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Research

Evergreen forest types of the central plains in Cambodia: floristic composition and ecological characteristics

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Current vegetation maps show evergreen forests of Cambodia as one homogenous forest type. However, ecological field studies in the central plains demonstrated a heterogenous mosaic of different evergreen forest types, each with a unique species composition and ecological characteristics. Based on six botanical expeditions, we describe four lowland evergreen forest types: 1) riverine forest dominated by *Dipterocarpus costatus* (Dipterocarpaceae); 2) tall dipterocarp forest dominated by *Anisoptera costata* (Dipterocarpaceae); 3) swamp forest dominated by *Macaranga triloba* (Euphorbiaceae); and 4) 'Sralao', an open forest with a monodominance of *Lagerstroemia cochinchinensis* (Lythraceae). Ordination by non-metric multi-dimensional scaling (NMDS) indicated that the four forest types represent well-separated floristic entities with Sralao as the most deviant community. The highest species diversity was found in the riverine forest ($\bar{H}$ = 2.65), followed by tall dipterocarp forest ($\bar{H}$ = 2.53) and swamp forest ($\bar{H}$ = 2.34), whereas the Sralao forest had the lowest species diversity ($\bar{H}$ = 1.64). We argue that botanical fieldwork remains essential to refine vegetation maps otherwise based on remote sensing, and that knowledge of species composition is essential to conserve Indochina's vanishing evergreen forest biodiversity.

Keywords: biodiversity, ecology, importance value index, principal component analysis, tree species diversity, tropical forest

Introduction

Lowland tropical forests consist of highly diverse ecosystems and geographically distinct species compositions (Turner 2001, Corlett 2014). In Southeast Asia, the lowland forests are severely threatened by logging and the expansion of large-scale plantations and agriculture (Wilcove et al. 2013, Warren-Thomas et al. 2018, Namkhan et al. 2021). A dramatic loss of lowland forest has been observed in mainland Southeast Asia, with high-vulnerability areas especially found within the Mekong Basin (Namkhan et al. 2021).

Detailed information about forest species composition, diversity patterns and community assemblages is essential for managing ecosystems for their environmental and

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conservation value (Kacholi et al. 2015), for biodiversity (Hunter 1999, Newton and Kapos 2002, Corlett 2016), to identify threatened and rare species (Sharrock 2020), for silviculture (Pond et al. 2014), and for carbon measurements (Mitchard et al. 2014). Remote sensing (RS) and biomass maps are widely used by governments and by conservation projects because they are spatially continuous and typically easier to obtain than field data (Brosofske et al. 2014). However, these maps may have significant regional biases, as they do not estimate vegetation biomass directly and thus may miss significant spatial variations in the forest structure (Pierce et al. 2009, Mitchard et al. 2014). Especially in tropical and sub-tropical areas, with a high number of tree species, accurate forest type identification by RS is often not possible (Shepard et al. 2004, Koch 2013, Olivero et al. 2016). Maps generated from RS (Mitchard et al. 2014) or simple vegetation maps (Houghton et al. 2001) has proven unsuccessful in the Amazon to capture the main gradient in species composition and hence forest carbon compared to data recorded on the ground. Hence, describing and characterising forest types through field plots remains essential for calibrating and validating RS maps (Mitchard et al. 2014). Globally, the hyperdiverse tropical lowland forest is where attention needs to be focused (Corlett 2016).

Systematic collection of Cambodia's flora and fauna, and surveys that investigate different forest types within Cambodia, are very limited (Strange et al. 2007, Theilade and de Kok 2015). Botanical studies were conducted in the first half of the 20th century, mainly by French botanists. These studies, for the most part, are presented as species lists (Lecomte and Guibier 1926, Béjaud 1932, Maurand 1938) and floristic accounts (Lecomte 1907–1942, Forbé and Trojani 1930).

Rollet (1972) categorised the tall forests of central Cambodia as 'evergreen forests'. However, the most frequently used vegetation map of Cambodia by Legris and Blasco (1971) identified and mapped a range of different forest types based on canopy cover, tree stature and leaf phenology. The map includes only two classifications within the central lowlands: dense semi-deciduous forest and Dipterocarpaceae forests.

A land use map from 2004 based on satellite imagery distinguished three vegetation types in the central lowlands: evergreen forest, semi-deciduous forest and deciduous forest (JICA 2002). None of the vegetation maps provided information about the distinctive floristic composition, the structure of plant communities, frequency of species or biodiversity in the mapped forest types. Existing vegetation maps guiding the management and conservation of the central lowlands solely characterise evergreen, semi-evergreen and deciduous forests (Forest Administration 2010). For decades, governmental organisations and non-governmental organisations (NGOs) have relied on these vegetation maps to evaluate and prioritise conservation programmes.

More recent botanical expeditions have indicated that the forests in the central lowlands of Cambodia consist of up to seven distinct forest types: Deciduous dipterocarp forest, Mixed deciduous forest, Mixed pine–broad leaf forest, Semi-evergreen forest, Evergreen forest, Evergreen swamp forest and Riparian forest, as well as Open grasslands (Hayes et al. 2015). However, the evergreen forests assumed to be the most species-rich have never been systematically surveyed, and our understanding of their botanical composition as well as alpha and beta diversity is still cursory.

The objective of the study

The aim of the study was to explore the evergreen forest of the central lowlands of Cambodiato: 1) document different forest types and describe ecological characteristics; i.e. richness, density, basal area and importance value index (IVI); 2) compare the tree species composition, diameter distribution and the patterns of diversity and community structure of the different forest types.

Methods

Study site

Cambodia has a monsoon climate with distinct wet and dry seasons. The dry season lasts from approximately November to May, and the wet season from June to October (CTSP/FA 2003). Annual rainfall in the central lowlands is 1600–2200 mm. Sandy, alluvial and loamy soils are interspersed in the area at 0–200 m a.s.l.

The Prey Lang forest complex is located in the central lowland plains of Cambodia and is the largest, continuous lowland evergreen forest in Cambodia (Hayes et al. 2015, Fig. 1). It is characterised as evergreen forest bordered by semi-evergreen and dry dipterocarp forest and recognised as a crucial ecosystem in the Indo-Burmese hotspot, since it is the sole intact remnant forest of Indochina's once extensive lowland forest (McNeely 1975, Birdlife International 2005). The Prey Lang forest features rare and endemic species (Hayes et al. 2015), including a rare type of evergreen freshwater swamp forest (Theilade et al. 2011), and the area is recognised as vital to the national reserve network owing to its importance for plant conservation (Strange et al. 2007, Schmidt and Theilade 2010, Theilade et al. 2011, Hayes et al. 2015).

The greater Prey Lang forest complex is a primary watershed located between the Mekong Basin and the Tonle Sap Lake, and regulates water and sediment flow to the Mekong River and the Tonle Sap Lake, which is known for its highly productive fisheries (Michaud 2013). The Prey Lang Wildlife Sanctuary, covering 432 000 ha of mainly evergreen and dry dipterocarp forest, was formally established in 2016.

Approximately 80% of the most valuable and endangered native tree species of Cambodia are found in Prey Lang (CTSP/FA 2003). Valuable species include luxury timbers such as the rosewood species *Dalbergia cochinchinensis*, *D. oliveri* and a range of other species such as *Shorea roxburghii*, *Hopea odorata*, *Pterocarpus macrocarpus* and *Afzelia xylocarpa*, which are often illegally logged (McDonald 2004, Hayes et al. 2015).

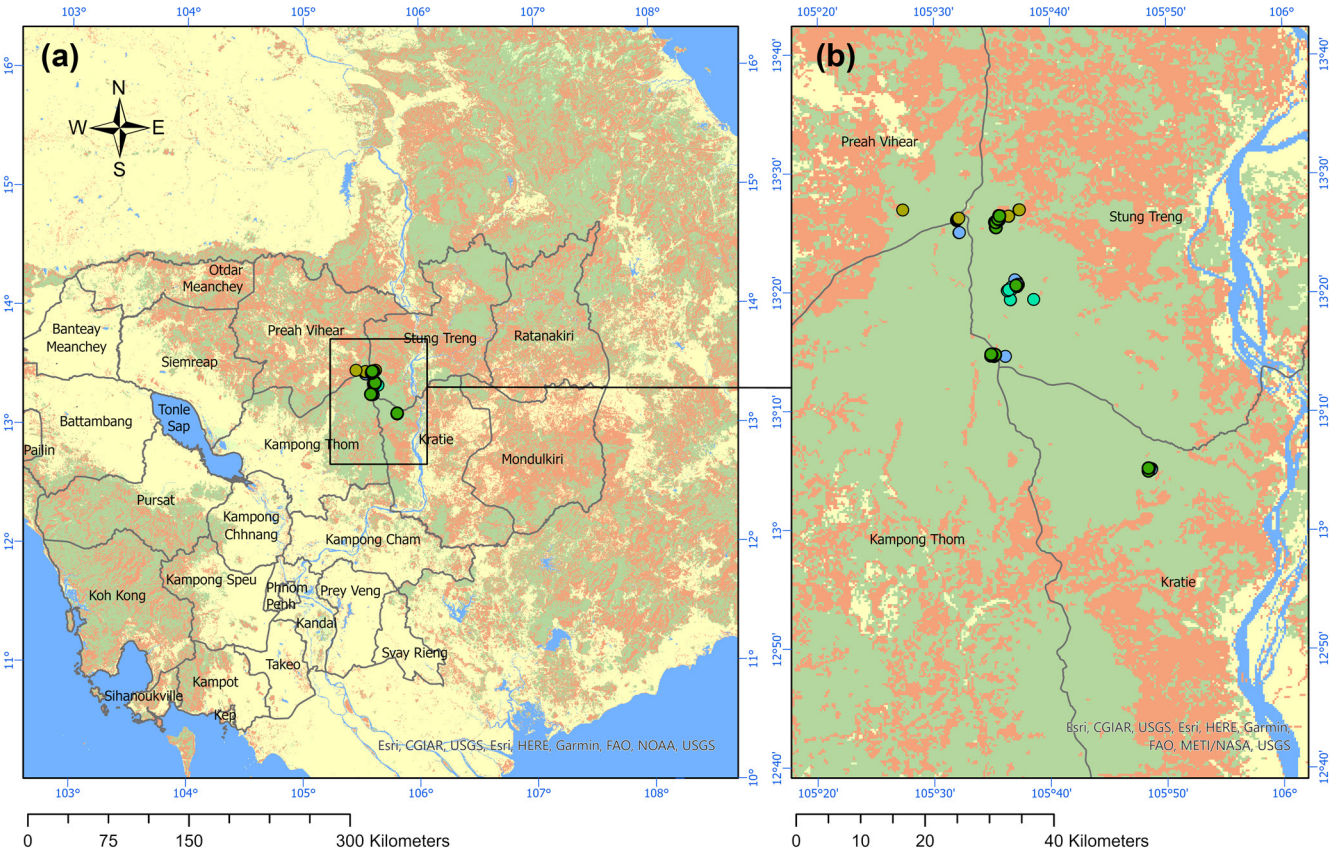


Figure 1. Study area. (a) Map of Cambodia and surroundings; (b) study area: location of surveyed plots within Prey Lang. Blue circles denote riverine forest plots, dark green circles tall dipterocarp forest plots, light green circles swamp forest plots and olive-brown circles Sralao forest plots. Land cover adapted from GlobCover 2009 (© ESA 2010 and UCLouvain <http://due.esrin.esa.int/page_globcover.php>). (Colour classification/codes are: green, forest; blue, water; yellow, open land; reddish-brown, land cover types, with more or less open vegetation.)

Roughly 250 000 people, the majority of them indigenous Kuy, live near the Prey Lang forest and depend on the forest for their livelihoods (Jiao et al. 2015). The Prey Lang, which means 'our forest' in the Kuy language, is also a vital part of Kuy cultural and spiritual life (Turreira-García et al. 2018). Resin extracted from the genus *Dipterocarpus* is the most significant source of cash income for forest communities (Hüls Dyrmose et al. 2017). Resin trees are protected according to the National Forestry Legislation (Ministry of Agriculture, Forestry and Fisheries 2003), but have been logged illegally for decades (Evans et al. 2003), and are now endangered (IUCN Red List 2021).

Ecological survey

Six botanical expeditions were conducted in 2007, 2008, 2009, 2011, 2012 and 2013. The first expeditions revealed considerable variation in forest height, structure and species composition in different parts of the forest, which necessitated distinction between at least four evergreen forest types. During the expeditions in 2011 and 2012, structured focus group discussions (n = 4) were held with local Kuy residents to record the traditional classification of forest, which confirmed our observations.

Sample plots were distributed in primary forest along random transect lines with a spacing of 100 m between plots. A total of 119 Gentry plots (50 × 10 m) were established in four different evergreen forest types as recognised by local guides (Fig. 1a–b, Table 1). The first plot began at an arbitrarily chosen point approximately 3–5 m from a trail. The consecutive plots were oriented perpendicular to the trail, further inside the forest. A maximum of ten plots was situated along each transect line. The plots were situated in forest with no environmental gradient of the terrain and we assumed that plots could be treated as independent.

In each plot, all trees with a diameter at breast height (DBH) above 10 cm were recorded and identified by a team of forest botanists. Trees were included if the centre of the base was inside the plot. Vernacular names were recorded with assistance from local Kuy guides. The geographical location of each plot was recorded using a GPS device. Kuy guides classified the forest type for each transect and sample plot using their traditional classification system.

Table 1. Summary statistics for each forest type, specifying forest density, tree size and species diversity and richness. Mean value ± standard error.

Forest type	No. of plots	Density (ha^{-1})	Basal area ($m^2\ ha^{-1}$)	Diam (D_g) (cm)	Shannon index $\bar{H}$	Simpson index $1-\bar{D}$	No. of species (per 500 m^2)
Riverine	37	583.8 ± 24.8	35.0 ± 3.2	27.0 ± 0.8	2.65 ± 0.04	0.946 ± 0.006	17.2 ± 0.6
Tall dipterocarp	41	477.6 ± 14.8	39.9 ± 3.0	31.9 ± 1.2	2.53 ± 0.04	0.938 ± 0.005	15.3 ± 0.5
Swamp	19	529.5 ± 35.5	26.8 ± 1.3	26.1 ± 1.1	2.34 ± 0.08	0.915 ± 0.011	13.1 ± 0.9
Sralao	22	414.5 ± 27.3	33.2 ± 2.9	31.7 ± 1.1	1.64 ± 0.08	0.769 ± 0.026	7.8 ± 0.6

Voucher specimens were collected and deposited at TEX, PAUH, AAU, CMU and at the Forest and Wildlife Research and Development Institute, Cambodia. We consulted the Flora of Thailand (1963–2010), Flore générale de L'Indochiné (Lecomte 1907–1942), Lexique des arbres forestiers du Cambodge (Dy Phon and Rollet 1999) and Vietnam forest trees (FIPI 1996) to determine the species. BKF and CMU herbaria were visited to verify identifications. Names are according to <Worldfloraonline.org> and Flora of Thailand.

Forest profile drawings were prepared by botanical artists Katja Anker and Jaap Vermeulen, based on the species lists and species frequencies for each forest type and supported by a library of photos for each tree species showing leaf characteristics, bark, branching and root characteristics.

Data analysis and comparison of forest plots

Tree data collected during the field expeditions were entered in a database prepared in MS-Access. Subsequently, we exported the complete dataset including 119 plots with 3003 individual trees for further analysis in the statistical software packages R (ver. 4.0.0, <www.r-project.org>) and SAS (ver. 9.4). To understand the degree to which the plot samples provided a complete picture of the species assemblages of the presumed forest types, we calculated species accumulation curves using the accumcomp function of the BiodiversityR package in R. Unconditional standard error estimates for the cumulative number of species were calculated using 999 permutations of the plot data. To analyse similarities between plots within each forest type and between plots categorised as different forest types, Jaccard indices were calculated (number of common species divided by total number of species) for each pair of plots and summarised for pairs of forest types. This was done using the 'vegan' package of R. We also calculated summary statistics for each species within plots and on average for each plot and forest type. This was done in the statistical software package SAS. Summary statistics included density (number of stems per ha), basal area ($m^2\ ha^{-1}$), quadratic mean diameter (cm), number of species, the Shannon–Wiener ($\bar{H}$) diversity index and the Simpson diversity index ($1-\bar{D}$). A comparison of the estimated mean values across forest types was carried out using the GLM Bonferroni (Dunn) t tests. Furthermore, for each species in each forest type we calculated frequency, relative frequency (percentage of total frequency), relative density (percentage of total density), relative dominance (percentage of total basal area) and importance value index (sum of relative frequency, density and dominance). Finally, to achieve a general impression of the differences between forest types we carried out ordination using non-metric multi-dimensional scaling (NMDS) implemented using the metaMDS function in the 'vegan' package of R. For this purpose we used Jaccard distances and allowed up to 200 iterations (random starts) for the algorithm to converge.

Results

Ecological characteristics

Focus group interviews with Kuy residents yielded information about the traditional characterisation of different forest types. Ecological surveys were done in four of the evergreen forest types recognised by Kuy and botanists: riverine, tall dipterocarp, swamp forest and 'Sralao' (*Lagerstroemia*) forest.

Riverine forest

The riverine forest is 30–35 m tall, and dense, with emergent canopy trees such as *Dipterocarpus costatus*, *Anisoptera costata* and *Heritiera javanica* reaching up to 45–50 m. Three canopy layers are present, which are rich in epiphytes and lianas. The forest floor is open and dominated by occasional *Areca triandra*, *Calamus* sp. and *Pandanus* sp. This forest type occurs along streams and tributaries of the Mekong River to the east of Porong River and in the central parts of the greater Prey Lang forest complex, which is traversed by smaller forest streams. The soil is alluvial and loamy, and remains moist during the dry season.

Tree species composition in the riverine forest

A total of 1078 trees was recorded, representing 140 species and 96 genera from 48 families, in the 37 plots totalling 1.85 ha (see Supporting information). The dominant species according to IVI were *Chisocheton cumingianus* (C.DC.) Harms ssp. *balansae* (C.DC.) Mabb. (Meliaceae) (IVI 16.5%), *Dipterocarpus costatus* C.F.Gaertn. (Dipterocarpaceae) (IVI 13.3%), *Mastixia pentandra* Blume spp. *chinensis* (Merr.) Matt. (Cornaceae) (IVI 11.8%), *Syzygium syzygioides* (Miq.) L.M.Perry (Myrtaceae) (IVI 11%) and *Anisoptera costata* Korth. (Dipterocarpaceae) (IVI 10.9%). The dominant families (IVI) were Dipterocarpaceae, Myrtaceae and Meliaceae (Table 2), and these families accounted for 27% of all trees recorded (mean density, $\bar{N}$).

The riverine forest had the highest Shannon–Wiener index (2.65), the highest number of species (mean 17.2 species per 500 m^2) and the highest density (583.8 ha^{-1}) and the second highest basal area (35.0 $m^2\ ha^{-1}$) of the four forest types (Table 1). A profile of characteristic species and their distribution is shown in Fig. 2.

Table 2. Floristic description of the four forest types, number of genera and species, frequency and importance value index (IVI) by family.

Family	Genera (species)	Riverine (37 plots)		Tall dipterocarp (41 plots)		Swamp (19 plots)		Sralao (22 plots)	
		Freq.	IVI (%)	Freq.	IVI (%)	Freq.	IVI (%)	Freq.	IVI (%)
Anacardiaceae	12 (12)	0.108	2.1	0.122	2.3	0.158	4.7	0.273	5.7
Annonaceae	11 (13)	0.27	4.3	0.268	4.7	0.158	3.5	0.545	13.4
Apocynaceae	1 (1)	0	0	0.049	0.7	0	0	0	0
Asparagaceae	1 (2)	0.108	1.3	0	0	0	0	0	0
Bignoniaceae	4 (4)	0.054	0.8	0.024	0.4	0	0	0.091	1.8
Bonnetiaceae	1 (1)	0.081	1.5	0	0	0	0	0	0
Capparaceae	3 (3)	0.027	0.3	0.049	0.7	0.105	1.4	0	0
Celastraceae	6 (7)	0.189	3.5	0.244	4.7	0.474	13.1	0	0
Chrysobalanaceae	3 (3)	0.216	4.2	0.22	5.3	0.316	10.7	0	0
Clusiaceae	7 (18)	0.568	10.1	0.439	7.5	0.632	13.1	0.045	1.2
Combretaceae	6 (13)	0.108	2.2	0.195	3.2	0.158	2.6	0.636	21.5
Connaraceae	1 (1)	0	0	0.024	0.4	0	0	0	0
Cornaceae	3 (3)	0.459	12.7	0.244	6	0.158	7.7	0	0
Dilleniaceae	4 (5)	0.054	0.8	0.073	1.1	0.053	0.7	0.045	0.9
Dipterocarpaceae	13 (19)	0.892	42.4	0.976	75.7	0.421	11.1	0.136	5.9
Ebenaceae	4 (23)	0.595	14.9	0.951	23.2	0.263	4.7	0.409	12.5
Elaeocarpaceae	6 (12)	0.459	10	0.341	6	0.421	9.1	0.091	1.9
Euphorbiaceae	10 (10)	0.135	1.8	0.122	1.8	0.632	19.8	0	0
Fagaceae	5 (7)	0.405	6.2	0.463	9.1	0.053	0.9	0	0
Gentianaceae	3 (4)	0.378	6.8	0	0	0.316	5.3	0.045	1
Gnetaceae	1 (1)	0.027	0.3	0	0	0	0	0	0
Hyperiaceae	3 (3)	0.108	3.4	0.073	1.1	0	0	0.727	30
Irvingiaceae	4 (4)	0.405	10	0.39	11	0.316	5.6	0.091	1.7
Lamiaceae	4 (5)	0.081	1.2	0.024	0.8	0.158	2.7	0.227	7.3
Lauraceae	14 (17)	0.459	8.4	0.488	9.3	0.526	12.1	0.091	2.2
Lecythidaceae	3 (2)	0.081	1	0	0	0	0	0.091	1.7
Leguminosae, Caesalpinioideae	11 (11)	0.189	3.2	0.244	6.4	0.316	7.8	0.182	4.5
Leguminosae, Mimosoideae	3 (3)	0.027	0.3	0.049	0.8	0	0	0.727	29.9
Leguminosae, Papilionoideae	3 (4)	0.027	0.3	0.024	0.7	0	0	0.136	5.1
Lythraceae	3 (4)	0.216	9.5	0.073	1.1	0	0	1	107
Malvaceae	17 (19)	0.595	12.9	0.39	8.9	0.316	9.7	0.409	10.1
Melastomataceae	5 (9)	0.514	10.4	0.195	3.3	0.737	20.6	0	0
Meliaceae	13 (15)	0.757	20.4	0.341	5.1	0.263	7.4	0	0
Moraceae	4 (10)	0.135	2.6	0.146	5	0	0	0	0
Myristicaceae	7 (10)	0.432	8.1	0.122	2.9	0.579	23.6	0	0
Myrtaceae	4 (22)	0.946	25.2	0.927	26.6	0.947	32.4	0	0
Palmae	1 (1)	0	0	0	0	0.316	6.2	0	0
Peraceae	3 (3)	0.432	7.8	0.122	2.1	0	0	0.045	0.9
Phyllanthaceae	17 (25)	0.568	13.6	0.659	16.5	0.789	23.8	0.409	9
Polygalaceae	3 (6)	0.27	5	0.439	9.1	0.684	19.2	0	0
Proteaceae	1 (1)	0.054	0.6	0	0	0	0	0	0
Putranjivaceae	3 (3)	0.054	0.7	0.049	0.7	0.053	0.7	0	0
Rhamnaceae	1 (1)	0	0	0	0	0	0	0.045	1.2
Rhizophoraceae	3 (3)	0.162	2.4	0.049	0.8	0.053	2.8	0	0
Rosaceae	1 (1)	0.027	0.3	0	0	0	0	0	0
Rubiaceae	5 (5)	0.081	1.1	0.146	2.2	0	0	0.273	8.7
Rutaceae	4 (4)	0.135	1.9	0.146	2.7	0	0	0.182	3.9
Sapindaceae	17 (20)	0.811	16.7	0.951	29	0.368	7.8	0.409	11.1
Sapotaceae	2 (2)	0.027	0.3	0.049	0.7	0	0	0	0
Simaroubaceae	2 (2)	0.027	0.4	0	0	0.053	0.8	0	0
Symplocaceae	1 (2)	0.054	0.6	0	0	0	0	0	0
Theaceae	1 (1)	0.027	0.3	0	0	0	0	0	0
Unknown	3 (4)	0.243	4.8	0.024	0.3	0.211	8.3	0	0

Tall dipterocarp forest

The tall dipterocarp forest is characterised by a high diversity of species, multiple layers and a dense canopy at 35–45 m with emergent species such as *Dipterocarpus costatus*, *Irvingia malayana* and *Anisoptera costata* reaching up to 50 m. Tall dipterocarp forest is found on alluvial, moist and loamy soils. Giant trees (i.e. from 60 cm DBH, and up to 300 cm DBH) are abundant. The forest floor is dark and with little undergrowth.

Tree species composition in the tall dipterocarp forest

A total of 978 trees was recorded representing 124 species and 77 genera from 41 different families, in the 41 plots totalling 2.05 ha (Supporting information). The tall dipterocarp forests are dominated by *Anisoptera costata* (Dipterocarpaceae) (IVI 27.2%), *Vatica odorata* (Griff.) Symington (Dipterocarpaceae) (IVI 20.9%), *Dipterocarpus costatus* (Dipterocarpaceae) (IVI 19.1%), *Xerospermum noronhianum* (Blume) Blume (Sapindaceae) (IVI 14.4%) and *Nephelium melliferum* Gagnep. (Sapindaceae) (IVI 11%). The three dominant families are Dipterocarpaceae, Sapindaceae and Myrtaceae; these families accounted for 43.3% of all trees recorded (mean density, $\bar{N}$). The tall dipterocarp forest exhibited the highest basal area (39.9 m^2 ha^{-1}) of the four forests types. Considerable diversity of species is also present in the tall dipterocarp forests with the second highest Shannon–Wiener index (2.53), and second highest number of species (15.3 species per 500 m^2) of the four forest types, but the second lowest density (477.6 ha^{-1}) (Table 1). The profile sketch Fig. 3 in shows the characteristic species and structure of this forest type.

Freshwater swamp forest

The swamp forest is found on peaty soils with shallow stagnant water. It has a patchy distribution covering a few to several hectares with the largest identified area covering about 35 ha. The swamp forest is characterised by hydrophytic trees with pneumatophores (aerial roots) and stilt roots, and a permanent or long-term seasonal inundation. The canopy is open, irregular and reaches 10–20 m in height with taller trees towards the edges of the swamp. *Livistona saribus* emerges as an indicator species, reaching heights of 30–35 m. The dense understory is dominated by clusters of tree ferns, rattans and smaller trees, and dense stands of *Calamus* spp., *Areca triandra* and *Licuala* palms. The forest type is extremely rare and endemic to Cambodia, with limited floristic resemblance to other swamp forests in the region (Theilade et al. 2011).

Tree species composition in the freshwater swamp forest

A total of 491 trees wasrecorded, representing 65 species and 54 genera, from 32 families in the 19 plots totalling 0.95 ha (Supporting information). Reference to IVI indicated that the canopy layer is dominated by *Xanthophyllum* sp. (Polygalaceae) (IVI 18.2%), *Macaranga triloba* (Euphorbiaceae) (IVI 17.9%), *Syzygium albiflorum* (Myrtaceae) (IVI 16%), *Myristica iners* (Myristicaceae) (IVI 14.3%) and *Pternandra caerulescens* (Melastomataceae) (IVI 13.2%). Dominant families are Myristicaceae, Myrtaceae and Phyllantaceae and these families accounted for 29.8% of all trees recorded (mean density, $\bar{N}$). The swamp forest

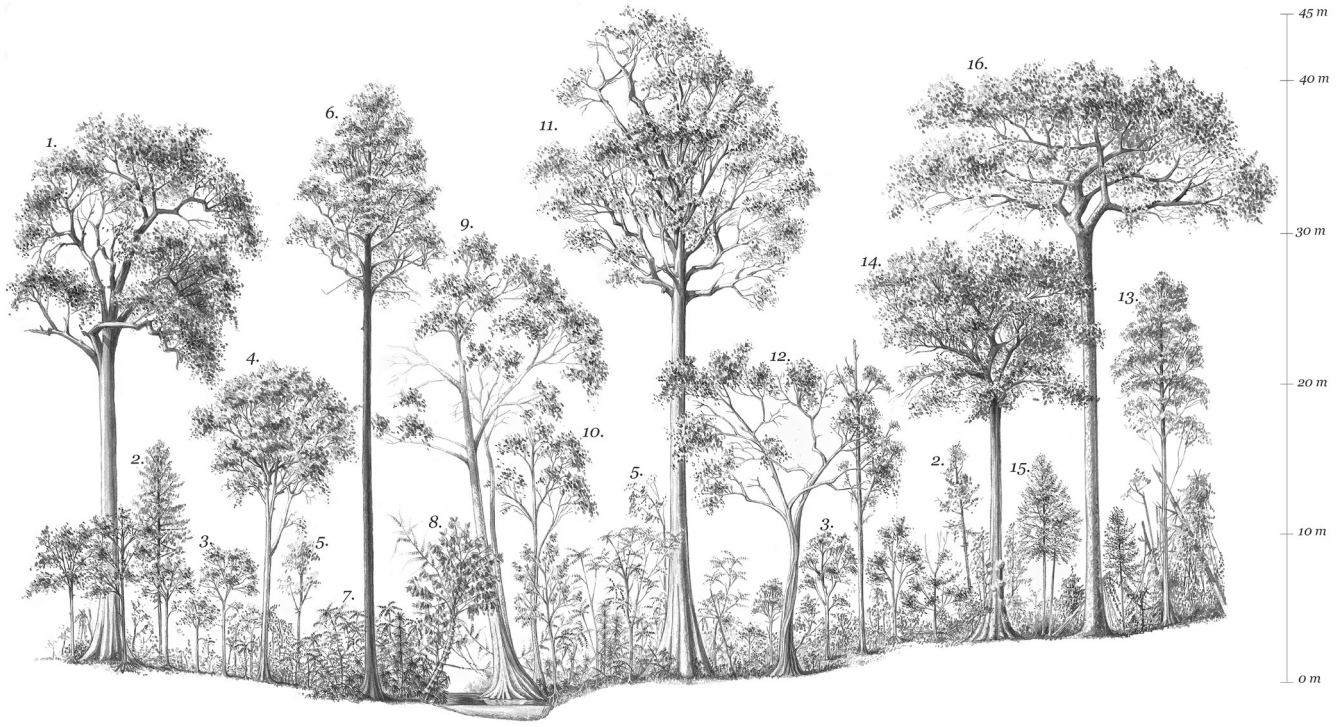


Figure 2. Profile drawing showing characteristic species of the riverine forest. From left to right 1) *Irvingia malayana*, 2) *Nephelium melliferum*, 3) *Mastixia pentandra*, 4) *Balakata baccata*, 5) *Chisocheton cumingianus*, 6) *Hopea odorata*, 7) *Pandanus* spp., 8) *Fagraea racemosa*, 9) *Lagerstromia* sp., 10) *Elaeocarpus floribundus*, 11) *Heritiera javanica*, 12) *Syzygium grande*, 13) *Vatica odorata*, 14) *Anisoptera costata*, 15) *Diospyros* sp. and 16) *Dipterocarpus costatus.* Most frequent species were *Chisocheton cumingianus* ssp. *balansae*, *Syzygium syzygioides* and *Dipterocarpus costatus.* Drawing by Katja Anker and Jaap Vermeulen.

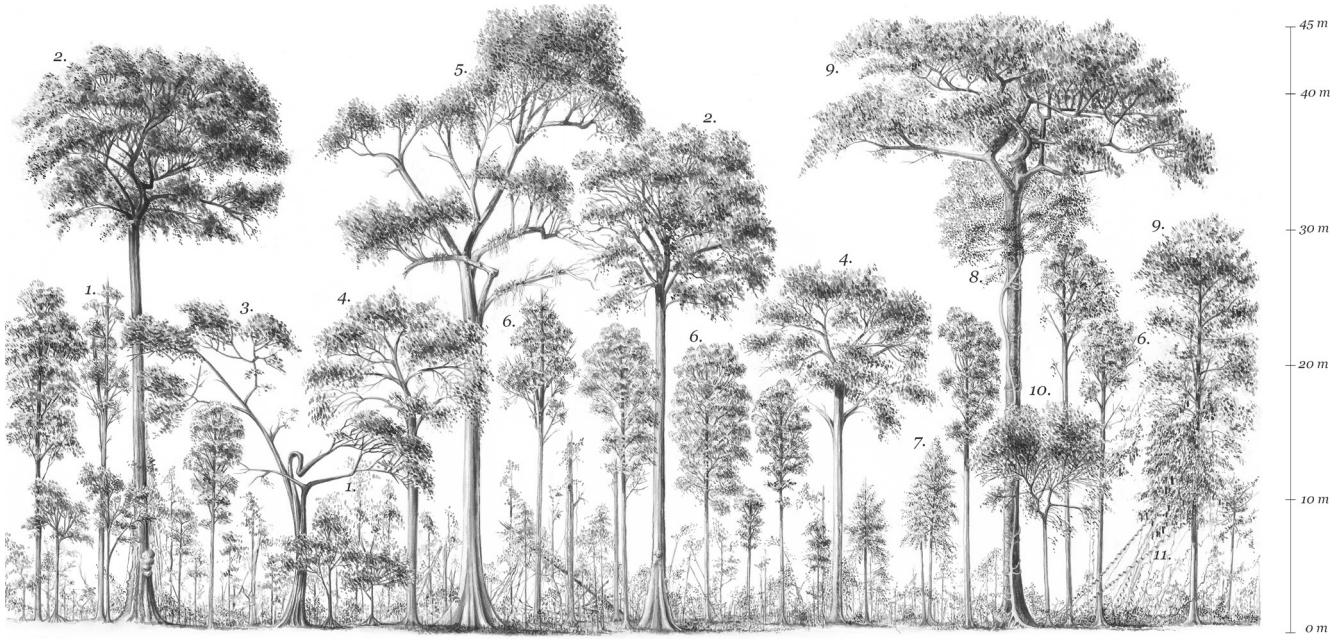


Figure 3. Profile drawing showing characteristic species of tall dipterocarp forest. From left to right 1) *Nephelium melliferum*, 2) *Anisoptera costata*, 3) *Syzygium grande*, 4) *Lithocarpus elegans*, 5) *Irvingia malayana*, 6) *Vatica odorata*, 7) *Diospyros crumenata*, 8) *Ficus* sp., 9) *Dipterocarpus costatus*, 10) *Syzygium albiflorum* and 11) *Entada* sp. Most frequent species were *Anisoptera costata*, *Vatica odorata* and *Dipterocarpus costatus*. Drawing by Katja Anker and Jaap Vermeulen.

is distinguished by the abundance of hydrophytic *Syzygium*, *Myristica*, *Pternandra* and *Macaranga* trees. The swamp forest is the only forest type with Palmae (Arecaceae) present in the canopy (trees above 10 cm DBH), represented by the palm *Livistona saribus* (Fig. 4 . According to the NMDS analysis there is no coincidence between Sralao and the swamp forest. The swamp has the lowest basal area (26.8 m^2 ha^{-1}) and mean DBH (Fig. 7), and the second lowest number of species (13.1 per 500 m^2) in comparison with the other forest types (Table 1). The swamp forest is considered a unique forest type for the region and contains several rare and endangered species (Theilade et al. 2011).

Sralao – an evergreen forest with some deciduous elements

The Sralao forest is 15–25(–30) m in height, open and characterised by the predominance of the species *Lagerstroemia cochinchinensis* Pierre, easily recognised by its almost white bark and fluted base. Sralao is the Khmer word for *L. cochinchinensis*. The Sralao forest is found mainly on well-drained, sloping soils. A total of 456 trees was recorded, representing 51 species and 42 genera from 26 families in the 22 plots totalling 1.1 ha (Supporting information). The most dominant species are *L. cochinchinensis* (Lythraceae) (IVI 106.2%), *Cratoxylum formosum* ssp. *pruniflorum* (Hypericaceae) (IVI 29.4%), *Xylia xylocarpa* var. *kerrii* (Leguminosae, Mimosoideae) (IVI 29.3%), *Schleichera oleosa* (Sapindaceae) (IVI 10.4%) and *Nauclea officinalis* (Rubiaceae) (IVI 8.5%). The three dominant families in the Sralao forests are Lythraceae, Hypericaceae and Leguminosae (Mimosoideae) (IVI%) (Table 2), and these families accounted for 61.9% of all trees recorded (mean density, $\bar{N}$). The Sralao forest presents the lowest density (414.5 ha^{-1}), the lowest number of species (7.8 per 500 m^2) and the lowest Shannon–Wiener index (1.64) of all four forest types. However, the quadratic mean diameter (D_g, cm) of the trees is the second highest, mainly due to the fluted trunks of *L. cochinchinesis*. The family Myrtaceae, which is dominant in riverine, tall dipterocarp and swamp forests; Melicaeae, dominant in riverine forest; and Myristicaceae, dominant in the swamp forest, are not present in the Sralao forest. A profile showing characteristic species and their distribution is illustrated in Fig. 5.

Species composition and species richness across the four forest types

A total of 52 families was identified, 15 of which occurred in all forest types. Of the recorded 52 families, nine were represented by only one species. A total of 3003 individual trees was recorded, representing 194 identified species. Only ten species were present in all four forest types, and only two out of 20 of the top-five dominant species (IVI%) overlap in the different forest types. These were *Anisoptera costata* and *Dipterocarpus costatus,* which were dominant in the riverine and tall dipterocarp forests. Arecaceae > 10 cm DBH was only present in the swamp forest. Nineteen of the surveyed species are on the IUCN red list (see Supporting information). The highest species richness was recorded for the riverine forest (17.2 species per 500 m^2) and tall dipterocarp forest (15.3



Figure 4. Profile drawing showing characteristic species of the swamp forest. From left to right 1) *Shorea guiso*, 2) *Archidendron clypearia*, 3) *Areca triandra*, 4) *Sindora siamensis*, 5) *Myristica iners*, 6) *Fagraea racemosa*, 7) *Livistona saribus*, 8) *Macaranga triloba*, 9) *Licuala spinosa*, 10) *Syzygium albiflorum*, 11) *Cibotium barometz*, 12) *Litsea* sp., 13) *Dipterocarpus costatus* and 14) *Pternandra caerulescens*. Most frequent species were *Macaranga triloba*, *Pternandra caerulescens* and *Syzygium albiflorum*. Drawing by Katja Anker and Jaap Vermeulen.



Figure 5. Profile drawing showing characteristic species of the Sralao forest. From left to right 1) *Lagerstroemia cochinchinensis*, 2) *Ficus* sp., 3) *Xylia xylocarpa*, 4) *Cratoxylum formosum*, 5) *Entada* sp. and 6) *Schleichera oleosa*. Most frequent species were *L. cochinchinensis*, *C. formosum* and *X. xylocarpa.* Drawing by Katja Anker and Jaap Vermeulen.

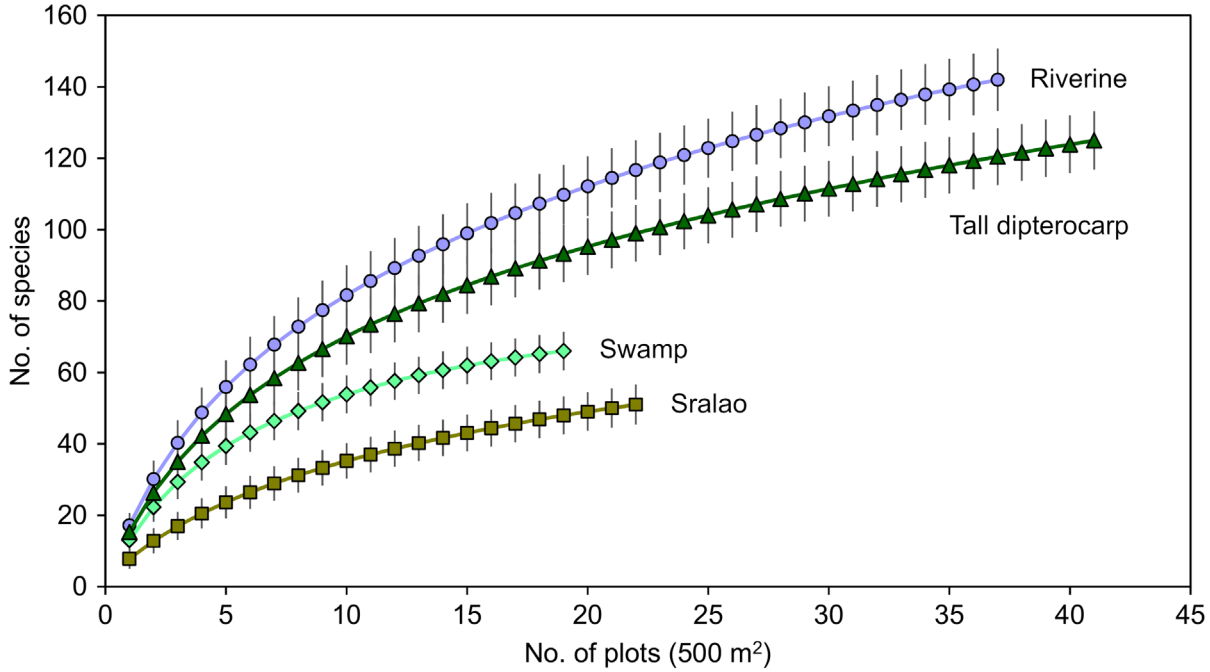


Figure 6. Species accumulation curves, unconditional (not constrained by existing number of plots), 999 permutations. Error bars represent mean values ± two standard deviations.

species per 500 m^2), followed by swamp forest (13.1 species per 500 m^2) and the Sralao (7.8 species per 500 m^2). Of the 140 species recorded for the riverine forest, 23% were only observed in this forest type. Likewise, 9% of 65 species were unique for the swamp forest, 18% of 124 species were unique to the tall dipterocarp forest and 31% of 51 species were unique for the Sralao forest. A species overlap was observed between all four forest types (Table 3).

Species diversity and species accumulation curves

Among the four forest types, riverine and tall dipterocarp were the most complex in terms of species diversity, with Shannon–Wiener indices of 2.65 and 2.53, respectively, and Simpson's indices of 0.946 and 0.938, respectively. The least diverse forest was Sralao with a Shannon–Wiener diversity value of 1.64, and a Simpson's index of 0.769 (Table 1).

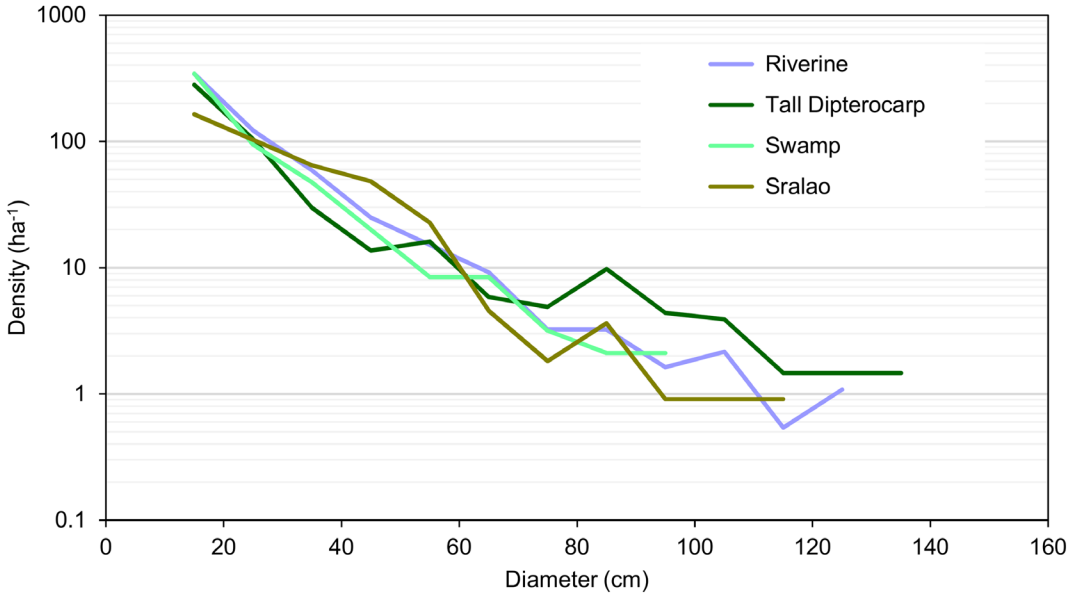


Figure 7. Diameter distributions (mean density $\bar{N}$, ha^{-1}) for the four forest types. Diameter classes are 10 cm wide. Note the logarithmic y-axis.

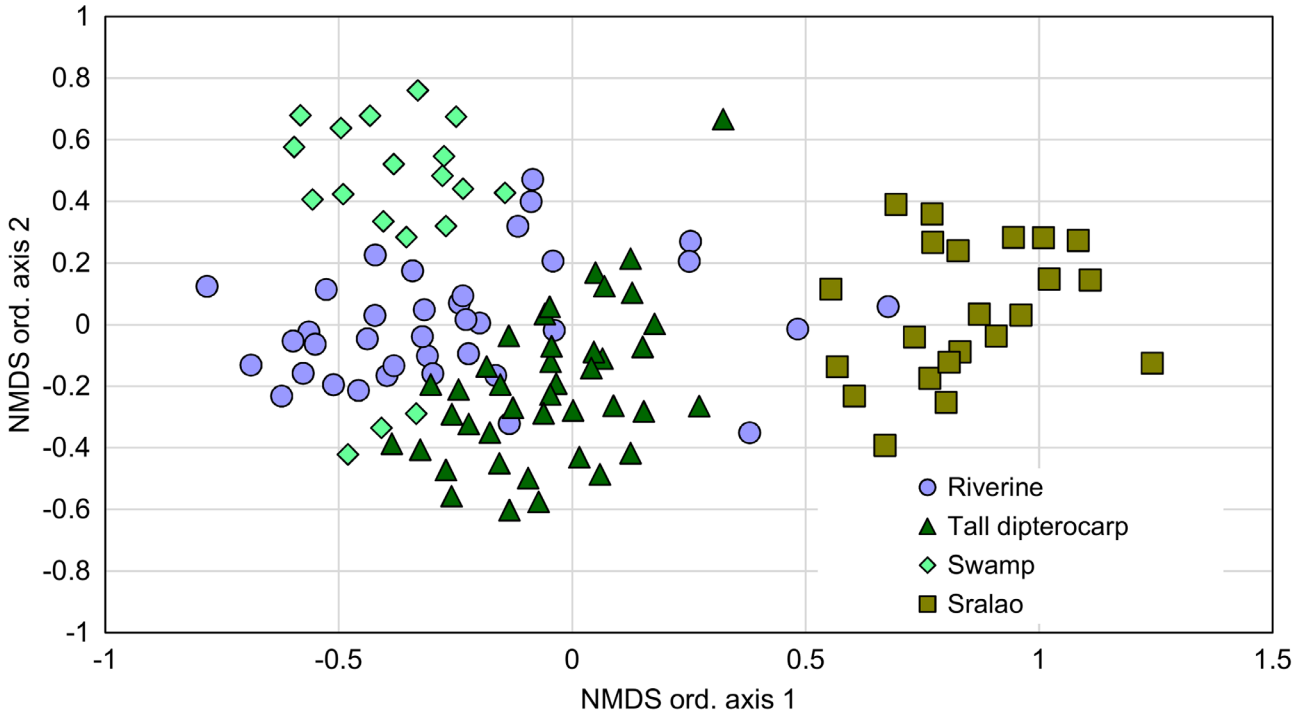


Figure 8. Ordination results based on non-metric multi-dimensional scaling (NMDS), meta-MDS (forest type) and Jaccard distances. The algorithm converged after 68 iterations (random starts).

GLM Bonferroni (Dunn) t tests showed that significant differences in the Shannon–Wiener indices were significant between the Sralao and all other forest types ($p < 0.05$), and additionally between riverine and swamp forest ($p < 0.05$). In contrast, there were no significant differences between the riverine and tall dipterocarp forest ($p > 0.05$), or between the tall dipterocarp and the swamp forest ($p > 0.05$). The species accumulation curves for all four forest types are shown in Fig. 6. For the swamp forest, the species-accumulation curve appeared to be reaching a plateau, so the 19 plots measured seemed to capture much of the floristic diversity in this forest type. By contrast, the riverine and tall evergreen dipterocarp forest types were more species rich; therefore, the 37 and 41 plots, respectively, did not really suffice for the species-accumulation curves to start reaching a plateau.

Density, basal area and mean diameter of the forest types

The density of trees calculated for each diameter class in the four forest types exhibited an inverse J-shape, with the majority of individuals found in the diameter range 20–30 cm (Fig. 7). The riverine forest had the highest density (583.8 ha^{-1}) followed by the swamp forest (529.5 ha^{-1}), tall dipterocarp (477.6 ha^{-1}) and Sralao (414 ha^{-1}). The GLM Bonferroni (Dunn) t tests showed that the density of the riverine forest was significantly higher than for tall dipterocarp (477.6 ha^{-1}) ($p < 0.05$) and Sralao (414 ha^{-1}) ($p < 0.05$) (Table 1). Furthermore, the t tests showed a significant difference between the swamp forest and the Sralao ($p < 0.05$).

Tall dipterocarp forest had the highest basal area (39.9 m^2 ha^{-1}) followed by riverine (35 m^2 ha^{-1}), Sralao (33.2 m^2 ha^{-1}) and swamp forest (26.8 m^2 ha^{-1}). The basal area differed significantly between tall dipterocarp forest and swamp forest ($p < 0.05$).

Tall dipterocarp forest and Sralao showed almost similar quadratic mean diameter (D_g, cm) at 31.9 and 31.7 cm, respectively, followed by riverine forest (27.0 com) and swamp forest (26.1 cm). No significant difference was found between tall dipterocarp forest and Sralao ($p > 0.05$), or between the swamp and riverine forest ($p > 0.05$), while significant differences were found between riverine forest and tall dipterocarp forest ($p < 0.05$), and all other combinations of forest types.

Tall dipterocarp forest had the greatest density of giant trees; that is, with a diameter above 60 cm (Fig. 7). The highest DBH value recorded within the plots was 164 cm, observed for *Anisoptera costata* (Dipterocarpaceae), followed by *Irvingia malayana*, at 137 cm. Both of these large trees were found in the tall dipterocarp forest. Several trees with a DBH > 300 cm were recorded outside the plot network.

Table 3. Number of species shared between forest types.

Forest type	Riverine (n = 140)	Tall dipterocarp (n = 124)	Swamp (n = 65)	Sralao (n = 51)
Riverine	–	95	54	28
Tall dipterocarp	95	–	51	25
Swamp	54	51	–	9
Sralao	28	25	9	–

Table 4. Summary of Jaccard similarity indices (i.e. # in intersection divided by # in union) calculated for pairs of plots within the four evergreen forest types in the central lowlands, Cambodia.

Forest type		Riverine	Tall dipterocarp	Swamp	Sralao
Riverine	Mean	0.113	0.080	0.055	0.025
	Stdev.	0.080	0.051	0.046	0.049
	#pairs	666	1517	703	814
Tall dipterocarp	Mean	0.080	0.138	0.042	0.013
	Stdev.	0.051	0.080	0.039	0.019
	#pairs	1517	820	779	902
Swamp	Mean	0.055	0.042	0.132	0.003
	Stdev.	0.046	0.039	0.114	0.008
	#pairs	703	779	171	418
Sralao	Mean	0.025	0.013	0.003	0.265
	Stdev.	0.049	0.019	0.008	0.123
	#pairs	814	902	418	231

Similarity between forest types

Jaccard similarity indices (Table 4) indicated that the most homogeneous forest type, characterised by the highest similarity among plots within the same forest type, was the Sralao (mean 0.265), followed by tall dipterocarp (0.138) and swamp forest (0.132) and finally the riverine forest (0.113) as the least homogeneous forest type. The highest Jaccard similarity between forest types was observed for tall dipterocarp and riverine forests (0.08), followed by riverine and swamp forests (0.055). The least similar pair of forest types was the Sralao and swamp (Table 4).

The results of NMDS ordination are shown in Fig. 8. Generally, the four forest types are well defined. The point cloud representing the Sralao is well separated from the point clouds representing the other forest types, except for a couple of riverine plots. Similarly, the swamp forest is separated from the other forest types except for three plots. The difference in the composition of swamp and Sralao is clear, as also indicated by the low mean similarity (0.003; Table 4) and the low number of shared species (n = 9; Table 3). The riverine forest is well-separated from swamp forest but shows a small overlap with the tall dipterocarp forest. In turn, the plots of the latter forest type form a well-delineated point cloud, although a single plot falls relatively far from the main concentration of points at a level corresponding to swamp forest along the second ordination axis (Fig. 8).

Unidentified species

Unfortunately, it was impossible to secure fertile collections of all tree species despite one of the authors being an experienced tree climber. Therefore, there are a few unidentified plant specimens at TEX, AAU and Chiang Mai, which will require further scrutiny. According to local guides, a number of tree species flower during the rainy season, between May and October, when roads are inaccessible. Moreover, many rare elements of these forests still await collection.

Discussion

Tropical forests

Cambodian vegetation maps are based on remote sensing. This is also the case for the central lowlands, which have been characterised as homogenous evergreen forest. However, our plot data showed that the evergreen forest can be characterised as four distinct forest types, differing in structure and species composition. The distribution of the four forest types was related to the coarseness of the alluvial deposits and subtle topographical variation. Hence, riverine and tall dipterocarp forest were found on loamy soil; Sralao on more dry, coarse and often gently sloping soil; and the swamp forest on waterlogged and humus-rich soil. Even if high-resolution satellite images had revealed a difference in forest types, they would not have been able to tell which species composition accounted for such difference.

This is in line with earlier surveys, which found that the evergreen forests of central lowlands in Cambodia varied considerably with respect to species diversity and composition, and concluded that it should not be recognised as a single 'vegetation type' (McDonald 2004). Comparing an extensive plot-based dataset with remote sensing data for the Amazon, Mitchard (2014) showed that describing and characterising forest types through field plots, which consist of species identification and tree measurements, remains essential to fill data gaps and better understand the variation of biodiversity in complex tropical forest systems. Furthermore, differences in species composition between forest types can matter greatly for determining carbon stocks (Mitchard et al. 2014).

Traditional ecological knowledge can provide valuable support for forest botanists and ecologists in the classification of forest types, as described from studies in collaboration with the Tsimane peoples in the Bolivian Amazon (Riu-Bosoms et al. 2014), the Matsigenka of the Peruvian Amazon (Shepard et al. 2004), and among different indigenous peoples in the Venezuelan Amazon (Olivero et al. 2016). Habitat knowledge, as well as the clear notion of ecological zones based on indicator species, flooding regimes, soil, traditional uses by humans (Shepard et al. 2001, Campos et al. 2012) and anthropogenic disturbances (Gilmore et al. 2010) are utilized by indigenous peoples to distinguish different forest types (Shepard et al. 2004). Thus, forest types and habitats can be described in greater detail when botanical field surveys and indigenous knowledge are combined with remote sensing, as remote sensing on its own is far from omniscient when it comes to forest type recognition (Shepard et al. 2004). In

this study, Kuy ecological knowledge fascilitated the recognition and identification of different forest types in the field as well as species identification. The Kuy forest classification was found to correspond to the classification based on the plot data used to characterise and compare vegetation types.

Evergreen forests are a heterogeneous assemblage

In addition to the freshwater swamp forest discovered in 2011 (Theilade et al. 2011), we described three evergreen forest types. Each forest type has a unique floristic composition, as well as a distinct diversity of species, size distribution and structural composition. Former studies in the central lowlands have not recognised these forest types (Birdlife International 2005, Hayes et al. 2015). However, tree species richness, density, basal area and IVI are known to vary within evergreen forest types as subtle changes in soil and hydrology are translated into different forest species compositions (Shepard et al. 2004, Campos et al. 2012, Mitchard et al. 2014, Balslev et al. 2017, Myster 2017). In both Laos and Vietnam the results of lowland forest inventories point to appreciable changes in floristic composition along relatively short spatial gradients (Satdichanh et al. 2015, Van and Cochard 2017), with the occurrence of several distinct forest types in close proximity (Claridge 1996, Satdichanh et al. 2015).

The lowland riverine forest and swamp forest are also described by Claridge (1996) in Laos, as significant and rare ecosystems of Southeast Asia. The swamp forest is also found in the Mekong floodplains of Vietnam, although large areas of such forests have been drained (Phuong 2007). As with the Sralao forest, domination by *Lagerstroemia* is also described by Rollet (1960) and Blanc et al. (2001) in lowland forests of southern Vietnam. In both studies the *Lagerstroemia* dominance is regarded as a secondary forest, probably a result of early shifting cultivation.

In comparison to other lowland forests in Indochina, the four forest types in Prey Lang exhibit a density that ranges between 414.5 and 583.8 stems ha^{-1}; in lowland forest studies from Vietnam the density is found to be 287–439 ha^{-1} (Tran et al. 2013), 389–540 ha^{-1} (Blanc et al. 2001) and 496–734 stems ha^{-1} (Millet et al. 2010). In peninsular Malaysia mean density is found at 530 ha^{-1} (Kochummen et al. 1990), which is close to the density of the swamp forest (529.5 ha^{-1}), and at 584 ha^{-1} (Okuda et al. 2003) close to the density of the riverine forest (583.8 ha^{-1}). In comparison, density is found to be considerably higher in the dipterocarp forest on nutrient-poor soil in Lambir, Malaysian Borneo, with 637 stems ha^{-1} (Lee et al. 2004). The basal area of the four forest types ranges between 26.8–39.9 m^2 ha^{-1}. The estimated pan-tropical average of 36.0 m^2 ha^{-1} (Dawkins 1959) is exceeded in the tall dipterocarp forest (39.9 m^2 ha^{-1}) with a high percentage of trees in high DBH classes. In comparison, the basal area of lowland forests in Vietnam is found to be 29.3 m^2 ha^{-1} (Rundell 1999) and between 31.33 and 69.41 m^2 ha^{-1} (Blanc 2001). In the Malaysian Peninsular, the basal area is found to be 26 m^2 ha^{-1} (Satdichanh et al. 2015), 33–37 m^2 ha^{-1} (Kochummen et al. 1990) and 35 m^2 ha^{-1} in Laos (Sovu et al 2009).

Hayes et al. (2015) accounted for 111 plant species in Prey Lang Wildlife Sanctuary. The present study recorded 194 tree species (> 10 cm DBH) of which only six: *Irvingia malayana*, *Dehaasia cuneata*, *Xerospermum noronhianum*, *Pterospermum littorale* var. *littorale*, *Elaeocarpus hygrophilus* and *Diospyros filipendula* were found across all four forest types. Among 52 recorded plant families, 15 were present in all forest types. Of the 20 dominant species (IVI) found in the four forest types, only two dominant species coincided in the different forest types. The dominant *Lagerstroemia cochinchinensis* of the Sralao forest did not coincide with the dominant species of any of the other forest types. Groundcover and subcanopy structures also differed considerably between the four forest types.

Dipterocarpaceae, the dominant family of the lowland forest in Southeast Asia (Whitmore 1984, Corlett and Primack 2005), was found to be dominant in the tall dipterocarp (75.7 IVI) and riverine forests (42.4 IVI), but less abundant in the swamp forest (11.1 IVI) and especially in the Sralao forest (5.9 IVI). Myrtaceae, another commonly found family in the lowlands, was dominant in the swamp (32.4 IVI), tall dipterocarp (26.6 IVI) and riverine (25.2 IVI) forests, but was completely absent in the Sralao forest. The riverine and swamp forests differed from the tall dipterocarp and Sralao forests by the difference in indicator species, such as the occurrence of *Myristica iners* and *Pternandra caerulescens*. The palm *Livistonia saribus* was found to be endemic to the swamp forest. In addition to Dipterocarpaceae, typical family affinities in the lowland forest floras such as the Lythraceae, Leguminosae (Fabaceae) and Myristicaceae (Rundell 1999), were also among the dominant families in the four forest types.

Conservation status

Deforestation by large-scale illegal logging has severely affected the Prey Lang forest (Brofeldt et al. 2018), and the extensive evergreen old-growth forest of Prey Lang is rapidly decreasing (Argyriou et al. 2019, IFOROS 2021). A total of 19 tree species recorded (10%) is threatened (IUCN 2021). As about 20% of the world's tree species are either Data Deficient (13.2%) or Not Evaluated (8.3%) this is likely to be a conservative estimate (BGCI 2021). Species composition has an impact on related ecological services such as biodiversity conservation and carbon storage (Slik et al. 2013, Mitchard et al. 2014). Logging targeting the 'giant' trees (> 60 cm DBH), especially in the riverine and tall dipterocarp forests, may lead to a considerable decrease in the above ground carbon storage (Slik et al. 2013) and directly exacerbate local climate effects associated with deforestation, such as changes in temperature, precipitation patterns and water cycles (Zhang et al. 1996).

Finally, the different forest types have different cultural connotations and value to the local and indigenous people. A previous study found that 80% of local households had a major income from tapping oleoresin from trees of the Dipterocarpaceae family (Hüls Dyrmose et al. 2017). Similarly, the spirit forests of the indigenous Kuy correspond to the biodiversity-rich riverine and tall dipterocarp forests.

Hence, these two forest types have a special importance to the spiritual and cultural well-being of the local indigenous people. This is supported by Jiao et al. (2015), who documented the negative impact of deforestation on local household economies in the central lowlands, Cambodia. Dipterocarp forests yield far more than timber. Their service values for carbon sequestration and as carbon sinks, and for conservation of biodiversity, can only be realised if the world community invests in their restoration and future maintenance (Ashton et al. 2021).

Conclusion

Four evergreen forest types are described from the central lowlands in Cambodia, each with a unique species composition and ecological characteristics. We show that vegetation maps based solely on satellite images may omit significant differences in forest composition and structure, and need to be ground-truthed. Knowledge of plant diversity and distribution is a prerequisite for conservation planning and carbon stock assessments, and for a greater understanding of local and indigenous production systems and spiritual well-being. Prey Lang Wildlife Sanctuary, in the central lowlands of Cambodia, spans a continuous range of at least four evergreen forest types, as well as semi-evergreen and dry dipterocarp forests, and should receive the highest priority for conservation.

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Author contributions

Ida Theilade: Conceptualisation (lead); Data curation (equal); Formal analysis (supporting); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Resources (equal); Writing – original draft (equal); Writing – review and editing (equal). **Phourin Chhang**: Conceptualisation (supporting); Data curation (supporting); Investigation (equal); Methodology (equal); Validation (equal). **Lars Schmidt**: Data curation (equal); Writing – review and editing (supporting). **Henrik Meilby**: Data curation (equal); Formal analysis (lead); Writing – review and editing (supporting). **Martin van de Bult**: Validation (lead). **Katrine Friborg**: Formal analysis (equal); Writing – original draft (lead); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://dx.doi.org/10.5061/dryad.hmgqnk9kf> (Theilade et al. 2022).

Supporting information

The supporting information associated with this article is available from the online version.

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