

# Topographical patterns of species composition in a deciduous dipterocarp forest in Kratie Province, Cambodia

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Paper submitted 2 July 2021, revised manuscript accepted 3 January 2022.

## មូលនិយមសង្ខេប

យើងបានរករកពីទម្រង់នៃសមាសភាពប្រភេទព្រៃក្នុងឡូត៍គំរូតាងអចិន្ត្រៃយ៍ទំហំ៤ហិកតា ដើម្បីវាយតម្លៃពីរបាយតាមរយៈកម្ពស់នៃប្រភេទព្រៃឈ្មោះផ្សេងៗគ្នា ក្នុងខេត្តក្រចេះ ភាគខាងលិចនៃប្រទេសកម្ពុជា។ លំដាប់រយៈកម្ពស់ត្រូវបានកំណត់ពីកំពូលភ្នំដល់ទំនាបលិចទឹកនៃឡូត៍គំរូតាង លក្ខខណ្ឌដី និងព្រៃប្រែប្រួលតាមលំដាប់កម្រិតកម្ពស់។ យើងក៏បានប្រើសន្ទស្សន៍ (index of importance value) សម្រាប់ប្រភេទដែលលុបក្នុងឡូត៍គំរូតាង (0,0៤ ហិកតា) ហើយការវិភាគរង្វាស់បែប non-metric multi-dimensional scaling ត្រូវបានប្រើដើម្បីបង្ហាញពីទម្រង់នៃសមាសភាពប្រភេទ។ ព្រៃឈ្មោះដែលស្ថិតនៅក្នុងឡូត៍គំរូ ត្រូវបានចែកចេញជា៤ក្រុម (Groups 1-4)។ ប្រភេទសាមញ្ញចំនួន២ បានបង្ហាញពីទម្រង់ចែកដាច់ពីគ្នាតាមបណ្តោយរយៈកម្ពស់គឺ ដើមរាំងភ្នំ (*Shorea siamensis*) ជាប្រភេទមានចំនួនលើសលុបនៅតំបន់ខ្ពស់ (ក្រុម១) និងបន្ទាប់មកគឺ ដើមខ្លុង (*Dipterocarpus tuberculatus*) ដើមផ្លិត (*Shorea obtusa*) ឬជួនកាលពពួកដើមឈ្លឹក (*Terminalia*) (ក្រុមទី៤) ដែលមានចំនួនលើសលុបនៅតាមវាល និងទំនាបលិចទឹក។ ក្រុមទី៣ត្រូវបានកំណត់ដោយភាពសម្បូរលើសលុបនៃដើមខ្លុង (*D. tuberculatus*) នៅតាមវាល និងទំនាបលិចទឹកដែលពួកវារាវាងដល់ការដុះឡើងវិញនូវប្រភេទផ្សេងៗទៀត។ ក្រុមទី២មានល្បាយនៃ *dipterocarps* ចំនួនបីប្រភេទលាយឡំគ្នាដែលត្រូវបានសម្គាល់ដោយវត្តមាននៃប្រភេទរុក្ខជាតិជាច្រើន ជាមួយនឹងព្រៃស្រទាប់ក្រោមក្រាស់។ ព្រៃប្រភេទនេះគ្រប់ដណ្តប់តាមជើងជម្រាល និងតាមទីវាលខ្ពស់ៗដែលបង្កើតបានជាតំបន់ព្រៃដែនរវាងព្រៃក្រុមទី១ និងទី៣-៤។ លទ្ធផលសិក្សារបស់យើងបានបង្ហាញថា ព្រៃឈ្មោះជាច្រើនប្រភេទអាចដុះលាយឡំគ្នាក្នុងទំហំដីជាច្រើនហិកតា ទោះបីវាបានបង្ហាញពីទម្រង់ព្រៃដាច់ពីគ្នាទៅ

CITATION: Ito E., Furuya N., Ohnuki Y., Miyamoto K., Araki M., Tamai K., Shimizu T., Iida S., Kanzaki M., Monda Y., Kabeya N., Yagi T., Shimizu A., Toriyama J., Tith B., Keth S., Ly C., Op P., Chann S. & Kiyono Y. (2022) Topographical patterns of species composition in a deciduous dipterocarp forest in Kratie Province, Cambodia. *Cambodian Journal of Natural History*, 2022, 18–37.

តាមលំដាប់រយៈកម្ពស់ក៏ដោយ។ ដើម្បីការពារព្រៃឈ្មោះអោយបានគង់វង្ស គ្រប់សមាសភាពព្រៃតាមលំដាប់រយៈកម្ពស់ (មិនមែន ជ្រើសតែប្រភេទដែលមានចំនួនតិចទេ) ត្រូវតែទទួលបាននូវកិច្ចខិតខំប្រឹងប្រែងអភិរក្ស។

## Abstract

We explored species composition patterns in a 4 ha permanent sample plot to assess the topographical distributions of various types of deciduous dipterocarp forest in Kratie Province, eastern Cambodia. A toposequence was identified from hill tops to flood plains in the plot and soil and forest floor conditions varied along the toposequence. We also used an index of “importance value” for dominant species in each quadrat (0.04 ha) and non-metric multi-dimensional scaling analysis to visualize patterns of species composition. The deciduous dipterocarp forest in our study plot could be subdivided into four types (Groups 1–4). Two common types clearly separated along the toposequence: strong dominance of *Shorea siamensis* (*raing phnom* in Khmer) on hills (Group 1), and, dominance of *Dipterocarpus tuberculatus* (*khlong*), *Shorea obtusa* (*phchek*), or sometimes *Terminalia* species on plains and flood plains (Group 4). Group 3 was characterized by strong dominance of *D. tuberculatus* scattered throughout the plains and flood plains and suggested limited regeneration of other species. Group 2 comprised a mixture of three dipterocarps characterized by a high number of tree species and large amounts of forest floor vegetation. This forest type occupied foot slopes and the higher sides of the plains, which formed the boundary area between Group 1 and Groups 3–4. Our results indicate that various types of deciduous dipterocarp forests can coexist within a scale of several hectares, although they exhibit separation along the toposequence. To appropriately preserve deciduous dipterocarp forests, all types of forest composition along toposequences (rather than solely types that are limited in abundance) must be included in forest conservation efforts.

**Keywords** Conservation, dry dipterocarp forest, forest fire, forest floor vegetation, forest type, spatial heterogeneity, topography, tree recruitment.

## Introduction

Identification of forest types in combination with their associated topographies and soil conditions is essential for understanding forest ecosystems. In Cambodia, deciduous forests are predominant, comprising 38.2% of the forested area (Ministry of Environment [MoE], 2018). Deciduous forests primarily occur within five provinces (Mondulakiri, Preah Vihear, Kratie, Stung Treng, and Ratanakiri) in northeast Cambodia; these comprise 79.0% of deciduous forests in Cambodia (MoE, 2018). In the Cambodian Forestry Administration (FA) forest classification system, deciduous forests include deciduous (dry) dipterocarp forests and dry mixed deciduous forests (FA, 2018). Deciduous dipterocarp forests are described as “*forêt claire*” (Rollet, 1972) or deciduous dipterocarp forests or woodlands (Rundel, 1999); they exist throughout Indo-Burma (Ashton, 2014) and on skeletal or arid soils up to approximately 600 m elevation in Cambodia (Rollet, 1972; Rundel, 1999).

Deciduous dipterocarp forests have been further subdivided into four types (or subtypes of forest) in Cambodia, each representing distinct combinations of a small number of deciduous species of Dipterocarpaceae (Rollet, 1972). One type of deciduous dipterocarp forest is characterized by dominance of *Dipterocarpus tuberculatus*

Roxb. (*khlong* in Khmer), *Shorea obtusa* Wall. ex Blume (*phchek*), and *Terminalia alata* Heyne ex Roth (*chhlik*) of the Combretaceae, which favours plinthite soils (“laterite” in Rollet, 1972). This most predominant type of forest exhibits generally moderate species richness, and a similar floristic structure extends broadly across mainland Southeast Asia (Rundel, 1999). The second forest type is characterized by strong dominance of *Shorea siamensis* Miq. (*raing phnom*), which is the most tolerant of dry habitat conditions among the deciduous species of dipterocarps (Rundel, 1999). This type of forest occupies sites with eroded leptosols (or lithosols) or skeletal soils, such as soils that occur over young basalt flows (Rollet, 1972; Rundel, 1999). The third forest type is characterized by strong dominance of *Dipterocarpus obtusifolius* Teijsm. ex Miq. (*tbeng*) (Rollet, 1972). This type grows on sandy soils that experience seasonal flooding (Rundel, 1999; Hiramatsu *et al.*, 2007; Ito *et al.*, 2017b). The above three types were also reported by Tani *et al.* (2007). The fourth type exhibits the greatest species richness with characteristic dominance by *Dipterocarpus intricatus* Dyer (*trach*) in upper stature (Rundel, 1999; Hiramatsu *et al.*, 2007). Soil conditions under this forest type generally consist of sandy siliceous soil horizons over clay or laterite layers at 20–40 cm depth (Rundel, 1999).

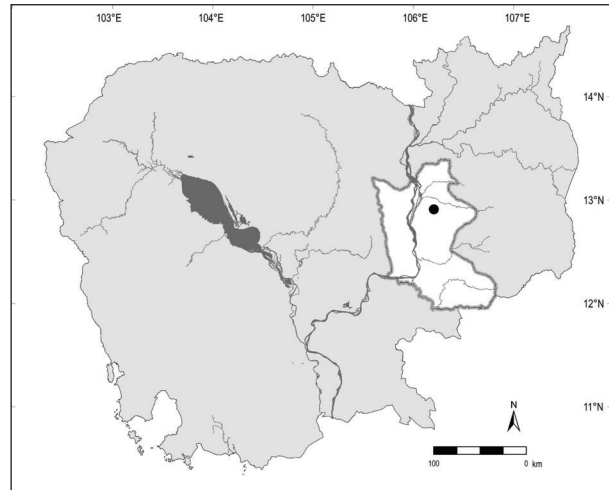
As described above, these four types of deciduous dipterocarp forests have been categorized based on the topography, geology, and soils within the habitat. However, the findings thus far have only described typical habitat patterns; they have not sufficiently examined how these types are distributed in space, at which scale, and what features exist near the boundaries between the different forest types, i.e., transitional forms between the different types of deciduous dipterocarp forests. Determining the spatial distribution patterns of typical and transitional forms, as well as their spatial scales, would provide key information regarding the conservation and sustainable use of these forests. Such data would provide necessary information for conservation planning, such as the extent of area to conserve, the site characteristics to include, and the nature of sustainable forest conditions for each site.

The objective of the present study was to determine the spatial distribution patterns of the first and second types of deciduous dipterocarp forests, and the transitional forms between these within an area of several hectares. The study was conducted on the terrace surface of the Mekong River in Kratie Province, on the east side of the river. Although most topography is flat in Kratie Province, some undulations are present in forested areas. Topographical patterns reflect soil conditions and govern water/groundwater flows, and thus potentially affect tree or understory species composition and stand structure. We established a 4 ha permanent sample plot, assessed spatial heterogeneity in vegetation properties, and examined relationships between species composition (or distribution) and topographic patterns.

## Methods

### Research site

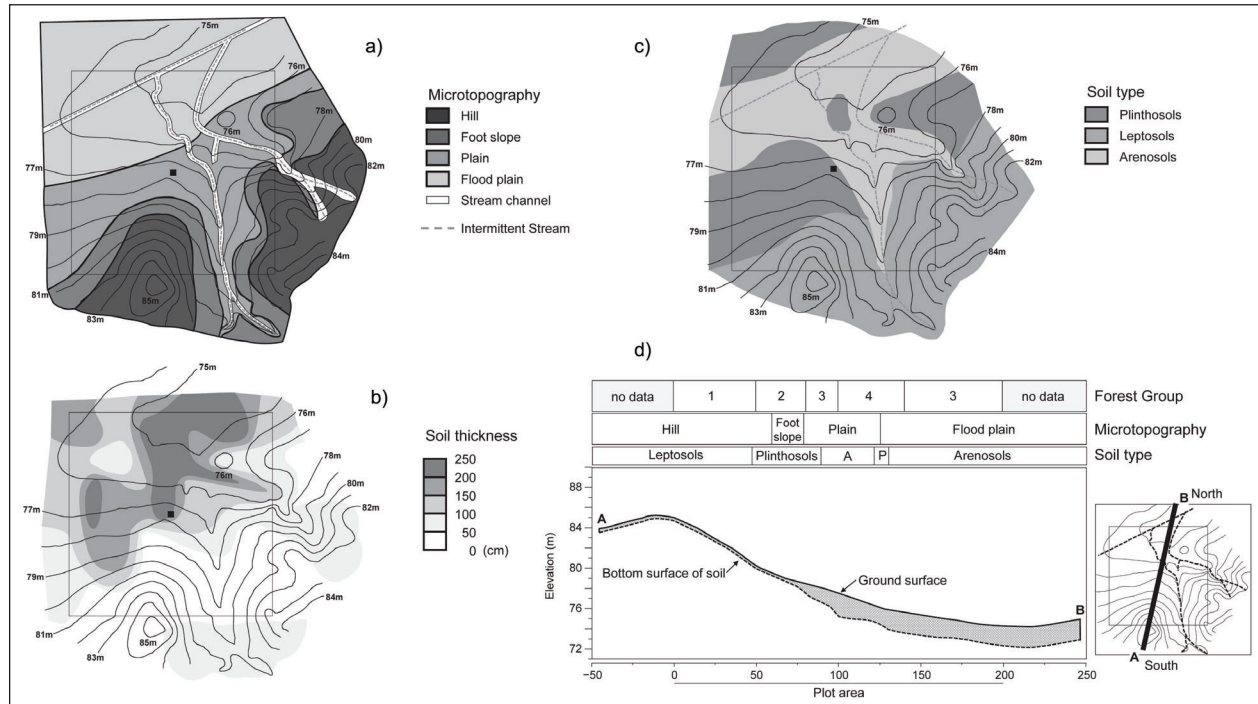
Our 4 ha study plot (200 × 200 m) included a meteorological observation site and was located 50 km north of the Kratie provincial capital in eastern Cambodia (12.92°N, 106.20°E; elevation: 74–85 m; Fig. 1). The region has a dry season extending from November to April. Annual rainfall (mean ± standard deviation) was 1,643 ± 272 mm during 2000–2010 (National Institute of Statistics, 2012) and mean annual temperature was 27 °C (Iida *et al.*, 2016). Tertiary and quaternary sedimentary rocks and basalts underlie forests located on the Mekong River terrace (Ohnuki *et al.*, 2008; Toriyama *et al.*, 2010; Ohnuki *et al.*, 2012). These forests experience a fire regime caused by surface fires almost every year, and the aboveground portion of dead forest floor vegetation almost burns during the dry season. Logging or fuelwood collection



**Fig. 1** Location of study site (solid circle) in Kratie Province (white area), Cambodia. Dark gray areas and lines indicate water bodies and rivers, respectively.

was not allowed in the study forest. However, illegal logging did occur occasionally. There was no grazing.

The study plot encompassed a toposequence from hill tops (i.e., elevated sections in the southeastern portion of the plot) to foot slopes, plains and flood plains (i.e., flat areas in the northwestern portion of the plot). The main stream flows from west to northeast, and two small streams enter from the south (Fig. 2A). The soil types were outlined by Ito *et al.* (2017a) (Fig. 2B). Soil thickness measurements were conducted using a dynamic cone penetrometer at 41 points in and around the study plot (Ohnuki *et al.*, 2008; adding 17 points to Ito *et al.*, 2017a; Fig. 2C). Topography, soil type, and soil thickness were associated with each other in the study plot (Fig. 2D). The hills contained leptosols (Food & Agriculture Organization soil classification), in which the basaltic bedrock was often exposed. Leptosols are shallow (<1 m deep and primarily <50 cm deep) debris soils (Figs. 2B–C; Ohnuki *et al.*, 2012). Plinthosols (i.e., clay soils that possess a hard plinthite layer with large accumulations of iron) are distributed in the foot slopes and plains, except near small streams (Ohnuki *et al.*, 2012). In the area of plinthosols located at the foot slope near the arenosol boundary, fine debris and large weathered basalt debris (probably transported from the hill tops) occur at a thickness of >50 cm within a 1 m deep soil pit (Ohnuki *et al.*, 2014). Arenosols (i.e., thick sandy soils) are located in the flood plains and plains near the streams. Coarse-rounded quartzite gravel has been found on the ground surface along the stream (Ohnuki *et al.*, 2022). Plinthosols and arenosols exhibit significantly deeper soils (1.0–2.5 m deep), compared



**Fig. 2** Topographical and soil conditions of study plot. A) Microtopographic classification, B) soil types, C) soil thickness, and D) topographic cross section. Soil type and soil thickness are modified from Ito *et al.* (2017a). Dashed gray lines indicate intermittent streams. Square boundary line and solid black symbol indicate 4 ha study plot (200 × 200 m) and meteorological flux observation tower, respectively.

with leptosols (Figs. 2B–C; Ito *et al.*, 2017a). Water storage capacity in the study plot is directly proportional to soil thickness, considering an effective porosity identical to the three soil types ( $0.15 \text{ m}^3 \text{ m}^{-3}$ , Ohnuki *et al.*, 2008).

### Tree census

We divided the 4 ha plot into 1,600 quadrats each measuring  $5 \times 5 \text{ m}$ . Within the plot, we recorded the girth of all standing woody stems with values  $\geq 5 \text{ cm}$  at 1.3 m above ground level (diameter at breast height, DBH) to the nearest 1 mm. These data were collected in the dry season of mid-February 2017. We also identified trees to species level and recorded the position of each individual based on the  $5 \times 5 \text{ m}$  quadrat location. Coppiced stems were included in basal area and stem density measurements. Scientific names of species are presented in Annex 1. Though the glabrous type and hairy type of *T. alata* have not been confirmed as distinct species, they differ substantially in habitat and leaf phenology (Ito *et al.*, 2017a) and are treated separately for convenience in this paper. Stand structure parameters calculated from tree census data included basal area ( $\text{m}^2 \text{ 25 m}^{-2}$ ), stem density (number of stems  $25 \text{ m}^{-2}$ ) and maximum stem diameter (cm) for all species in each  $5 \times 5 \text{ m}$  quadrat.

### Forest floor vegetation census

As an index of aboveground forest floor vegetation biomass, we investigated spatial variation in the height of understory vegetation (hereafter, understory height) at 747 points within the 4 ha plot on 4–5 September 2011. Understory height (cm) was measured by reading the height of any plant (primarily grasses) touching a vertically standing measuring rod. Data were interpolated onto a 0.5 m mesh grid and then averaged for each  $5 \times 5 \text{ m}$  quadrat.

Aboveground forest floor biomass was destructively investigated on 20 November 2012. Floor vegetation was sampled in  $0.5 \times 0.5 \text{ m}$  areas at the corners of sixteen  $50 \times 50 \text{ m}$  quadrats within the 4 ha plot except in the centre of the plot (location of our meteorological tower). Each sampling area was located 2 m forward from the corner of quadrats towards the flux tower. This was to avoid the influence of foot traffic and concrete-post setting on sampling data. Following sorting of samples into the leaves of shrubs or juvenile trees, the stems and branches of shrubs or juvenile trees, and grasses, these were oven-dried and weighted.

### Fire regime census

The spatial distribution of the fire regime was examined from 29 January to 1 February 2014. We recorded whether the base of each standing tree had been burnt or not and then calculated the percentage of burnt trees in each of four hundred 10 × 10 m quadrats constituting the 4 ha plot. In quadrats without standing trees, we visually determined the percentage of burnt areas. The fire regime was also directly observed from 10 February to 10 March in 2012 and 2013 at the corners of sixteen 50 × 50 m quadrats within the 4 ha plot except for the centre of the plot. In these instances, we recorded whether the area within 5 m in four directions from the fixed observation point was burning or not.

### Species composition analysis in 20 × 20 m subplots

For species composition analyses, we pooled tree census data from 16 neighbouring 5 × 5 m quadrats and treated them as a single 20 × 20 m subplot (i.e., 100 total subplots within the 4 ha plot). The dominant tree species was defined as the species with the highest importance value (IV index) for each 20 × 20 m subplot. IV indexes for every species in each quadrat were calculated as follows:

$$IV_i = (\%N_i + \%G_i) / 2$$

where %N<sub>*i*</sub> is the proportion of stems of species *i* relative to the total number of stems for all species, and G<sub>*i*</sub> is the proportion of basal area of species *i* relative to the total basal area of all species (Nguyen & Baker, 2016). To compare our data with the results of previous studies, we calculated IV indexes only when stems with DBH ≥ 10 cm were selected.

To explore patterns of species composition for each 20 × 20 m subplot, we employed non-metric multi-dimensional scaling (NMDS) (Kenkel & Orlóci, 1986) with the “vegan” package (Oksanen *et al.*, 2019) in R (R Core Team, 2020). Bray–Curtis dissimilarity (Beals, 1984) in species composition was calculated based on the IV indexes, which was used to identify grouping patterns of quadrats using NMDS. We used the “vegdist” and “metaMDS” functions for these analyses.

To determine groups of quadrats, we used hierarchical cluster analysis with the “cluster” package (Maechler *et al.*, 2019) in R (R Core Team, 2020). Bray–Curtis dissimilarity was also used for the hierarchical cluster analysis, wherein the quadrats were grouped based on the number of groups objectively determined with the largest silhouette value. We used the “hclust” and “silhouette” functions for these analyses.

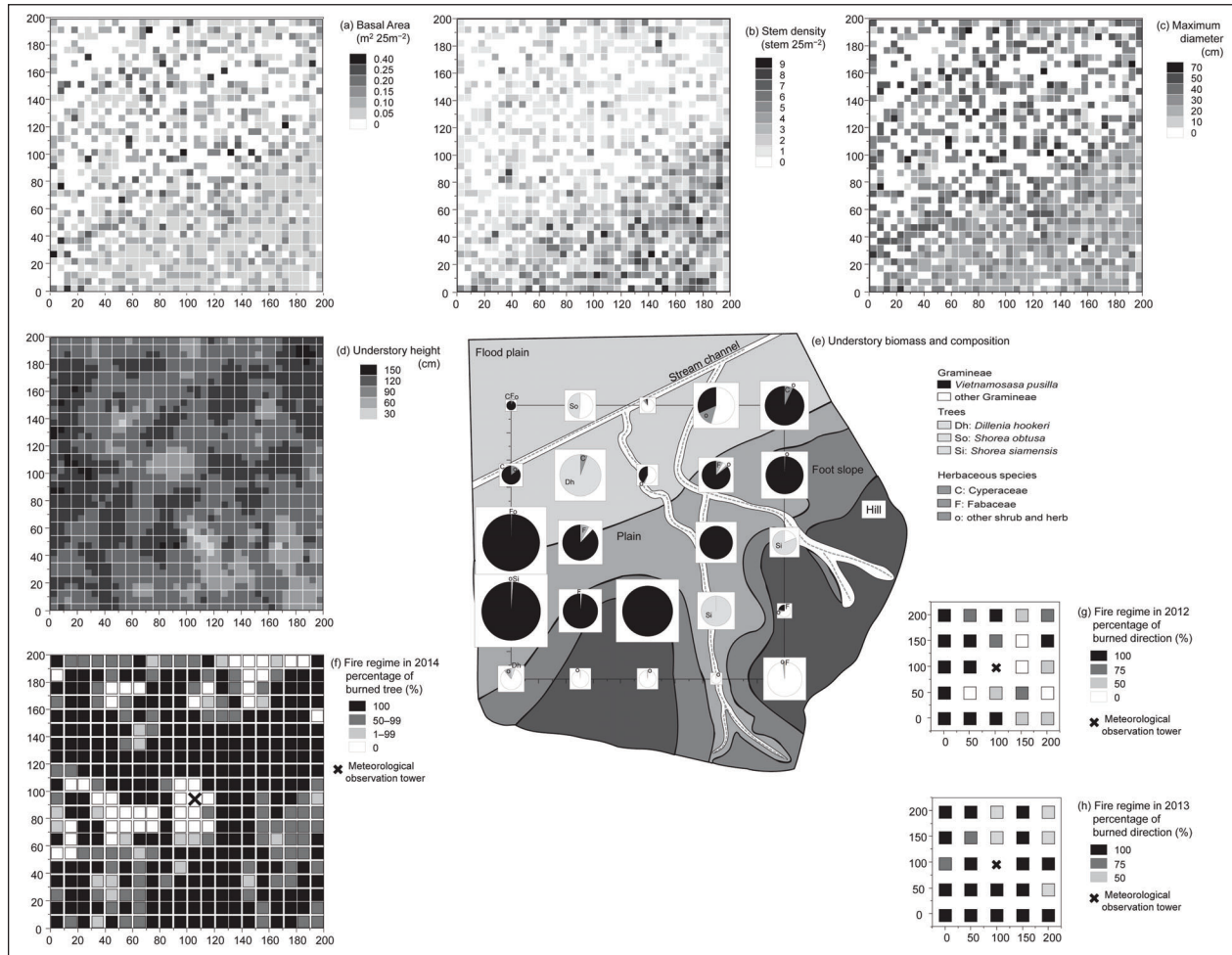
One-way analysis of variance and post hoc Tukey–Kramer honest significant difference tests were used to evaluate differences in understory height among the 20 × 20 m subplots with different dominant tree species. These were also used to determine differences in basal area, stem density, the number of total species, the number of dipterocarp species (or number of non-dipterocarp species) in each subplot, as well as understory height and aboveground understory biomass among the NMDS-identified groups mentioned above. The size (DBH) distributions of the three dipterocarp species and other non-dipterocarp species were examined using NMDS-identified groups. This analysis was conducted in JMP statistical software (ver. 10.0, SAS Institute Inc., North Carolina, USA).

## Results

### Forest properties and spatial characteristics

For free-standing stems with DBH ≥ 5 cm, our study plot comprised 13.76 m<sup>2</sup> ha<sup>-1</sup> in basal area, 555.5 stem ha<sup>-1</sup> for stem density, and a total of 46 tree species. For free-standing stems with DBH ≥ 10 cm, the study plot comprised 12.88 m<sup>2</sup> ha<sup>-1</sup> in basal area, 358.8 stem ha<sup>-1</sup> in stem density, and 36 tree species in total (Table 1, Annex 1).

The spatial distribution of three forest properties (basal area, stem density and maximum stem diameter) are shown in Figs. 3A–3C. Of the 1,600 quadrats (5 × 5 m), 999 (62.4% of the total) contained at least one tree individual with DBH ≥ 5 cm (hereafter referred to as with-tree quadrat). Quadrats not including individuals with DBH ≥ 5 cm (*n* = 601) were frequently found in the northwest area of the plot; fewer such quadrats were found in the southeast area (Fig. 3). Based on the same three forest properties (basal area, stem density, and maximum stem diameter), the plot was also generally divided into two areas (i.e., northwest and southeast). For with-tree quadrats, basal area was slightly higher in the northwest area (Fig. 3A), stem density was slightly higher in the southeast area (Fig. 3B) and maximum stem diameter was considerably higher in the northwest area (Fig. 3C). In terms of microtopography (Fig. 2A), stem density was lower in the flood plains and higher on hills (Fig. 3B), while maximum stem diameter was greater on flood plains and smaller on hills (Fig. 3C).



**Fig. 3** Spatial distribution of selected forest properties in the study plot. A) Basal area, B) stem density, C) maximum DBH, D) understory height, E) understory biomass and its composition, F) fire regime in 2014, G) fire regime in 2012, and H) fire regime in 2013. The scales of pie charts in Fig. 3E are proportional to the total amount of understory biomass (Annex 2). In Fig. 3F, the area around the observation tower has been cleared to prevent the spread of fire.

**Table 1** Structural properties of deciduous dipterocarp forest trees at study site in Kratie Province, Cambodia.

| Metric / species                                  | 5–10 cm DBH | ≥10 cm DBH | Total |
|---|-------------|------------|-------|
| <b>Basal area (m<sup>2</sup> ha<sup>-1</sup>)</b> | 0.88        | 12.88      | 13.76 |
| <i>Dipterocarpus tuberculatus</i>                 | 0.07        | 4.17       | 4.24  |
| <i>Shorea obtusa</i>                              | 0.01        | 2.40       | 2.41  |
| <i>Shorea siamensis</i>                           | 0.52        | 2.19       | 2.72  |
| <b>Stem density (stems ha<sup>-1</sup>)</b>       | 197.3       | 358.8      | 556.0 |
| <i>Dipterocarpus tuberculatus</i>                 | 14.8        | 91.5       | 106.3 |
| <i>Shorea obtusa</i>                              | 3.5         | 43.8       | 47.3  |
| <i>Shorea siamensis</i>                           | 114.3       | 109.3      | 223.5 |
| No. of species (spp. 4 ha <sup>-1</sup> )         | 38          | 36         | 46    |

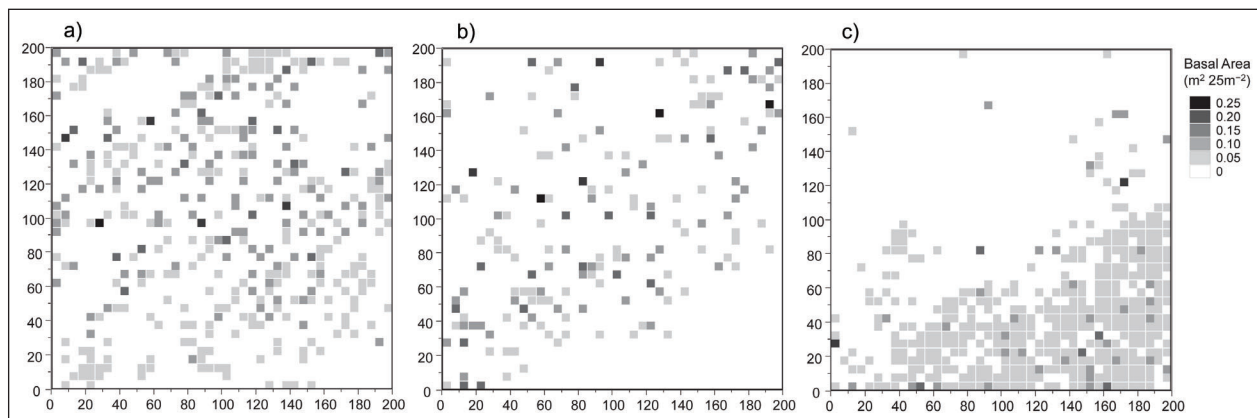
Topographical locations were clearly linked to forest floor vegetation (Figs. 3D–E). Lower understory heights were primarily found in the hills and flood plains (Fig. 3D). The spatial distribution of understory height varied from 15 to ca. 140 cm tall (Fig. 3D). Our field observation and destructive survey of the biomass of understory vegetation indicated that in the plain and foot slope, the top layer of herbaceous communities primarily consisted of dense dwarf bamboo grass (*Vietnamosasa pusilla*), whereas the lower layer often consisted of other herbaceous species belonging to the Gramineae and Fabaceae (Fig. 3E). The understory biomass in these areas ranged from 3.5 to 7.2 Mg ha<sup>-1</sup>. In the flood plain, *V. pusilla* and other Gramineae were abundant, but their biomass was not significant (1.1–5.0 Mg ha<sup>-1</sup>). A small colony of

*Dillenia hookeri* (phlou bat; approximately 50 cm tall) and herbaceous species in the Cyperaceae were also observed near the main stream. Saplings of *S. obtusa* were found in one location (X50, Y200). In the southeast area, the grass layer was generally composed of herbaceous species of Gramineae ( $1.2\text{--}4.2\text{ Mg ha}^{-1}$ ). *Shorea siamensis* saplings were found in some parts of this area. *Cycas siamensis* (brong) was present, but rare and not found in the destructive sampling plots. Details of understory vegetation biomass obtained from the destructive survey in 24 sites are shown in Annex 2. The spatial distribution of fire is shown in Figs. 3F–H. The percentage and distribution of areas burnt varied from year to year. Visual comparisons of these spatial distributions indicated that understory height and biomass appeared to be less associated with the frequency of fire.

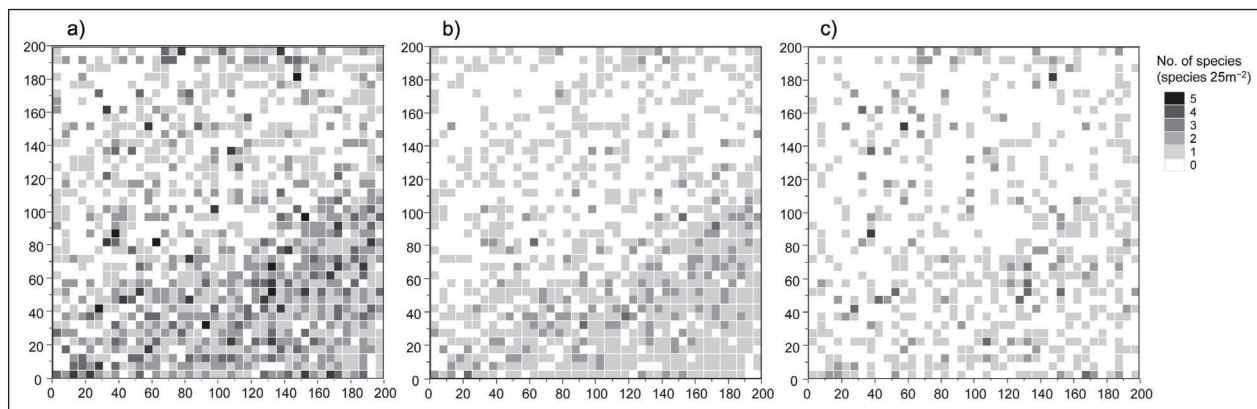
#### Spatial distributions of dominant dipterocarp species and other species

The study plot contained three dominant dipterocarp species. These were *D. tuberculatus*, *S. obtusa*, and *S. siamensis*, which respectively comprised 30.8%, 17.5% and 19.7% of the total basal area of the plot and 19.1%, 8.5% and 40.2% of the total number of stems, respectively (Table 1, Annex 1). *Dipterocarpus tuberculatus* was evenly distributed in the plot, although its basal area was larger in the northwest area (Fig. 4A). *S. obtusa* was scattered in the northwest area (Fig. 4B) and *S. siamensis* was distributed throughout the southeast area (Fig. 4C).

The maximum number of tree species that appeared in a  $5 \times 5\text{ m}$  quadrat was five (Fig. 5A). Among the with-tree quadrats ( $n = 999$ ), the mean number of tree species present in a quadrat was 1.6 and 570 quadrats (57.1%)



**Fig. 4** Spatial distributions of predominant dipterocarp species in study plot. Basal areas of A) *Dipterocarpus tuberculatus*, B) *Shorea obtusa*, and C) *Shorea siamensis*.



**Fig. 5** Spatial distributions of species richness in study plot. A) All species, B) three dominant dipterocarp species, and C) all other species.

contained only one species (Fig. 5A). The numbers of quadrats containing *D. tuberculatus*, *S. obtusa* and *S. siamensis* were 369, 169 and 428, respectively (Figs. 4A–4C). The three dominant dipterocarp species were rarely distributed together, in co-occurring in only six quadrats (Fig. 5B). Among the with-tree quadrats, at least one of the three dominant dipterocarp species occurred in 825 quadrats (82.6%) (Fig. 5B). Of the 129 quadrats (12.9%) in which two species of dipterocarps occurred, 76 quadrats (58.9% of the 129 quadrats) included *D. tuberculatus* and *S. siamensis*, 28 quadrats (21.7%) included *S. obtusa* and *S. siamensis* and 25 quadrats (19.4%) included *D. tuberculatus* and *S. obtusa*.

Other non-dipterocarp species (43 species in total) occurred in 521 (52.1% of total) quadrats among the 999 with-tree quadrats. On rare occasions, 3–4 non-dipterocarp species appeared in a quadrat (Fig. 5C).

#### Dominant species and species composition groups (IV index and NMDS analysis)

Six tree species were considered dominant based on the IV index for each 20 × 20 m subplot (Fig. 6). The dominant

tree species in the largest number of plots was *D. tuberculatus* ( $n = 46$ ), which dominated a large portion of the northwest area. The second most dominant tree species in the subplots was *S. siamensis* ( $n = 30$ ), which dominated all of the southeast area. The third most dominant tree species in the plots was *S. obtusa* ( $n = 16$ ), and the plots dominated by this species occurred near the boundary between southeastern and northwestern areas. These three dipterocarp species were dominant in 92% of the subplots. The other eight subplots were dominated by three *Terminalia* spp. The glabrous type of *T. alata* ( $n = 3$ ) was dominant near the boundary between the two main areas, similar to *S. obtusa*. The hairy types of *T. alata* ( $n = 3$ ) and *T. mucronata* ( $n = 2$ ) were occasionally dominant near the northwest corner of the study plot. Understory height was significantly lower in subplots dominated by *S. siamensis*, compared with subplots dominated by other species ( $F = 54.4$ ,  $p < 0.0001$ ).

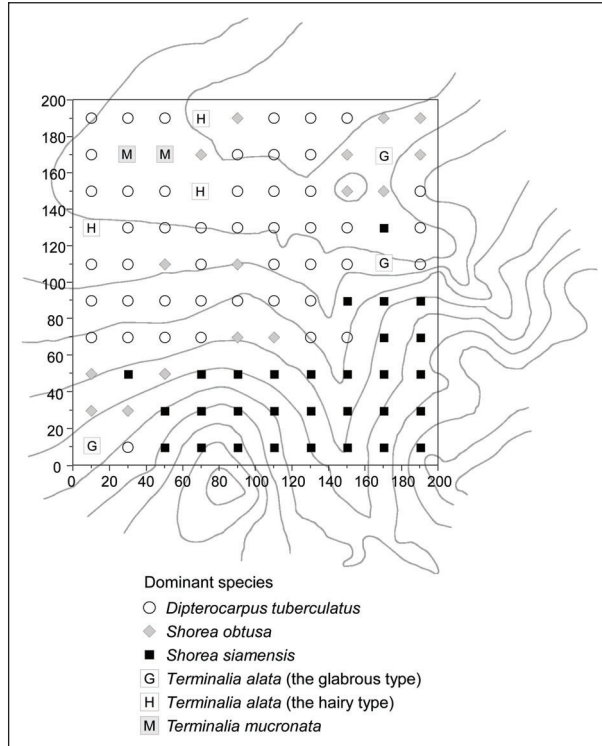
Hierarchical cluster analysis determined four distinct groups among the 20 × 20 m subplots. NMDS analysis showed that Group 1 was tightly clustered (Fig. 7A), dominated by *S. siamensis* without exception (Fig. 7B, Table 2) and occupied the southeast area (Fig. 7C). Group

**Table 2** Characteristics of groups separated in the non-metric multi-dimensional scaling analysis.

|  | Group                                    |   |   |   |
|--|--|---|---|---|
|  | 1  | 2   | 3                                       | 4   |
| Dominant species*  | <i>S. siamensis</i> (24)                 | <i>D. tuberculatus</i> (10), <i>S. obtusa</i> (10), <i>S. siamensis</i> (6), <i>T. alata</i> (glabrous) (3) | <i>D. tuberculatus</i> (18)             | <i>D. tuberculatus</i> (13), <i>S. obtusa</i> (6), <i>T. alata</i> (hairy) (3), <i>T. mucronata</i> (2) |
| No. of subplots  | 24                                       | 34  | 18                                      | 24  |
| Microtopography  | Hills                                    | Foot slope / upper plain  | Flood plain / lower plain               | Flood plain / lower plain   |
| Stem density† (stems 0.04 ha <sup>-1</sup> )             | 43.3 ± 8.5 <sup>a</sup><br>[27–65]       | 20.3 ± 10.4 <sup>b</sup><br>[8–51]  | 11.3 ± 5.1 <sup>c</sup> [5–25]          | 12.1 ± 4.8 <sup>c</sup><br>[6–25]   |
| Basal area† (m <sup>2</sup> 0.04 ha <sup>-1</sup> )      | 0.55 ± 0.09 <sup>ab</sup><br>[0.39–0.72] | 0.62 ± 0.21 <sup>a</sup><br>[0.22–1.06]   | 0.47 ± 0.17 <sup>b</sup><br>[0.16–0.76] | 0.51 ± 0.19 <sup>ab</sup><br>[0.11–0.88]  |
| No. of species† (0.04 ha <sup>-1</sup> )                 | 5.9 ± 1.8 <sup>ab</sup> [3–10]           | 6.6 ± 2.6 <sup>a</sup> [3–15]   | 4.6 ± 1.5 <sup>b</sup> [1–7]            | 6.0 ± 1.5 <sup>ab</sup> [4–9]   |
| No. of dipterocarp species† (0.04 ha <sup>-1</sup> )     | 2.3 ± 0.7 <sup>b</sup> [1–3]             | 2.7 ± 0.5 <sup>a</sup> [2–3]  | 1.7 ± 0.5 <sup>c</sup> [1–2]            | 2.0 ± 0.5 <sup>bc</sup> [1–3]   |
| No. of non-dipterocarp species† (0.04 ha <sup>-1</sup> ) | 3.6 ± 1.4 <sup>a</sup> [1–7]             | 3.9 ± 2.4 <sup>a</sup> [1–12]   | 2.9 ± 1.4 <sup>a</sup> [0–5]            | 3.9 ± 1.5 <sup>a</sup> [2–6]  |
| Understory height† (cm)                                  | 69 ± 16 <sup>c</sup> [29–127]            | 87 ± 16 <sup>a</sup> [16–135]   | 82 ± 16 <sup>b</sup><br>[25–123]        | 84 ± 19 <sup>b</sup><br>[36–142]  |
| Aboveground understory biomass (Mg ha <sup>-1</sup> )    | 3.0 ± 1.4 <sup>a</sup><br>[1.2–6.2]      | 4.4 ± 1.3 <sup>a</sup><br>[2.6–7.2]   | 2.6 ± 1.7 <sup>a</sup><br>[1.1–7.0]     | 4.3 ± 1.3 <sup>a</sup><br>[1.6–7.0]   |

\* Figures in parentheses indicate the number of subplots dominated by that species. † Values represent mean ± standard deviation [range]. Figures on the same row with different superscript letters indicate significant differences ( $p < 0.05$ ).



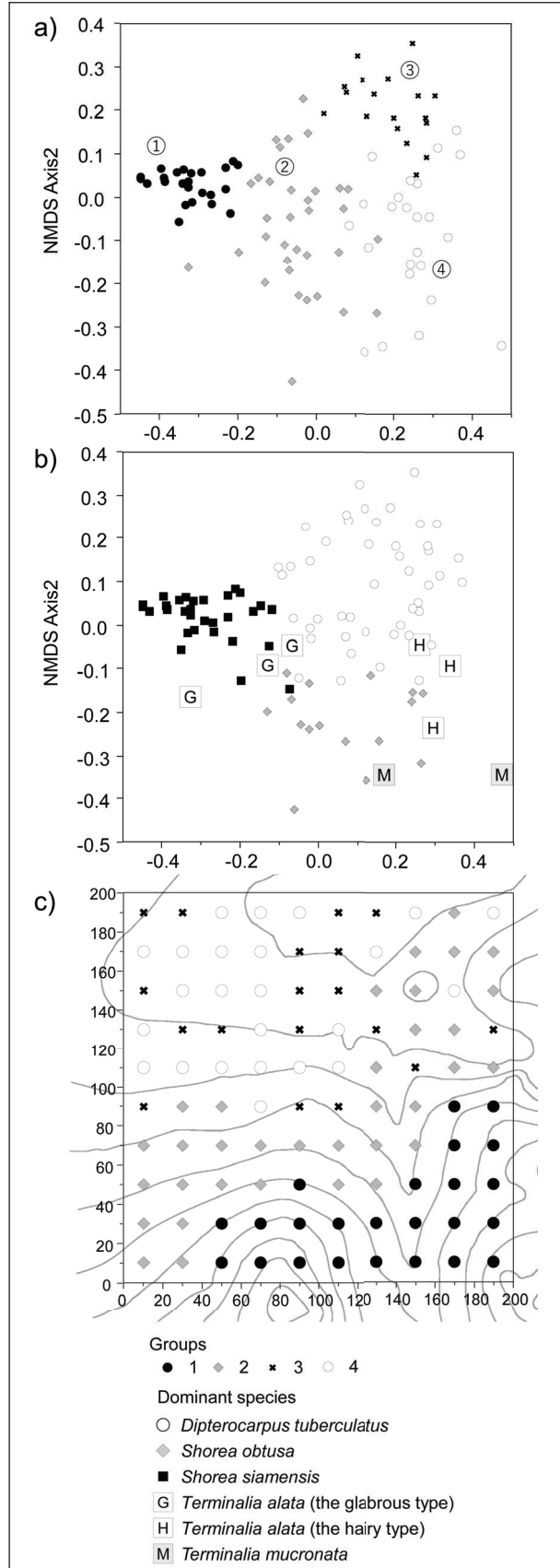


**Fig. 6** Spatial distributions of the dominant tree species for each 20 × 20 m subplot. Gray lines indicate elevation contours.

3 was also clustered (Fig. 7A), dominated by *D. tuberculatus* without exception (Fig. 7B, Table 2) and scattered in the northwest area (Fig. 7C). Groups 2 and 4 were more diffusely arranged (Fig. 7A) and dominated by various species (Fig. 7B, Table 2). Group 2, in which *S. siamensis* and the glabrous type of *T. alata* occasionally dominated, in addition to *D. tuberculatus* and *S. obtusa*, was distributed in the border between the northwest and southeast areas. In contrast, Group 4, where the hairy type of *T. alata* and *T. mucronata* occasionally dominated in addition to *D. tuberculatus* and *S. obtusa*, was scattered in the northwest area (Fig. 7C, Table 2).

Stem density was higher in Group 1 in the southeast area, followed by Group 2 at the border between northwest and southeast areas. Values of stem density were

**Fig. 7** (right) Non-metric multidimensional scaling (NMDS) based on the species compositions of 100 subplots. A) NMDS by identified groups (stress value = 0.137), B) NMDS by dominant species, and C) spatial distributions of groups with elevation contours (gray lines).



lower in Groups 3 and 4 in the northwest area. Basal area did not differ in a manner similar to stem density among groups; it was smaller in Group 3, which was only dominated by *D. tuberculatus*, and significantly differed from Group 2 (Table 2). The number of species was larger in Group 2 and smaller in Group 3. The number of non-dipterocarp species did not differ among groups; thus, differences in the total number of species between groups were attributed to differences in the number of dipterocarp species (Table 2). Understory height was significantly larger in Group 2, followed by Groups 3 and 4; it was lowest in Group 1 (Table 2).

The size (DBH) distributions of the dipterocarp and non-dipterocarp species (*T. alata* and others) are shown according to group (Fig. 8). Although *D. tuberculatus* was found in all four groups, the shape of the DBH distribution differed between Group 1 and the other groups. Group 1 had no large-diameter trees, whereas it contained many small-diameter trees (Fig. 8A). In the other groups, the peak of the diameter distribution was in the range of 15–30 cm (Fig. 8A). For the size distribution of *S. obtusa*, a peak distribution in the medium size class was observed for all groups (Fig. 8B). The size distribution of *S. siamensis* differed markedly among groups (Fig. 8C). Very few *S. siamensis* individuals were present in Groups 3 and 4, whereas many such individuals were found in Group 1. In Groups 1 and 2, when sufficient individuals were present, the size distribution exhibited an “L” shape; smaller size was associated with greater number of individuals. Populations of the glabrous type of *T. alata* were commonly found in Groups 1 and 2, but the size distribution was not L-shaped (Fig. 8D). The hairy type of *T. alata* was found rather evenly in each class of Group 4, although there were not enough individuals to determine the size distribution (Fig. 8D). The overall size distribution of the other non-dipterocarp species was L-shaped, except for Group 3 (Fig. 8E). However, the number of individuals of each species was small, and only *Xylia xylocarpa* in Group 2 could be regarded as having an L-shaped distribution on a species basis. The maximum DBH for each non-dipterocarp species is listed in Annex 1.

## Discussion

### Deciduous dipterocarp forest at the study site

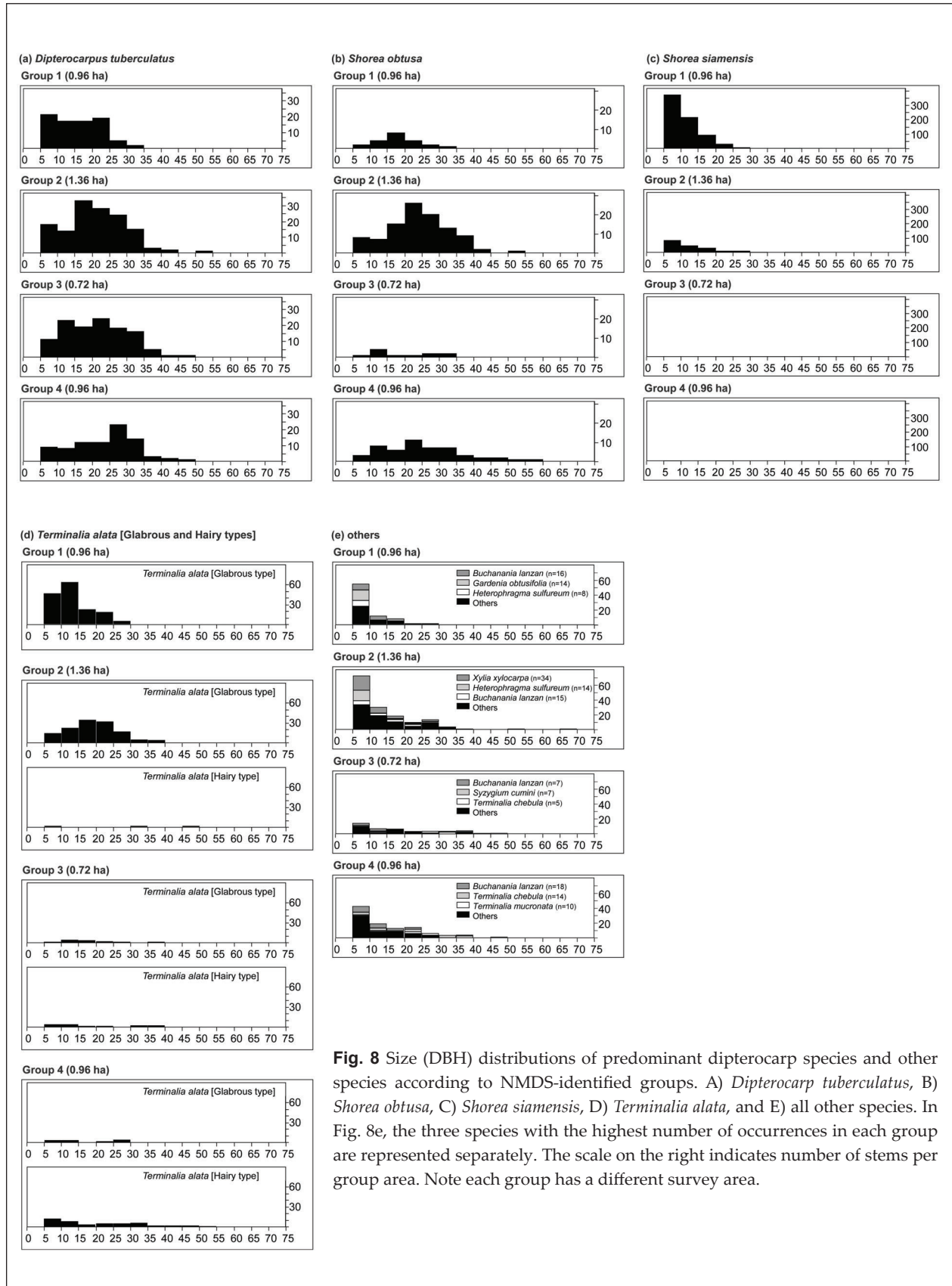
The overwhelming dominance of one or two deciduous dipterocarp species at the stand level is considered a defining feature of deciduous dipterocarp forests (Bunyavejchewin, 1983; Bunyavejchewin *et al.*, 2011; Nguyen & Baker, 2016). Our study site was also charac-

terized by the local existence of one or two of the three deciduous dipterocarp species (Fig. 5B). We expected our study plot would contain two types of deciduous dipterocarp forests: one forest dominated by *D. tuberculatus* and *S. obtusa* (=the first type in the introduction), and another forest dominated by *S. siamensis* (=the second type in the introduction). The former type corresponded to Group 4 in our NMDS analysis and occurred on the plains and flood plains, whereas the latter corresponded to Group 1 and exclusively occurred on hills (Table 2, Fig. 7). In addition to these two common types, our NMDS analysis suggested the existence of Group 3, which was strongly dominated by *D. tuberculatus*, and Group 2, which was a mixture of all three dipterocarp species (Table 2). Our study also clarified the distributions of Group 3 and Group 2: Group 3 was distributed in a patchy manner within Group 4, and Group 2 occupied the foot slopes between Group 4 and Group 1 (Fig. 7).

Group 4 has been reported in several studies of deciduous dipterocarp forest in Cambodia, including in the Phnom Prich Wildlife Sanctuary (Pin *et al.*, 2013), in the Mondulkiri Protected Forest (Pin *et al.*, 2013), and in Kratie Province (DDF3 in Tani *et al.*, 2007). A forest type similar to Group 1, dominated by *S. siamensis*, has been reported in Mondulkiri Province (DDF2 in Tani *et al.*, 2007). However, this forest type was not exactly the same as ours because several indicator or dominant species (*Quercus kerii*, *Dipterocarpus obtusifolius* and *T. mucronata*) were absent from Group 1 in our study. There is also a deciduous dipterocarp forest study in southwestern Cambodia (Phnom Samkos Wildlife Sanctuary), but the species were not described and the details of the forest type are unknown (Wood, 2012). To the best of our knowledge, the existence of Group 2 and Group 3 in Cambodia is unique to our study.

### Comparison of species composition with deciduous dipterocarp forests in continental Southeast Asia

The species composition of our study site is similar to other deciduous dipterocarp forests in continental Southeast Asia in terms of dominant dipterocarp species, but differs in several respects. The species composition (Annex 1) and forest characteristics (Tables 1–2) of our site were most similar to deciduous dipterocarp forests in Yok Don National Park in central Vietnam (Nguyen & Baker, 2016), which is located 170 km due east of our study site. Compared to the Doi Inthanon National Park, Chiangmai, Thailand, our site differed from the pine-dipterocarp forest in the intermediate zone (850–1400 m above sea level [asl]) in terms of the absence of *Pinus* spp., and from the deciduous dipterocarp forest in the lowlands (400–850 m asl) in terms of high abun-



**Fig. 8** Size (DBH) distributions of predominant dipterocarp species and other species according to NMDS-identified groups. A) *Dipterocarp tuberculatus*, B) *Shorea obtusa*, C) *Shorea siamensis*, D) *Terminalia alata*, and E) all other species. In Fig. 8e, the three species with the highest number of occurrences in each group are represented separately. The scale on the right indicates number of stems per group area. Note each group has a different survey area.

dances of *D. tuberculatus* and accompanying species (i.e., low abundance of *Canarium subulatum*) (Robbins & Smitinand, 1966; Bunyavejchewin, 1983; Teejuntuk *et al.*, 2002; Nguyen & Baker, 2016). The overall difference of our study site from deciduous dipterocarp forests in northern Thailand involves the non-universal presence of *S. obtusa*, i.e., *S. obtusa* was not present everywhere in our study site (Santisuk, 1988).

Although the topographical properties of our study site were similar to those in the Sakaerat deciduous dipterocarp forest of northeastern Thailand (i.e., frequent comparatively low, undulating hills with a slightly dry climate and shallow soils), the species composition differed from the Sakaerat forest in terms of the absence of *Shorea roxburghii*, presence of *D. tuberculatus* (Sahunalu, 2009) and absence of *D. intricatus* (Sakurai *et al.*, 1998). Our study forest also differs from a semi-Indaing forest (*D. tuberculatus* forest in Burma, a tropical dry deciduous forest based on the Burmese classification), in terms of the absence of teak *Tectona grandis* (Stamp, 1924; Hundley, 1961; Davis, 1964).

Our observation of co-occurring dominant deciduous dipterocarp species is also consistent with the species compositions of other forests in the region. For example, in lowland Thailand (Bunyavejchewin, 1983; Rundel & Boonpragob, 1995; Teejuntuk *et al.*, 2002) and Vietnam (Nguyen, 2009 and references therein), several associations of dominant dipterocarp species (i.e., dominance type: Bunyavejchewin, 1983) have been reported: *S. obtusa* and *S. siamensis*; *D. tuberculatus* and *S. obtusa*; and combinations of the three species. However, the combination most frequently observed in the present study was the combination of *D. tuberculatus* and *S. siamensis*, likely because the wide distribution range of *D. tuberculatus* in the study plot included hill tops to which *S. siamensis* was limited (Figs. 4A, 4C).

Elevational differences in the distribution of these dominance types have been found in Thailand (Bunyavejchewin, 1983). For instance, the *S. siamensis* type, which is similar to our Group 1, was distributed at lower elevations around 280 m, while the *D. tuberculatus*-*S. obtusa* type, which is similar to our Group 4, was reported as occurring at altitudes of 300 to 900 m (Bunyavejchewin, 1983). However, our study site lacked elevational differences among the three dipterocarp species; more specifically, *S. siamensis*, *D. tuberculatus* and *S. obtusa* were separated within a toposequence with an elevational difference of 10 m.

Group 2 noticeably differed from our other groups in that the three species of dipterocarps were often equally dominant (Table 2). It is also similar to the forest type

reported by Ogawa *et al.* (1961) as mixed savanna forest, which was later renamed mixed dry dipterocarp association (Bunyavejchewin, 1983). This forest type is characterized by component species which are numerous and well-mixed, with no distinct dominants (Ogawa *et al.*, 1961). The most commonly associated genera within mixed savanna forests are *Canarium*, *Gardenia*, *Heterophragma*, *Lannea*, *Terminalia*, *Vitex* and *Xylia* (Ogawa *et al.*, 1961), although our site also included *Adina*, *Lagerstroemia*, *Mangifera*, *Parinarium*, *Saurauia* and *Sindora* (Annex 1). Group 2 occupied the foot slopes on the border between the plains and hills. Its soil conditions were consistent with previous descriptions: commonly sandy clay loam or frequently underlain by fine sandy loam on plains, associated with stony sandy soils on hillsides (Ogawa *et al.*, 1961; Bunyavejchewin, 1983). Other striking features of Group 2 included larger basal area values, higher understory height and higher species richness (Table 2). The large basal area and high understory height suggest rich biomass in Group 2, which is consistent with a previous finding that the growth of rubber trees was highest on foot slopes along a toposequence (Okubo & Takeuchi, 1998).

#### Transitions between groups

One of our study objectives was to identify the forms of transition between deciduous dipterocarp forest types. Sharp boundaries often occur between different types of dominant dipterocarp species (Nguyen & Baker, 2016 and references therein), which is consistent with the separation of Group 1 from our other three groups (Fig. 7C). A key finding was that Group 2 functioned as the boundary area between Groups 1 and 4 (Fig. 7C). This separation of forest types was attributable to toposequence at a scale of several hundred meters (Fig. 2D), as reported in Kampong Thom Province (Hiramatsu *et al.*, 2007) and peninsular Thailand (Okubo & Takeuchi, 1998). Group 3 was scattered along with Group 4 in the plains and flood plains (Fig. 7C). The reasons for this scattered distribution are discussed below, along with factors responsible for the low abundances of tree species other than *D. tuberculatus* in Group 3.

#### Specific distribution patterns of deciduous dipterocarp and driving factors

*Absence of S. siamensis in plains vs. light environment and fire intensity*

*Shorea siamensis* was noticeably absent from the lower plain and flood plain (Figs. 4C, 8C). Marod *et al.* (2004) reported that the survival and growth rates of *S. siamensis* seedlings were dramatically greater in gaps than under

the closed canopy. Understory height is expected to have a monotonically increasing relationship with biomass of forest floor vegetation, implying a negative correlation between understory height and light transmittance. The light environment near the ground surface in the plain and flood plain may involve excessive shade for survival of *S. siamensis* seedlings, although this needs to be confirmed by seedling trials. Variation in understory biomass, i.e., fuel, also leads to differences in the intensity of combustion. The understory height in our study area (15–140 cm, Fig. 3D) corresponded to a high to very high fuel hazard (McCarthy *et al.*, 1999), whereas the understory biomass (1.1–7.2 Mg ha<sup>-1</sup>, Fig. 3E, Annex 2) corresponded to low to moderate surface fine fuel hazard (McCarthy *et al.*, 1999). Fire regimes in deciduous dipterocarp forests have been reported in detail for north and northeast Thailand (Stott, 1986). Fire intensity may appear to act as a critical environmental filter of tree species composition in our study plot, as reported previously for deciduous dipterocarp forests (Rundel & Boonpragob, 1995; Nguyen *et al.*, 2019). For instance, Nguyen *et al.* (2019) demonstrated that juveniles of *S. siamensis*, *S. obtusa* and *D. obtusifolius* require a comparatively long fire-free period to reach their fire-escape size, whereas juveniles of *D. tuberculatus* can become saplings despite an annual fire regime. The thin outer bark of low-height (<3 m) trees was noted as a possible reason for the fire vulnerability of *S. siamensis* (Nguyen *et al.*, 2019). In the present study, understory height differed significantly between hill tops, where *S. siamensis* is intensively distributed, and other areas (Table 2). The absence of *S. siamensis* was most likely because of light conditions, fire intensity, or both, depending on the amount of forest floor vegetation.

*Low prevalence of trees (or of trees other than D. tuberculatus) in plains vs. spatial heterogeneity in fire intensity*

Our Group 3, which occurred on the plains and flood plains, included fewer tree populations of species other than *D. tuberculatus* (Table 2, Fig. 8). In addition, when the flood plain was mapped at a fine resolution (5 × 5 m quadrats), a significant number of tree-less quadrats were present (Figs. 3A–3C). Factors limiting the presence of trees were smaller in scale than the toposequence and were presumably spatially heterogeneous within the plains and flood plains. Juveniles of *D. tuberculatus* are more resistant to fire, compared with other deciduous dipterocarps (Nguyen *et al.*, 2019), suggesting that spatial heterogeneity in fire intensity could be a limiting factor. As discussed in the previous paragraphs, low-intensity fire periods could be regularly expected where understory height and biomass were low (Figs. 3D–3E). On the other hand, a fire-free situation may occur more randomly, as suggested by the yearly variation in scat-

tered unburnt areas with remaining forest floor vegetation (Figs. 3F–3H). The survival of juvenile trees may only be possible in areas where a fire-free or low-intensity fire period lasts by chance for a comparatively long interval.

*Lower prevalence of trees or low understory height in the flood plain vs. stagnant water conditions*

In some areas of the flood plain where understory height and biomass were low (Figs. 3D, 3E), low-intensity fire periods might be expected to continue. However, Group 3 was distributed in such areas (Fig. 7C) and tree-less quadrats were often present (Figs. 3A–3C). Another factor limiting the presence of trees may be stagnant water conditions. Water retention was observed during the rainy season in the flood plain of our study area, including outside of the flow path (authors, unpublished data). The occurrence of Cyperaceae species and *D. hookeri* in these areas (Fig. 3E) is suggestive of a stagnant water environment. Thus, such conditions during the rainy season could also serve as factors limiting the survival of tree seedlings.

*Low recruitment of D. tuberculatus in Groups 2, 3 and 4 and S. obtusa in all groups vs. increase of fire events in recent years*

We documented lower numbers of small-sized trees of *D. tuberculatus* and *S. obtusa* in Groups 2, 3, and 4 (Fig. 8A) and in all four groups (Fig. 8B), respectively. In investigating the regeneration of various types of deciduous dipterocarp forest in central Vietnam, Nguyen & Baker (2016) documented the absence of *S. siamensis* saplings and raised concerns about the future regeneration of forest types dominated by the species. Pin *et al.* (2013) suggested that lower numbers of small *D. tuberculatus* trees in Monduliri Protected Forest were associated with more frequent fires. Our findings suggest that recruitment of *D. tuberculatus* and *S. obtusa* has somehow been suppressed in recent years. Ghazoul *et al.* (1998) reported that the reproductive output of *S. siamensis* was not affected when population density was reduced from 96 to 62 flowering trees ha<sup>-1</sup>, although it declined sharply when density was further reduced to 9 trees ha<sup>-1</sup>. In our 4 ha study plot, the density of flowering dipterocarp trees was 85 trees ha<sup>-1</sup> for *D. tuberculatus*, 34 trees ha<sup>-1</sup> for *S. siamensis* and 32 trees ha<sup>-1</sup> for *S. obtusa* (2014 census: Ito *et al.*, 2016). This suggests that the low recruitment of dipterocarp species was unlikely to be due to a lack of flowering trees. However, if fire intensity has increased in recent years, new tree recruitment may have been inhibited. In surveying the deciduous dipterocarp forests of Stung Treng Province before the 1970s, Legris & Blasco (1972) did not observe lower numbers of small trees of the three species of dipterocarps, indicating that their recruitment was steadily progressing in the forest

at that time. Climate-driven changes in drought and fire intensity in Southeast Asia may alter tree recruitment rates and cause long-term effects on the structure and species composition of deciduous dipterocarp forests (Nguyen *et al.*, 2019). Fire intensity may also be changing due to alterations in the composition of forest floor vegetation and amount of biomass. Forest fires may lead to soil degradation, such as soil erosion (Sakurai *et al.*, 1998) and nitrogen loss (Toda *et al.*, 2007), which may lead to further changes in forest floor vegetation.

Future studies are necessary to verify the above hypotheses, particularly for the development of conservation plans. Identification of site characteristics along the toposequence and species-specific mechanisms that govern tree recruitment are urgent tasks for this study area.

#### Practical proposals for forest conservation

The most practical finding of our study is that the foot slopes and upper side of plains were topographical locations where the three dipterocarp species coexisted with many other tree species (Group 2, Table 2). The number of species in Group 2 was higher than in Group 4, although this difference was not statistically significant (Table 2) and Group 4 has relatively moderate species richness (Rundel, 1999). This result implies that the foot slopes and surrounding areas are densely stocked with mother trees of deciduous forest tree species and are a high priority for protection. Thus, to appropriately conserve deciduous dipterocarp forests, the overall toposequence must be maintained. This should include hills (Group 1) and flood plains or plains (Group 4), where typical forms of deciduous dipterocarp forests appear, as well as their foot-slope transition zones (Group 2).

In an applied context, understory height, which is more easily visible than soil type and thickness, may be useful as an indicator for spatial classification in conservation planning. For example, when implementing a reforestation project in a deforested area, *S. siamensis* will be unlikely to grow in areas other than hills. In addition, locations to plant *S. siamensis* may be determined by understory height during the rainy season.

The general homogeneity of the deciduous dipterocarp forests in Southeast Asia is partly because they are adapted to edaphically or topographically dry sites (Stott, 1990). The toposequence of landforms found in our 4 ha study plot had an elevational difference of 10 m for a horizontal distance of 200 m (Fig. 2D). Similar topographic gradients of environmental and forest properties at the same scale has been reported in undulating lands in peninsular Thailand (Ohkubo & Takeuchi, 1998).

Our proposals for conservation can be applied to such toposequences of land forms, and the applicable area is expected to be considerably large.

#### Conclusions

We found clear spatial heterogeneity in vegetation at a scale of several hectares in Kratie Province, Cambodia. Strong associations of forest tree and forest floor vegetation with topographical properties were found along the toposequence. Various types of deciduous dipterocarp forests co-existed at this scale, although they were separated along the toposequence. We propose that along with the commonly limited forest types, the entire toposequence must be included in forest conservation efforts, because each type is established in an ecologically niche-differentiated manner along the toposequence. It is also crucial to determine the species-specific mechanisms governing tree distribution and such research will help to improve future forest conservation and reforestation projects.

#### Acknowledgements

This paper reports the results obtained by the global environment research coordination system funded by the Ministry of the Environment, Japan. Some field measurements were conducted as part of the following projects: 'Establishment of the integrated forest ecosystem observation site and network in the Lower Mekong (2008–2011)', 'Long-term monitoring of forest carbon dynamics in East Asia, the global research account for national institute', both funded by the Japanese Ministry of the Environment of Japan; 'Estimation and simulation of carbon stock change of tropical forests in Asia (2011–2014)' funded by the Japanese Ministry of Agriculture, Forestry and Fisheries, and the emergency project to develop the structure of promoting REDD action supported by the Japanese Forestry Agency. For permission to undertake the field research, the authors are deeply indebted to H.E. Dr. Ty Sokhun, secretary of state, H.E. Dr. Chheng Kimsun, Delegate of the royal government, head of the Forestry Administration in the Ministry of Agriculture, Forestry and Fisheries and Dr. Sokh Heng, director of the Institute of Forest and Wildlife Research and Development, Forestry Administration.

#### References

- Ashton, P.S. (2014) *On the Forests of Tropical Asia: Lest the Memory Fade*. Kew Publishing, UK.
- Beals, E.W. (1984) Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. *Advances in Ecolog-*

- ical Research, **14**, 1–55.
- Bunyavejchewin, S. (1983) Canopy structure of the dry dipterocarp forest of Thailand. *Thai Forest Bulletin (Botany)*, **14**, 1–132.
- Bunyavejchewin, S., Baker, P.J. & Davies, S.J. (2011) Seasonally dry tropical forests in continental Southeast Asia: structure, composition, and dynamics. In *The Ecology and Conservation of Seasonally Dry Forests in Asia* (eds W.J. McShea, S.J. Davies & N. Bhumpakphan), pp. 9–36. Smithsonian Institution Scholarly Press, Washington DC, USA.
- Davis, J.H. (1964) The forests of Burma. *Sarracenia*, **8**, 1–41.
- Forestry Administration [FA] (2018) Cambodia forest cover 2016. Phnom Penh, Cambodia: Forestry Administration, Cambodia.
- Ghazoul, J., Liston, K.A. & Boyle, T.J.B. (1998) Disturbance-induced density-dependent seed set in *Shorea siamensis* (Dipterocarpaceae), a tropical forest tree. *Journal of Ecology*, **86**, 462–473.
- Hiramatsu R., Kanzaki M., Toriyama J., Kaneko T., Okuda Y., Ohta S., Khorn S., Pith P., Lim S., Pol S., Ito E. & Araki M. (2007) Open woodland patch and the isolated stand of *Melaleuca cajuputi* in an evergreen forest of Kampong Thom, Cambodia: a transect study along a micro-topography gradient. In *Forest Environments in the Mekong River Basin* (eds Sawada H., Araki M., N.A. Chappell, J.V. LaFrankie & Shimizu A.), pp. 216–224. Springer, Tokyo, Japan.
- Hundley, H. (1961) The forest types of Burma. *Tropical Ecology*, **2**, 48–76.
- Iida S., Shimizu T., Tamai K., Kabeya N., Shimizu A., Ito E., Ohnuki Y., Chann S. & Keth N. (2016) Interrelationships among dry season leaf fall, leaf flush and transpiration: insights from sap flux measurements in a tropical dry deciduous forest. *Ecohydrology*, **9**, 472–486.
- Ito E., Chann S., Tith B., Keth S., Ly C., Op P., Furuya N., Ohnuki Y., Iida S. & Shimizu T. (2017a) Two phenological variants of *Terminalia alata* coexist in a dry dipterocarp forest. *Plant Species Biology*, **33**, 59–66.
- Ito E., Chann S., Tith B., Keth S., Ly C., Op P., Furuya N. & Monda Y. (2016) Reproductive size thresholds of dipterocarps in Cambodian dry forests. *Cambodian Journal of Natural History*, **2016**, 98–101.
- Ito E., Furuya N., Toriyama J., Ohnuki Y., Kiyono Y., Araki M., Sokh H., Chann S., Khorn S., Samreth V., So T., Tith B., Keth S., Ly C., Op P., Monda Y. & Kanzaki M. (2017b) Stand carbon dynamics in a dry Cambodian dipterocarp forest with seasonally flooded sandy soils. *Cambodian Journal of Natural History*, **2017**, 109–127.
- Kenkel, N.C. & Orlóci, L. (1986) Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. *Ecology*, **67**, 919–928.
- Legris, P. & Blasco, F. (1972) Carte Internationale Du Tapis Vegetal et des condition écologiques à 1/1.000.000, Notice de la carte Cambodge. Extrait des Travaux de la section Scientifique et Technique de l'institut Français de Pondichéry. Hors Série, No. 11-1972, 1–240.
- Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., Studer, M., Roudier, P., Gonzalez, J., Kozłowski, K., Schubert, E. & Murphy, K. (2019) *Finding Groups in Data: Cluster Analysis Extended Rousseeuw et al.* R package version 2.1.0. [Http://128.61.111.11/pub/CRAN/web/packages/cluster/cluster.pdf](http://128.61.111.11/pub/CRAN/web/packages/cluster/cluster.pdf) [accessed 19 October 2020].
- Marod, D., Kutintara, U., Tanaka H. & Nakashizuka T. (2004) Effects of drought and fire on seedling survival and growth under contrasting light conditions in a seasonal tropical forest. *Journal of Vegetation Science*, **15**, 691–700.
- McCarthy, G.J., Tolhurst, K.G. & Chatto, K. (1999) *Overall Fuel Hazard Guide*. Fire Management Research Report No.47. Department of Natural Resources and Environment, Melbourne, Australia.
- Ministry of Environment [MoE] (2018) *Cambodia Forest Cover 2016*. Phnom Penh, Cambodia. [https://redd.unfccc.int/uploads/54\\_3\\_cambodia\\_forest\\_cover\\_resource\\_\\_2016\\_english.pdf](https://redd.unfccc.int/uploads/54_3_cambodia_forest_cover_resource__2016_english.pdf) [accessed 1 November 2020].
- National Institute of Statistics (2012) *Statistical Yearbook of Cambodia 2011*. National Institute of Statistics, Ministry of Planning, Phnom Penh, Cambodia.
- Nguyen T.T. (2009) *Modelling growth and yield of dipterocarp forests in Central Highlands of Vietnam*. PhD thesis, Technische Universität München, Germany.
- Nguyen T.T. & Baker, P.J. (2016) Structure and composition of deciduous dipterocarp forest in Central Vietnam: patterns of species dominance and regeneration failure. *Plant Ecology & Diversity*, **9**, 589–601.
- Nguyen T.T., Murphy, B.P. & Baker, P.J. (2019) The existence of a fire-mediated tree-recruitment bottleneck in an Asian savanna. *Journal of Biogeography*, **46**, 745–756.
- Ogawa H., Yoda K. & Kira T. (1961) A preliminary survey on the vegetation of Thailand. *Nature and Life in Southeast Asia*, **1**, 21–157.
- Ohkubo S. & Takeuchi K. (1998) Evaluating potential land productivity in relation with catenary sequence of landform and soils in coastal area, peninsular Thailand. *Journal of the Japanese Institute of Landscape Architecture (Japan)*, **61**, 519–522 [in Japanese with English abstract].
- Ohnuki Y., Ito E., Toriyama J., Araki M. & Shimizu A. (2014) Site environments of deciduous forests at east bank of Mekong River, Cambodia. *Water Science*, **57**, 14–25 [in Japanese].
- Ohnuki Y., Keth S., Toriyama J., Chann S., Ito E., Tith B. & Araki M. (2012) Comparative study of soil thickness and soil physical properties on evergreen and deciduous forests in Cambodia. In *Proceedings of International Workshop on Forest Research in Cambodia, November 2011*, pp. 35–38. Phnom Penh, Cambodia.
- Ohnuki Y., Kimhean C., Shinomiya Y. & Toriyama J. (2008) Distribution and characteristics of soil thickness and effects upon water storage in forested areas of Cambodia. *Hydrological Processes*, **22**, 1272–1280.
- Ohnuki Y., Toriyama J., Ito E., Iida S., Kabeya N., Chann S. & Keth S. (2022) Fluctuation of soil water content in the tropical seasonal forests of Cambodia focusing on soil types and prop-

- erties. *Japan Agricultural Research Quarterly*, **56**, 177–187.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. & Wagner, H. (2019) *Vegan: Community Ecology Package*. R package version 2.5-6. <https://cran.r-project.org> [accessed 1 October 2020].
- Pin C., Phan C., Prum S. & Gray, T.N.E. (2013) Structure and composition of deciduous dipterocarp forest in the Eastern Plains Landscape, Cambodia. *Cambodian Journal of Natural History*, **2013**, 27–34.
- R Core Team (2020) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org/index.html> [accessed 15 October 2020].
- Robbins, R.G. & Smitinand, T. (1966) A botanical ascent of Doi Inthanon. *Natural History Bulletin of the Siam Society*, **21**, 205–227.
- Rollet, B. (1972) La végétation du Cambodge: deuxième partie. *Bois et Forêts des Tropiques*, **145**, 23–38 [in French].
- Rundel, P.W. (1999) *Forest Habitats and Flora in Lao PDR, Cambodia, and Vietnam*. WWF Indochina Programme, Hanoi, Vietnam.
- Rundel, P.W. & Boonpragob, K. (1995) Dry forest ecosystems of Thailand. In *Seasonally Dry Tropical Forests* (eds S. Bullock, H. Mooney & E. Medina), pp. 93–123. Cambridge University Press, Cambridge.
- Sahunalu, P. (2009) Stand structure and species composition in the long-term dynamic plots of Sakaerat deciduous dipterocarp forest, northeastern Thailand. *Journal of Forest Management*, **3**, 1–20.
- Sakurai K., Tanaka S., Ishiduka S. & Kanzaki, M. (1998) Differences in soil properties of dry evergreen and dry deciduous forests in the Sakaerat environmental research station. *Tropics*, **8**, 61–80.
- Santisuk, T. (1988) *An Account of the Vegetation of Northern Thailand (Geoecological Research)*. Franz Steiner Verlag Wiesbaden, Stuttgart, Germany.
- Stamp, L.D. (1924) *The Vegetation of Burma from an Ecological Standpoint*. Thacker Spink & Co., Calcutta, India.
- Stott, P. (1986) The spatial pattern of dry season fires in the savanna forests of Thailand. *Journal of Biogeography*, **13**, 345–358.
- Stott, P. (1990) Stability and stress in the savanna forests of mainland South-East Asia. *Journal of Biogeography*, **17**, 373–383.
- Tani A., Ito E., Kanzaki M., Ohta S., Khorn S., Pith P., Tith B., Pol S. & Lim S. (2007) Principal forest types of three regions of Cambodia: Kampong Thom, Kratie, and Mondolkiri. In *Forest Environments in the Mekong River Basin* (eds Sawada H., Araki M., N.A. Chappell, J.V. LaFrankie & Shimizu A.), pp. 201–213. Springer, Tokyo, Japan.
- Teejuntuk, S., Sahunalu, P., Sakurai K. & Sungpalee, W. (2002) Forest structure and tree species diversity along an altitudinal gradient in Doi Inthanon National Park, Northern Thailand. *Tropics*, **12**, 85–102.
- Toda T., Takeda H., Tokuchi N., Ohta S., Wacharinrat, C. & Kaitpraneet, S. (2007) Effects of forest fire on the nitrogen cycle in a dry dipterocarp forest, Thailand. *Tropics*, **16**, 41–45.
- Toriyama J., Ohta S., Ohnuki Y., Araki M., Kanzaki M., Det S., Lim S., Pol S. & Pith P. (2010) Physicochemical characteristics of plinthic and non-plinthic soils in dry deciduous forests on the east bank of Mekong, Cambodia. *Pedologist*, **54**, 2–10.
- Wood, T. (2012) Fire ecology of the dry dipterocarp forests of South West Cambodia. *Cambodian Journal of Natural History*, **2012**, 64–74.



### Annex 1 List of tree species occurring in the study plot

Khmer name: \* provided by local informants. Status: D = dominant dipterocarps, A = associating non-dipterocarps, M = minor spp., E = evergreen spp.

| Family / Species   | Khmer Name *             | Status | Tree density          |       | Basal area                      |       | Max. DBH (cm) |     |     |     |    |
|--|--------------------------|--------|-----------------------|-------|---------------------------------|-------|---------------|-----|-----|-----|----|
|  |                          |        | stem ha <sup>-1</sup> | %     | m <sup>2</sup> ha <sup>-1</sup> | %     | 1             | 2   | 3   | 4   |    |
| <b>Anacardiaceae</b>   |                          |        |                       |       |                                 |       |               |     |     |     |    |
| <i>Buchanania lanzan</i> Spreng                                | KAPRAONG                 | A      | 14.00                 | 2.52  | 0.211                           | 1.53  | 31.4          | 16  | 15  | 7   | 18 |
| <i>Buchanania reticulata</i> Hance                             | LEANG CHEY (sp. 1)       | M      | 1.00                  | 0.18  | 0.012                           | 0.09  | 16.7          | 3   | 1   |     |    |
| <i>Buchanania siamensis</i> Miq.                               | LEANG CHEY (sp. 2)       | M      | 1.75                  | 0.32  | 0.049                           | 0.36  | 26.8          | 5   | 2   |     |    |
| <i>Lannea coromandelica</i> (Houtt.) Merr.                     | -                        | M      | 0.50                  | 0.09  | 0.007                           | 0.05  | 17.0          |     |     |     |    |
| <b>Bignoniaceae</b>  |                          |        |                       |       |                                 |       |               |     |     |     |    |
| <i>Heterophragma sulfureum</i> Kurz                            | TA KUT TAMAT             | A      | 6.25                  | 1.13  | 0.075                           | 0.55  | 35.3          | 8   | 14  | 1   | 2  |
| <i>Stereospermum cylindricum</i> Pierre ex Dop                 | SANGKUOT THMAT           | M      | 0.25                  | 0.05  | 0.001                           | 0.00  | 5.7           |     |     | 1   |    |
| <b>Burseraceae</b>   |                          |        |                       |       |                                 |       |               |     |     |     |    |
| <i>Canarium subulatum</i> Guill.                               | TALAT / * Pon Svar       | M      | 0.25                  | 0.05  | 0.002                           | 0.02  | 10.3          |     |     |     | 1  |
| <b>Celastraceae</b>  |                          |        |                       |       |                                 |       |               |     |     |     |    |
| <i>Lophopetalum wallichii</i> Kurz                             | * Ta Ley                 | M      | 3.75                  | 0.68  | 0.096                           | 0.7   | 34.0          | 1   | 11  | 2   | 1  |
| <b>Combretaceae</b>  |                          |        |                       |       |                                 |       |               |     |     |     |    |
| <i>Terminalia alata</i> Heyne ex Roth [Glabrous type]          | CHHLIK                   | A      | 76.00                 | 13.68 | 1.82                            | 13.22 | 38.5          | 153 | 127 | 12  | 12 |
| <i>Terminalia alata</i> Heyne ex Roth [Hairy type]             | CHHLIK                   | A      | 15.50                 | 2.79  | 0.741                           | 5.38  | 52.4          | 3   | 13  | 46  |    |
| <i>Terminalia chebula</i> Retz var. <i>chebula</i> Retz        | SRORMOR                  | A      | 7.00                  | 1.26  | 0.277                           | 2.01  | 39.9          | 5   | 4   | 5   | 14 |
| <i>Terminalia mucronata</i> Craib & Hutch.                     | PRAM DOMLENG             | M      | 4.00                  | 0.72  | 0.221                           | 1.60  | 49.4          | 1   | 2   | 3   | 10 |
| <b>Dilleniaceae</b>  |                          |        |                       |       |                                 |       |               |     |     |     |    |
| <i>Dillenia ovata</i> Wall. ex Hook. f. & Thomson              | LOWEY                    | M      | 1.75                  | 0.32  | 0.012                           | 0.08  | 14.0          | 2   | 1   | 4   |    |
| <b>Dipterocarpaceae</b>  |                          |        |                       |       |                                 |       |               |     |     |     |    |
| <i>Dipterocarpus tuberculatus</i> Roxb.                        | KHLONG                   | D      | 106.25                | 19.13 | 4.235                           | 30.77 | 52.8          | 81  | 139 | 121 | 84 |
| <i>Shorea obtusa</i> Wall. ex Blume                            | PHCHEK                   | D      | 47.25                 | 8.51  | 2.413                           | 17.53 | 56.0          | 21  | 105 | 12  | 51 |
| <i>Shorea siamensis</i> Miq.                                   | RAING PHNOM              | D      | 223.25                | 40.19 | 2.716                           | 19.73 | 46.7          | 713 | 173 | 4   | 3  |
| <b>Ebenaceae</b>   |                          |        |                       |       |                                 |       |               |     |     |     |    |
| <i>Diospyros ehretoides</i> Wall. ex G. Don                    | CHHOEU ROMEANG / LOMEANG | M      | 2.00                  | 0.36  | 0.025                           | 0.18  | 23.0          | 2   |     |     | 6  |
| <i>Diospyros pilosanthera</i> Blanco var. <i>hefferi</i> Bakh. | TROR YING                | M (E)  | 0.25                  | 0.05  | 0.008                           | 0.06  | 20.1          |     |     |     | 1  |
| <b>Euphorbiaceae</b>   |                          |        |                       |       |                                 |       |               |     |     |     |    |
| <i>Aporosa octandra</i> (Buch.-Ham. ex D. Don) Vickery         | KRONG (sp. 1)            | M      | 0.25                  | 0.05  | 0.001                           | 0.01  | 7.7           | 1   |     |     |    |
| <i>Aporosa villosa</i> (Lindl.) Bail.                          | KRONG (sp. 2)            | M      | 0.75                  | 0.14  | 0.009                           | 0.07  | 19.0          |     |     | 3   |    |
| <i>Bridelia retusa</i> (L.) A.Juss.                            | CHHLIK PORK              | M      | 0.25                  | 0.05  | 0.001                           | 0.01  | 6.4           | 1   |     |     |    |
| <b>Guttiferae</b>  |                          |        |                       |       |                                 |       |               |     |     |     |    |
| <i>Garcinia cowa</i> Roxb.                                     | -                        | M      | 0.75                  | 0.14  | 0.003                           | 0.03  | 8.7           | 1   |     |     | 2  |

## Annex 1 Cont'd

| Family / Species  | Khmer Name *              | Status | Tree density          |      | Basal area                      |      | Max. DBH (cm) | No of trees in each group |    |   |   |  |  |   |
|---|---------------------------|--------|-----------------------|------|---------------------------------|------|---------------|---------------------------|----|---|---|--|--|---|
|   |                           |        | stem ha <sup>-1</sup> | %    | m <sup>2</sup> ha <sup>-1</sup> | %    |               | 1                         | 2  | 3 | 4 |  |  |   |
| <b>Lecythidaceae</b>                                    |                           |        |                       |      |                                 |      |               |                           |    |   |   |  |  |   |
| <i>Careya arborea</i> Roxb. / <i>C. sphaerica</i> Roxb. | KANN DOL                  | M      | 0.75                  | 0.14 | 0.01                            | 0.07 | 17.8          | 2                         | 1  |   |   |  |  |   |
| <b>Leguminosae</b>                                      |                           |        |                       |      |                                 |      |               |                           |    |   |   |  |  |   |
| <i>Acacia harmandiana</i> (Pierre) Gagnep.              | THMEAS TUK                | M      | 0.25                  | 0.05 | 0.011                           | 0.08 | 23.5          | 1                         |    |   |   |  |  |   |
| <i>Dalbergia cochinchinensis</i> Pierre                 | KRORNHOUNG                | M      | 0.25                  | 0.05 | 0.002                           | 0.02 | 10.9          | 1                         |    |   |   |  |  |   |
| <i>Dalbergia cultrata</i> Grah. ex Benth.               | * Ta Meaek                | M      | 2.00                  | 0.36 | 0.036                           | 0.26 | 21.5          | 3                         | 4  | 1 |   |  |  |   |
| <i>Dalbergia nigrescens</i> Kurz var. <i>nigrescens</i> | SNUOL                     | M      | 1.75                  | 0.32 | 0.156                           | 1.13 | 67.1          | 7                         |    |   |   |  |  |   |
| <i>Dalbergia oliveri</i> Gamb. ex Prain                 | NEANG NOUN                | M      | 0.25                  | 0.05 | 0.005                           | 0.04 | 15.9          |                           |    | 1 |   |  |  |   |
| <i>Pterocarpus macrocarpus</i> Kurz                     | THNONG KRAHAM             | M      | 0.75                  | 0.14 | 0.017                           | 0.12 | 28.6          | 1                         |    |   |   |  |  | 2 |
| <i>Spatholobus parviflorus</i> Kuntze                   | CHHAR / DORK CAV          | M      | 0.75                  | 0.14 | 0.005                           | 0.03 | 9.5           | 2                         | 1  |   |   |  |  |   |
| <i>Xylocarpus xylocarpa</i> (Roxb.) W. Theob.           | SOKROM                    | A      | 11.00                 | 1.98 | 0.126                           | 0.91 | 29.3          | 3                         | 34 | 1 | 6 |  |  |   |
| <b>Loganiaceae</b>                                      |                           |        |                       |      |                                 |      |               |                           |    |   |   |  |  |   |
| <i>Strychnos nux-blanda</i> Hill                        | PRAVEK                    | M      | 2.25                  | 0.41 | 0.015                           | 0.11 | 15.4          | 1                         | 4  | 1 | 3 |  |  |   |
| <b>Meliaceae</b>  |                           |        |                       |      |                                 |      |               |                           |    |   |   |  |  |   |
| <i>Azadirachta indica</i> A.Juss.                       | SDAO                      | M      | 0.25                  | 0.05 | 0.001                           | 0.00 | 5.7           |                           | 1  |   |   |  |  |   |
| <b>Myrtaceae</b>  |                           |        |                       |      |                                 |      |               |                           |    |   |   |  |  |   |
| <i>Syzygium cumini</i> (L.) Skeels                      | PRING BAI                 | M(E)   | 4.25                  | 0.77 | 0.219                           | 1.59 | 45.3          | 3                         | 7  | 7 |   |  |  |   |
| <b>Opiliaceae</b>                                       |                           |        |                       |      |                                 |      |               |                           |    |   |   |  |  |   |
| <i>Melentha suavis</i> Pierre                           | * Pricch                  | M      | 0.50                  | 0.09 | 0.003                           | 0.02 | 9.5           | 2                         |    |   |   |  |  |   |
| <b>Phyllanthaceae</b>                                   |                           |        |                       |      |                                 |      |               |                           |    |   |   |  |  |   |
| <i>Phyllanthus emblica</i> L.                           | KANTOUT PREY              | M      | 0.75                  | 0.14 | 0.018                           | 0.13 | 28.9          | 2                         | 1  |   |   |  |  |   |
| <b>Rubiaceae</b>  |                           |        |                       |      |                                 |      |               |                           |    |   |   |  |  |   |
| <i>Catunaregam longispina</i> (Roxb.) Tirveng           | LVIENG SOR                | M      | 3.00                  | 0.54 | 0.015                           | 0.11 | 11.9          | 5                         | 6  | 1 |   |  |  |   |
| <i>Catunaregam tomentosa</i> (Bl. ex DC.) Tirv.         | LVIENG KROHOM             | M      | 0.25                  | 0.05 | 0.003                           | 0.02 | 12.3          |                           |    | 1 |   |  |  |   |
| <i>Gardenia obtusifolia</i> Roxb.                       | BAKDORNG                  | M      | 4.50                  | 0.81 | 0.014                           | 0.10 | 8.8           | 14                        | 2  | 1 | 1 |  |  |   |
| <i>Mitragyna rotundifolia</i> (Roxb.) O.K.              | KHTOM / KHTOM PHNOM       | A      | 5.75                  | 1.04 | 0.107                           | 0.78 | 23.5          | 2                         | 13 | 2 | 6 |  |  |   |
| <i>Morinda coreia</i> Ham.                              | NHOR                      | M      | 1.00                  | 0.18 | 0.021                           | 0.15 | 29.6          | 2                         |    |   |   |  |  | 2 |
| <i>Neonauclea sessilifolia</i> Merr.                    | ROLEAY                    | M      | 0.25                  | 0.05 | 0.03                            | 0.21 | 38.8          |                           |    |   |   |  |  | 1 |
| <i>Pavetta tomentosa</i> Roxb. ex Sm.                   | PREAH CHHNET / PUK CHHMAR | M      | 0.25                  | 0.05 | 0.001                           | 0.00 | 5.4           | 1                         |    |   |   |  |  |   |
| <b>Sapotaceae</b>                                       |                           |        |                       |      |                                 |      |               |                           |    |   |   |  |  |   |
| <i>Madhuca stipulacea</i> Fletcher                      | SRAKUM                    | M(E)   | 1.00                  | 0.18 | 0.007                           | 0.05 | 13.8          | 2                         | 1  | 1 |   |  |  |   |
| <b>Tiliaceae</b>  |                           |        |                       |      |                                 |      |               |                           |    |   |   |  |  |   |
| <i>Grewia eriocarpa</i> Juss.                           | PO PLEAR                  | M      | 0.25                  | 0.05 | 0.001                           | 0.01 | 8.2           | 1                         |    |   |   |  |  |   |

**Annex 1 Cont'd**

| Family / Species        | Khmer Name * | Tree density |                       | Basal area |                                 | No of trees in each group |      |      |     |     |
|-------------------------|--------------|--------------|-----------------------|------------|---------------------------------|---------------------------|------|------|-----|-----|
|                         |              | Status       | stem ha <sup>-1</sup> | %          | m <sup>2</sup> ha <sup>-1</sup> | %                         | 1    | 2    | 3   | 4   |
| Verbenaceae             |              |              |                       |            |                                 |                           |      |      |     |     |
| <i>Vitex pinnata</i> L. | POPOUL       | M            | 0.50                  | 0.09       | 0.009                           | 0.07                      | 16.0 | 1    | 1   | 1   |
|                         | <b>Total</b> |              | 555.50                | 100        | 13.76                           | 100                       | 67.1 | 1041 | 689 | 203 |
|                         |              |              |                       |            |                                 |                           |      | 289  |     |     |

**Annex 2 Aboveground understorey biomass in the study plot**

| Location |     | Aboveground understorey biomass (Mg/ha) |                             |                 |            |                         |          |                      |                         |                      |   |
|----------|-----|---|-----------------------------|-----------------|------------|-------------------------|----------|----------------------|-------------------------|----------------------|---|
| x        | y   | Total                                   | <i>Vietnamosasa pusilla</i> | Other Gramineae | Cyperaceae | <i>Dillenia hookeri</i> | Fabaceae | <i>Shorea obtusa</i> | <i>Shorea siamensis</i> | Other shrubs & herbs | Remarks (emerging species)                        |
| 200      | 200 | 4.75                                    | 4.42                        |                 |            |                         | 0.27     |                      |                         | 0.06                 | Asteraceae  |
| 150      | 200 | 4.47                                    | 1.41                        | 2.43            |            |                         |          |                      |                         | 0.64                 | Liliaceae   |
| 100      | 200 | 1.60                                    | 0.07                        | 1.42            |            |                         |          |                      |                         | 0.11                 | Herb  |
| 50       | 200 | 3.09                                    |                             | 1.60            |            |                         |          | 1.49                 |                         |                      |   |
| 0        | 200 | 1.14                                    | 1.09                        |                 | 0.02       |                         | 0.02     |                      |                         | 0.02                 |   |
| 0        | 150 | 2.32                                    | 1.99                        |                 | 0.09       |                         |          |                      |                         | 0.24                 | <i>Heterophragma sulfureum</i> Kurz, <i>Vitex</i> |
| 50       | 150 | 5.04                                    |                             |                 | 0.28       | 4.77                    |          |                      |                         |                      |   |
| 100      | 150 | 2.13                                    | 0.89                        | 1.18            |            |                         |          |                      |                         | 0.06                 |   |
| 150      | 150 | 3.48                                    | 2.98                        | 0.16            |            |                         | 0.27     |                      |                         | 0.07                 | Schizaceae  |
| 200      | 150 | 4.64                                    | 4.62                        | 0.02            |            |                         |          |                      |                         | 0.00                 | Dioscoreaceae                                     |
| 200      | 100 | 2.95                                    |                             | 0.56            |            |                         |          |                      | 2.39                    |                      |   |
| 150      | 100 | 4.07                                    | 4.07                        |                 |            |                         |          |                      |                         |                      |   |
| 50       | 100 | 4.36                                    | 3.84                        | 0.18            |            |                         | 0.35     |                      |                         | 0.02                 | Liliaceae   |
| 0        | 100 | 6.98                                    | 6.95                        | 0.01            |            |                         | 0.00     |                      |                         | 0.04                 | <i>Vitex</i> sp.                                  |
| 0        | 50  | 7.17                                    | 7.10                        |                 |            |                         | 0.00     |                      |                         |                      |   |
| 50       | 50  | 4.28                                    | 4.23                        | 0.05            |            |                         |          |                      |                         |                      |   |
| 100      | 50  | 6.20                                    | 6.20                        |                 |            |                         |          |                      | 3.68                    |                      |   |
| 150      | 50  | 3.68                                    |                             |                 |            |                         |          |                      |                         |                      |   |
| 200      | 50  | 1.53                                    | 0.33                        | 1.06            |            |                         | 0.02     |                      |                         | 0.11                 |   |
| 200      | 0   | 4.23                                    |                             | 4.14            |            |                         | 0.01     |                      |                         | 0.08                 | Asteraceae  |
| 150      | 0   | 1.23                                    |                             | 1.22            |            |                         |          |                      |                         | 0.01                 |   |

**Annex 2 Cont'd**

| Location |   | Aboveground understorey biomass (Mg/ha) |                             |                 |            |                         |          |                      |                         |                      |                            |
|----------|---|---|-----------------------------|-----------------|------------|-------------------------|----------|----------------------|-------------------------|----------------------|----------------------------|
| x        | y | Total                                   | <i>Vietnamosasa pusilla</i> | Other Gramineae | Cyperaceae | <i>Dillenia hookeri</i> | Fabaceae | <i>Shorea obtusa</i> | <i>Shorea siamensis</i> | Other shrubs & herbs | Remarks (emerging species) |
| 100      | 0 | 2.10                                    |                             | 2.08            |            |                         |          |                      |                         | 0.02                 |                            |
| 50       | 0 | 2.12                                    |                             | 2.10            |            |                         |          |                      |                         | 0.01                 |                            |
| 0        | 0 | 2.62                                    |                             | 2.19            |            | 0.14                    |          |                      |                         | 0.29                 | Malvaceae                  |