).

Figure A3. Tree seedlings: species and individual counts (per 800 m^{2}) in each forest zone at NLPSF and PA, September–October 2022. Coloured bars indicate plant parts that are consumed as food by orangutans (Panda *et al*. 2023, Russon *et al*. 2009).

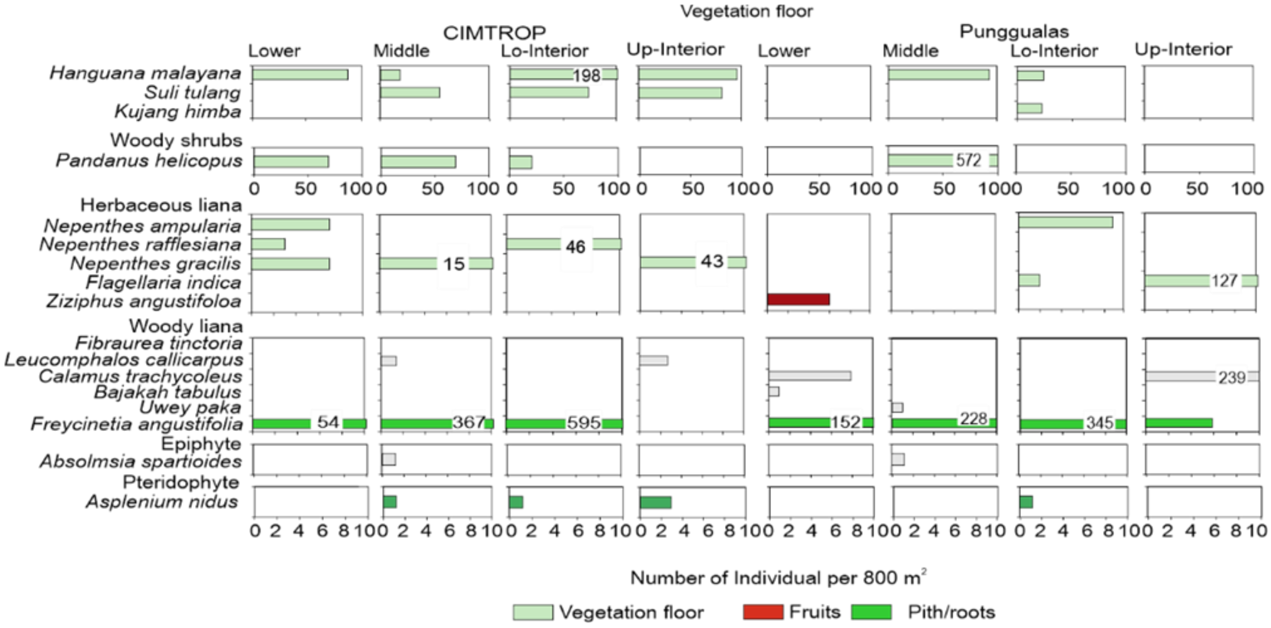


Figure A4. Forest-floor plants: species and individual counts (per 800 m^2) in each forest zone at NLPSF and PA, September–October 2022. Coloured bars indicate plant parts that are consumed as food by orangutans (Panda *et al*. 2023, Russon *et al*. 2009).

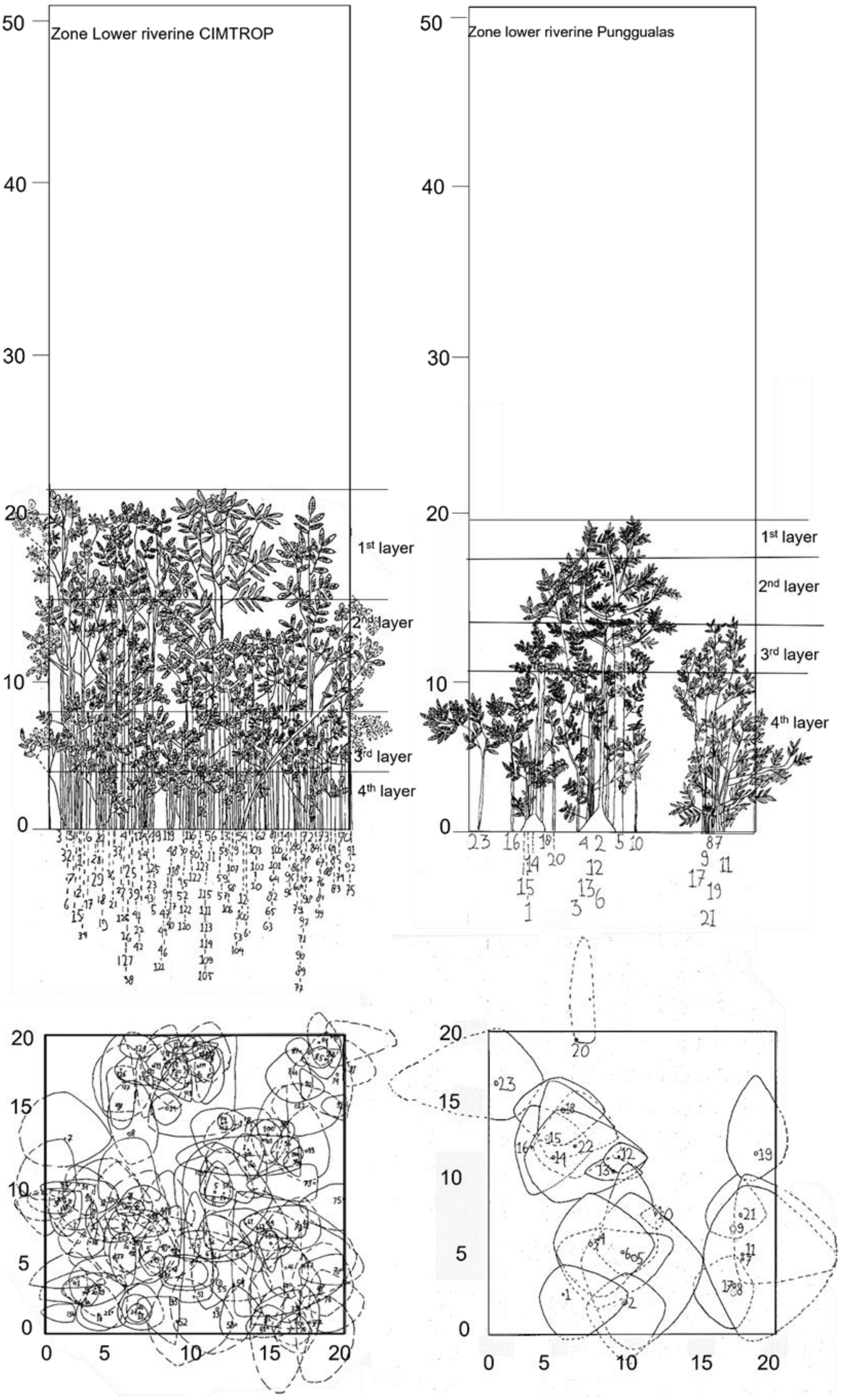


Figure A5. Forest profiles and their projections in the lower-riverine zone in the NLPSF (left) and Punggualas forest habitats (right), September and October 2022; Layers 1 to 4 are drawn to scale. The vegetation layer of the forest floor is not drawn.

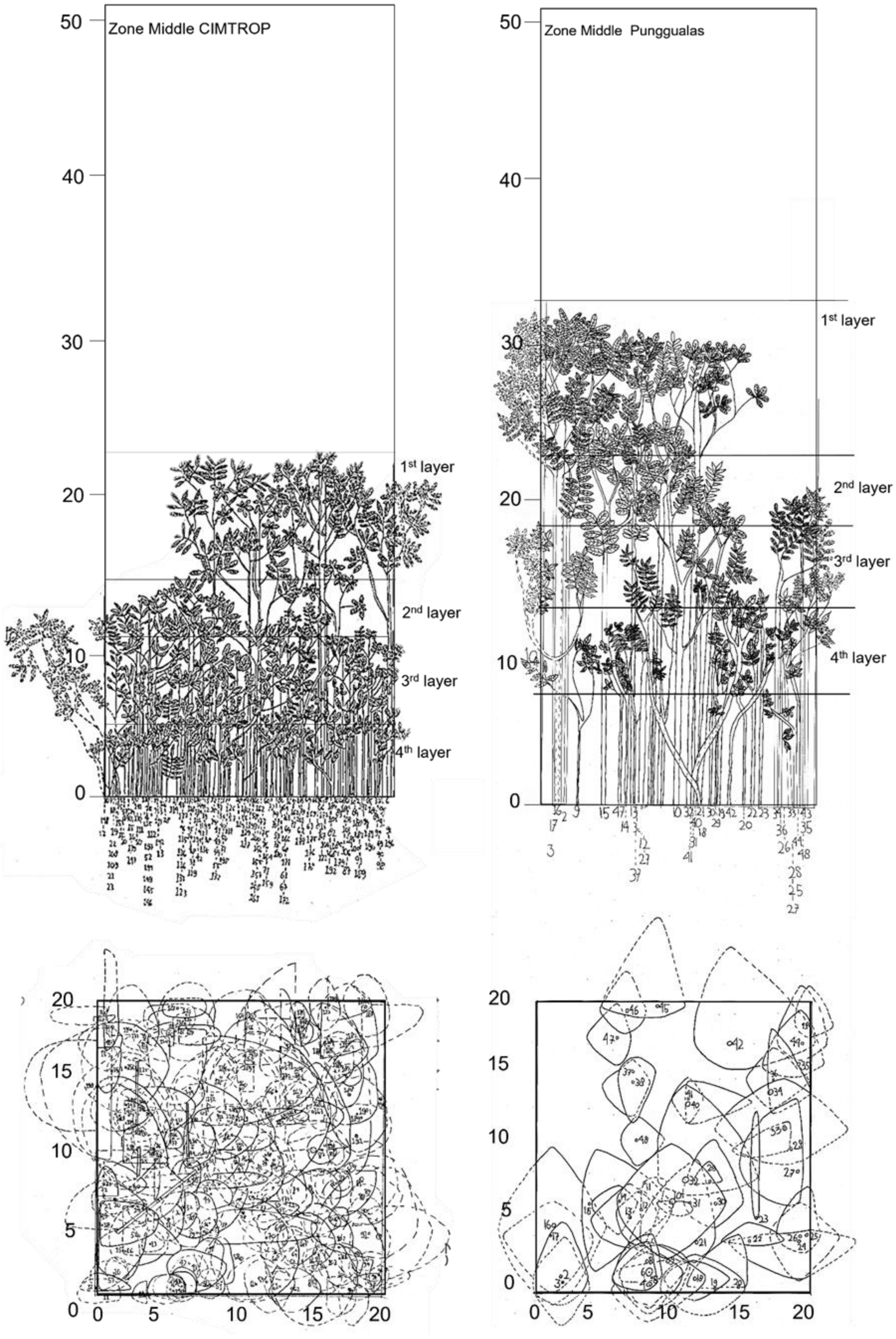


Figure A6. Forest profiles and their projections in the lower-riverine zone in the NLPSF (left) and Punggualas forest habitats (right), September and October 2022; Layers 1 to 4 are drawn to scale. The vegetation layer of the forest floor is not drawn.

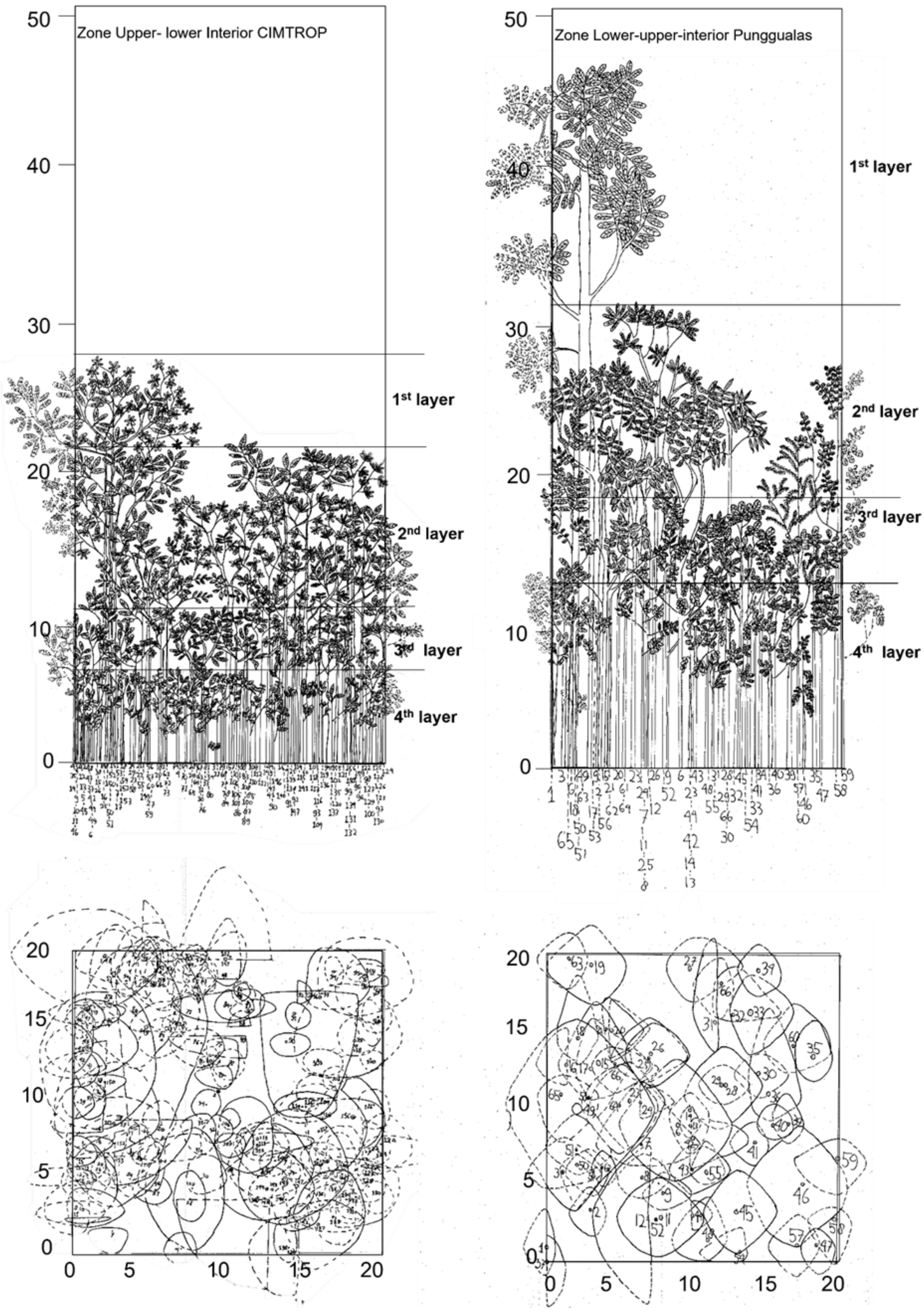


Figure A7. Forest profiles and their projections in the lower-riverine zone in the NLPSF (left) and Punggualas forest habitats (right), September and October 2022; Layers 1 to 4 are drawn to scale. The vegetation layer of the forest floor is not drawn.

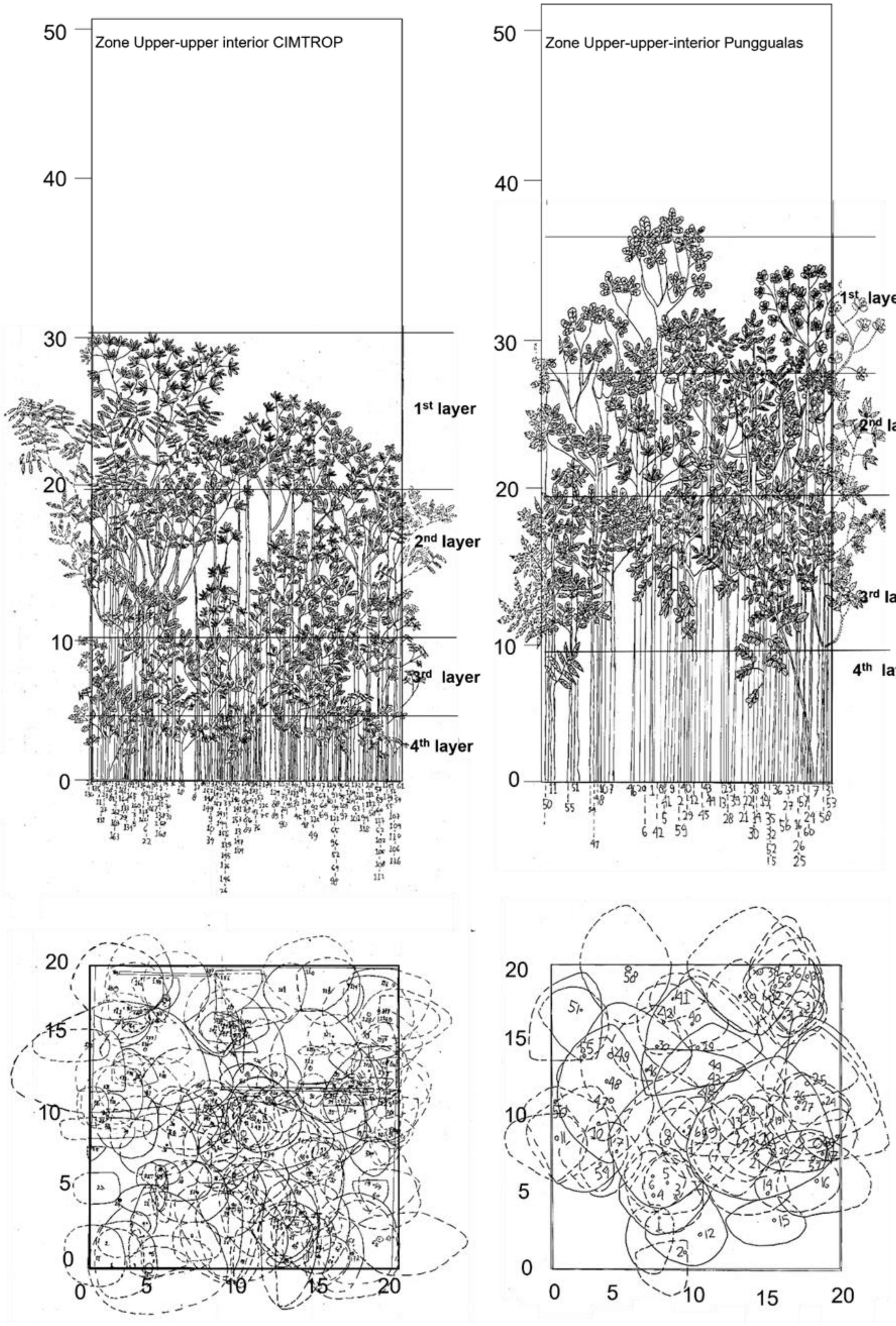


Figure A8. Forest profiles and their projections in the upper-upper interior zone in the NLPSF (left) and Punggualas forest habitats (right), September and October 2022; Layers 1 to 4 are drawn to scale. The vegetation layer of the forest floor is not drawn.