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COMPOSITION, STRUCTURE AND SPATIAL PATTERNS OF THE TREE COMMUNITY IN A FIRE-INFLUENCED, DECIDUOUS DIPTEROCARP-OAK FOREST, WESTERN THAILAND

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ABSTRACT

We present a quantitative description of the composition and structure of the tree community in a fire-influenced seasonal dipterocarp-oak forest with grassland in a 4-ha (200 × 200 m) plot in Thung Yai Naresuan Wildlife Sanctuary, Thailand. A total of 86 woody species with stems ≥5 cm dbh were encountered. The plot was subdivided into closed-canopy forest and grassland sections based on the tree distributions, canopy openness estimates, and cover of graminoids. The tree canopy was strongly dominated by *Shorea siamensis* var. *siamensis*, and *Quercus kerrii* var. *kerrii*, and the subcanopy strata dominated by *Cycas pectinata* and *Aporosa villosa.* Tree basal area was greatest in the closed-canopy section, and stem densities were highest along the edge separating the two sections. Stem densities of trees 5–10 cm dbh were higher in grassland than closed-canopy forest, and for a few species, trees 5–10 cm dbh occurred exclusively in open-canopy conditions, possibly indicating fire tolerance. The height of graminoids, which serve as fuel for ground fires, was correlated with canopy openness. The dominance of only a single dipterocarp species represents a distinctive variant of deciduous dipterocarp forest, and the persistence of a significant population of *Cycas pectinata* illustrates the critical role this habitat type plays in threatened species conservation. The interface between closed-canopy forest and grassland at this site appears dynamic, with fire playing an important role in structuring the habitat.

Keywords**:** Biodiversity, tropical dry forest, *Quercus,* savanna, *Shorea,* Southeast Asia

INTRODUCTION

Tropical dry forests, which are characterized by pronounced seasonality in rainfall, are ecologically important and highly threatened ecosystems (Lerdau *et al.*, 1991; Miles *et al.*, 2006). Because of their open structure, ease of clearing and susceptibility to fire, suitability for livestock, and relatively fertile soils compared with rain forest ecosystems, tropical dry forests have been extensively cleared for cultivation and now occupy only a fraction of their original extent (Murphy & Lugo, 1986; Miles *et al.*, 2006), with the majority of remaining forest under threat of conversion to agriculture (Wikramanayake *et al.*, 2002).

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Tropical dry forests in SE Asia consist of distinctive plant communities that vary in structure and floristics (Rundel, 1999). One such community is dominated by Dipterocarpaceae (*Shorea* and *Dipterocarpus*) and Fagaceae (*Quercus*) (Rundel, 1999), and is labeled Dipterocarp-oak Forest (DoF, Maxwell, 2004) or Deciduous Dipterocarp Forest (DDF, Santisuk, 1988). In SE Asia, dipterocarp-oak forest often occurs in a mosaic with open grasslands, where tree density is low and the ground flora is dominated by graminoids, forming "savanna forest" (Stott, 1990). Research on the basic ecology of SE Asian deciduous dipterocarp-oak forest is sparse, particularly with respect to the dynamics of the grassland-forest boundary (Stott, 1990). Filling that gap requires baseline descriptions of the forest mosaic, including both closed-canopy forest and grassland components. With this in mind, we present results from a permanent vegetation plot focused specifically on this little-studied mosaic. We provide the first quantitative description of the composition, structure and spatial patterns of tree diversity in a fire-influenced, seasonal deciduous dipterocarp-oak forest with grassland in western Thailand. We describe the differences between the tree-dominated closed-canopy forest and grassland, and make inferences about how fire could be shaping the structure and spatial pattern of the tree community. Our study lays the groundwork for further research that seeks to understand the drivers and dynamics of this ecosystem.

Our study was in Thung Yai Naresuan Wildlife Sanctuary (15°00'–15°23'N, 98°30'–99°05'E, hereafter Thung Yai), a 3,622-km^2 protected area located in the 18,000-km^2 Western Forest Complex in western Thailand (Fig. 1), and which comprises part of the Thung Yai – Huay Kha Khaeng World Heritage Site (IUCN, 1991). Thung Yai harbors unique vegetation types across an elevation range from 250 to 1800 m asl (UNEP, 2007; Webb *et al.*, 2011). The Sanctuary name *Thung Yai* means *large grassland* in the Thai language (*thung* = grassland, *yai* = large), and refers to a 140-km^2 swath of *thung* (pronounced "toong") in the central region of the sanctuary. The *thung* is a mosaic of tree-dominated, seasonal deciduous dipterocarp-oak forest, and grassland habitat with scattered small trees and a ground flora dominated by deciduous graminoids (Fig. 2). The *thung* is subjected to fires of anthropogenic origin, is one of the highest-quality habitats for large mammals in the sanctuary, and harbors large populations of ungulates, especially gaur (*Bos gaurus*) and sambar (*Cervus unicolor*), and their top predator, tiger (*Panthera tigris*) (Steinmetz *et al.*, 2006, 2008).

METHODS

We established a 4-hectare permanent forest monitoring plot in the central *thung* of Thung Yai, located at 780 m elevation approximately 5 km from the Sesawo Ranger Station (Fig. 1). The topography of the site is flat. We demarcated a 200 m × 200 m plot, subdivided into 20-m × 20-m subplots, with a Suunto® KB-14 sighting compass (accuracy 0.17 degree) and a Leica DISTO® laser distance meter (accuracy ±3 mm). The subplots were demarcated with metal stakes.

We oriented the plot so that it contained similar proportions of both closed-canopy dipterocarp-oak forest and open-canopy grassland (Fig. 1). Past fire occurrence was apparent throughout the plot, with scorch height and bark damage indicating higher intensity in the grassland than in the closed-canopy forest. There is no known history of cultivation, logging, or domestic livestock in or around the plot (Nakhasathien & Stewart-Cox, 1990).

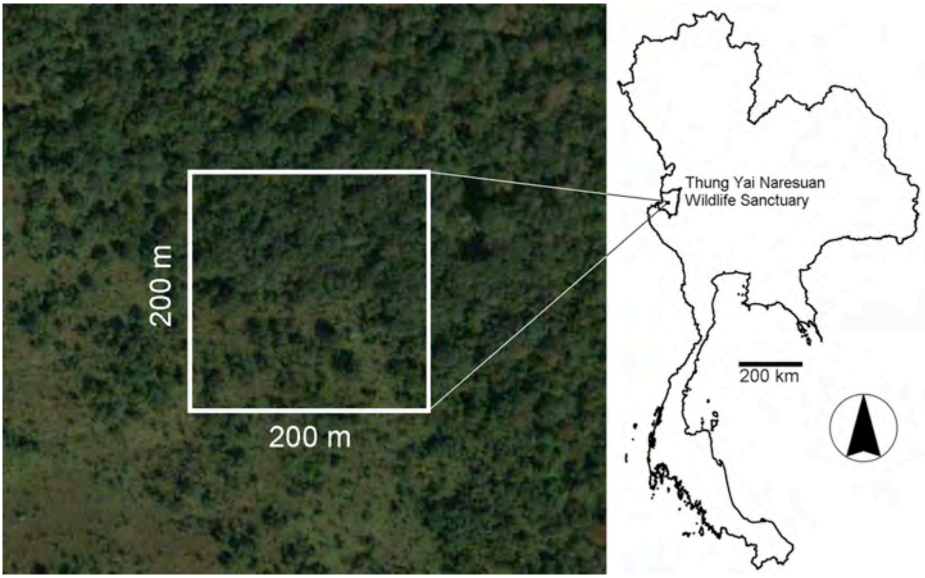

Figure 1. Map of Thailand showing Thung Yai Naresuan Wildlife Sanctuary and the location of the 4-ha plot, set across the interface between grassland (the SW portion of the plot) and closed-canopy forest (the NE portion of the plot). The GPS coordinates of the center of the plot are 15°20'11.1"N, 98°45'21.7"E, using a WGS-84 projection.

Mean (± SD) annual maximum and minimum temperatures were 33.6 ± 0.2 °C, and 20.5 ± 0.7 °C, respectively. Mean annual rainfall in Thung Yai during 1997–2005 was 1731 ± 217 mm (Thai Department of Meteorology, 2005), and concentrated between May and October, with typically <100 mm of rain per month in the dry season of November to April.

Tree surveys

Four surveys were conducted—April 2004, April 2005, December 2005 and April 2006—to census and measure every woody stem with a diameter (dbh) ≥5 cm at 1.4 m above the base. Stems were tagged 20 cm above the point of measurement and given Cartesian coordinates to the nearest 0.1 m. The height of each stem was estimated using a clinometer. All stems of multi-stemmed individuals were measured and tagged, but our maps show locations of individuals only. To calculate stem density we tallied only individuals (treating multiple-stemmed trees as singlets); however, we summed up all stems to calculate basal area. Stems of the cycad *Cycas pectinata* Buch.-Ham. and the palm *Phoenix loureiroi* Kunth var. *loureiroi* were included if all living leaves were above 1.4 m height. We also measured and tagged woody climbers ≥5 cm dbh. We counted and mapped clumps of the bamboo *Dendrocalamus strictus* (Roxb.) Nees.

Fertile herbarium specimens and vouchers were deposited at the Forest Herbarium Bangkok (BKF), Chiang Mai University Herbarium (CMU), Nationaal Herbarium Nederland (L) and Harvard University Herbaria (A).

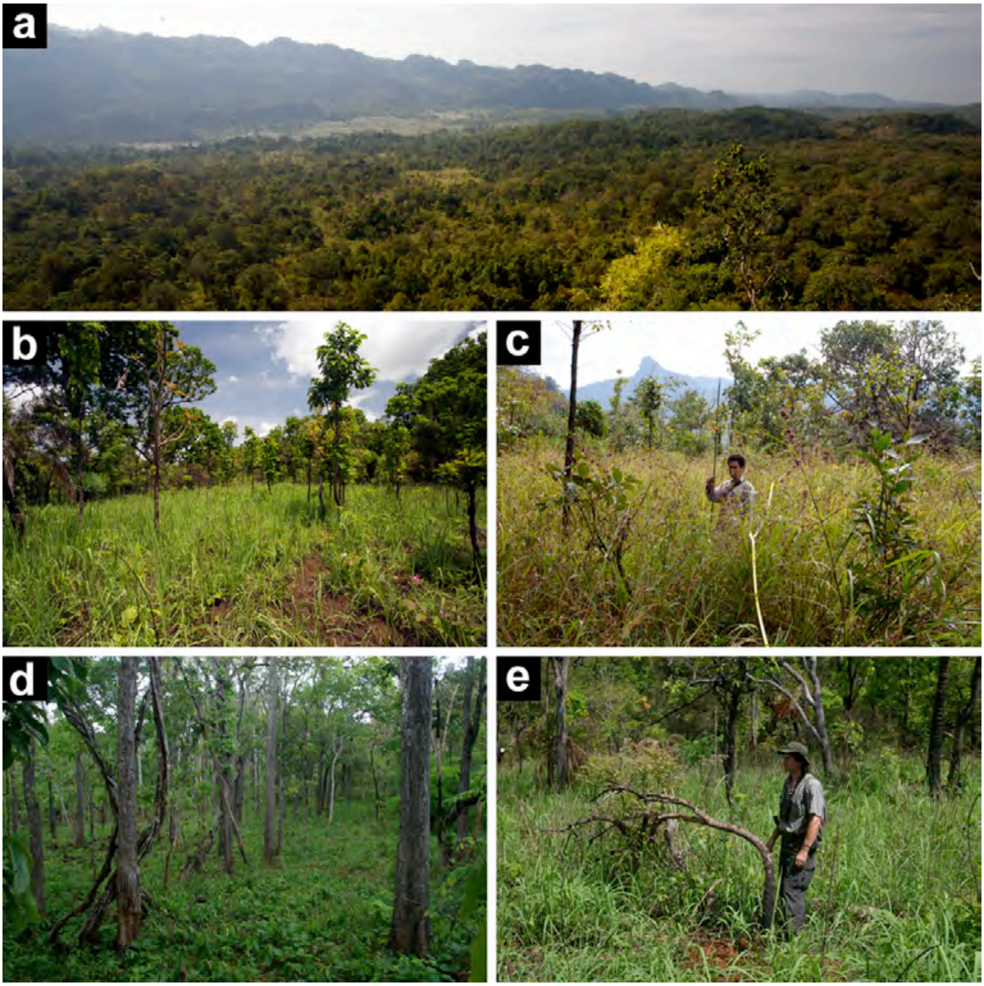

Figure 2. Deciduous dipterocarp-oak forest and grassland habitats in Thung Yai Naresuan Wildlife Sanctuary, western Thailand. (a) Oblique aerial view of the *thung* showing the vicinity of where plot was located, straddling the grassland closed-canopy forest approximately in the center of the photograph (dry season, December 2005). (b) Grassland habitat in the late dry season when graminoid height was low. Note the closed-canopy forest edge in the background (April 2006). (c) Grassland habitat in the middle of the dry season when graminoid height was high (December 2005). (d) Closed-canopy forest habitat (April 2005). (d) R. Steinmetz standing next to a *Stereospermum neurantham* specimen with a bent stem apparently resulting from repetitive browsing by gaur. *S. neurantham* was the only species exhibiting this peculiar form (April 2005).

Canopy openness and fuel load

Forest fire intensity depends on fuel load, which in mixed forest – graminoid systems should be related to tree canopy cover. To assess this relationship, we first took a canopy photograph in the center of each 20 × 20 m subplot ($n = 100$). Photographs were taken with a Canon 5D digital camera body with a 17-mm wide angle lens, which provided a 104° angle of view across the diagonal of the image. The camera was leveled with a circular bubble, with the bottom of the camera pointing north. Picture settings were for black and white, 400 ISO, maximum contrast, and red-filter effect. Canopy photographs were taken during a period of high cloud cover to maximize contrast between vegetation and sky. Images were 4368 × 2912 pixels (12.7 megapixels). Digital photographs of this type are useful in comparing the openness of the canopy across survey points (e.g. ranking) (ENGELBRECHT & HERZ, 2001).

From each photo point we then measured 2 m in each of the four cardinal directions, and measured the height of the tallest graminoid (to the nearest 5 cm, including inflorescence or infructescence stalk) within 20 cm of that point. This provided four graminoid height measurements, which were then averaged to relate with the photo-derived canopy openness value for that point (see below). Graminoid species were not recorded because we were most interested in the relative fuel load across space, and graminoid height served as a proxy for fuel load.

Raw canopy photographs were converted into bitmap images using Adobe Photoshop™ (Fig. 3). A properly exposed photograph had high contrast between vegetation and sky, and could be converted into a bitmap through automated functions of the software using a 50%

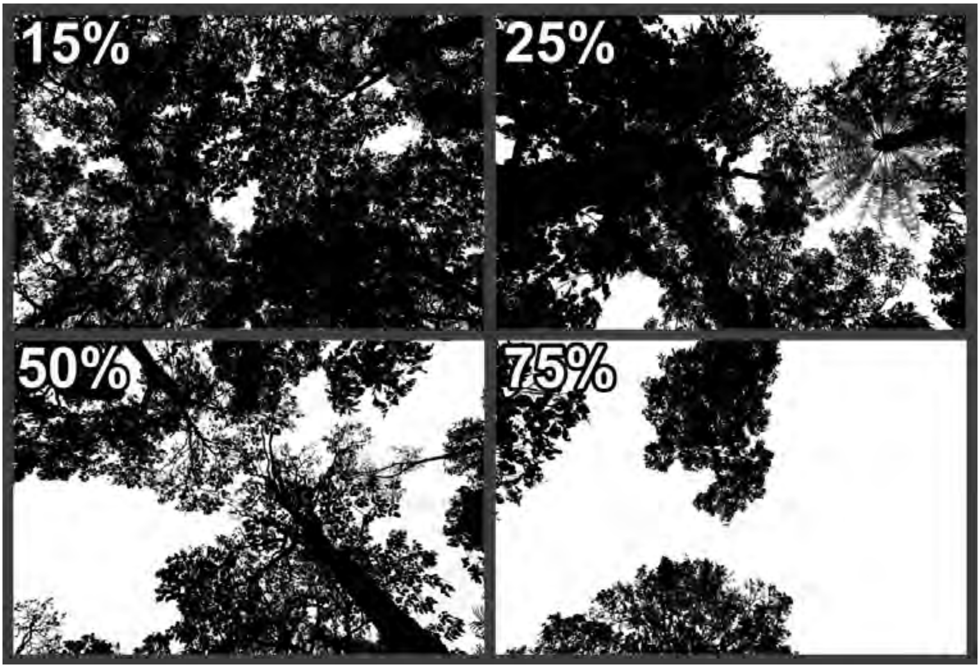

Figure 3. Examples of canopy photographs used to calculated canopy openness. Lens focal length was 17 mm. Calculated canopy openness values are given in each panel.

pixel value threshold (i.e. any pixel with a brightness value of ≤127 was given a value of 0 and pixels with values >127 were given a value of 255). For each image, we calculated the number of pixels corresponding to vegetation (value = 0) and sky (value = 1). This provided an unweighted approximation of canopy openness. The results are presented as the percentage of the image as sky.

We constructed a contour map of canopy openness by interpolating canopy openness values among all subplots, using the contour plot generator in SigmaPlot™ 11.0. Through visual approximation we then divided the 4-ha plot into three sections based on light level variation: closed-canopy forest (lowest canopy openness levels), open-canopy grassland (highest canopy openness levels) and edge (where levels transitioned between the above two plot sections).

Tree spatial analysis

We tested for non-random spatial patterning of species by applying a Kruskal-Wallis ANOVA to stem abundances across the 35 grassland subplots, 14 edge subplots and 51 closed-canopy forest subplots (as defined by the canopy photograph analysis, see Results). Statistical tests were performed for each species, and partitioned into trees ≥10 cm dbh and 5–9.9 cm dbh; tests were run only for species with at least 10 stems in each size class. Statistical tests were performed using IBM® *SPSS*® Statistics 20.

RESULTS

In the 4-ha plot we encountered 86 species ≥5 cm dbh, including the palm *P. loureiroi,* five woody climbers (*Celastrus monospermus* Roxb., *Celastrus paniculatus* Willd., *Cissus repens* Lam.*, Embelia tsjeriam-cottam* (Roem. & Schult.) A. DC. var. *tsjeriam-cottam* and *Spatholobus parviflorus* (Roxb.) Kuntze), the bamboo *Dendrocalamus strictus* (Roxb.) Nees, and the threatened cycad *Cycas pectinata* Buch.-Ham. (Table 1). Both Simpson's λ and the Shannon-Wiener index indicated high richness and evenness (λ = 0.071, *H*' = 3.23). The plot had 569 individuals (601 stems)/ha ≥5 cm dbh comprising 21.6 m^2/ha of woody basal area, and 330 individuals (343 stems)/ha ≥10 cm dbh comprising 20.6 m^2/ha basal area (Table 1).

By all measures (abundance, basal area and importance value), the plot was strongly dominated by *Shorea siamensis* Miq. var. *siamensis*, with *Quercus kerrii* var. *kerrii* ranking second in terms of basal area and importance value; the subcanopy was dominated by *Cycas pectinata* and *Aporosa villosa* (Lindl.) Baill. (Table 1). The most abundant species was *Shorea siamensis* with 315 individuals, followed by *Cycas pectinata* with 177 individuals and *Quercus kerrii* with 118 individuals. Other common species included *Zizyphus rugosa* Lam. var. *rugosa, Stereospermum neuranthum* Kurz, *Phyllanthus emblica* L., *Grewia eriocarpa* Juss., *Bridelia retusa* (L.) A. Juss. and *Dillenia parviflora* Griff. var *kerrii* (Craib) Hoogland.

A total of 109 *Stereospermum neuranthum* (Bignoniaceae) trees were in the plot, and most were bent to a 45–90° angle at about 1 m above the base (Fig. 2). This was evidently the result of repeated browsing by gaur, which accesses *Stereospermum* leaves by bending small trees down to feed (Schaller, 1967; Prayurasiddhi, 1997). In the southeast corner of the plot was a *ca.* 5-m diameter, 2-m deep sinkhole, which contained one individual each of *Magnolia baillonii* Pierre and *Mangifera caloneura* Kurz, species more typically found in either semi-evergreen forest or mixed-deciduous forest (van de Bult, 2003).

Table 1. Total abundances and basal areas (cm^2) of species with stems ≥5 cm dbh in 4 ha of deciduous dipterocarp-oak forest in western Thailand. RA = relative abundance, BA= basal area, RBA = relative basal area, IV = importance value (RA + RBA). Included in the list are large bamboos (*Dendrocalamus* spp.) and tree-like *Cycas pectinata* and *Phoenix loureiroi*. Abundance numbers are based on individuals (with multiple-stemmed individuals counted only once) and basal area is summed across all stems. For habit, D = deciduous, E = evergreen, T = tree, Tl = treelet, WC = woody climber, Sc=scandent, H= herb.

Species	Family	Habit	Abundance				RA	BA	RBA	IV
			Grassland	Edge	Closed-canopy forest	Total	(%)	(cm^2)	(%)	
Adenanthera microsperma Teijsm. & Binn.	Leguminosae, Mimosoideae	D,T		1	1	2	0.09	221.3	0.03	0.11
Albizia lebbeck (L.) Benth.	Leguminosae, Mimosoideae	D,T	1	1	0.04	45.4	0.01	0.05		
Albizia odoratissima (L.f.) Benth.	Leguminosae, Mimosoideae	E,T			3	3	0.13	1769.8	0.20	0.34
Antidesma acidum Retz.	Euphorbiaceae	D,T			2	2	0.09	55.9	0.01	0.09
Aporosa villosa (Lindl.) Baill.	Euphorbiaceae	D,T	30	45	88	163	7.16	25498.2	2.95	10.11
Bauhinia variegata L.	Leguminosae, Caesalpiniodeae	D,T	1	1	2	4	0.18	240.2	0.03	0.20
Bombax anceps Pierre var. *anceps*	Bombacaceae	D,T	6		6	12	0.53	4527.3	0.52	1.05
Bridelia retusa (L.) A. Juss.	Euphorbiaceae	D,T	59	13	39	111	4.87	6156.7	0.71	5.59
Canarium subulatum Guill.	Burseraceae	D,T	12		7	19	0.83	7417.8	0.86	1.69
Careya arborea Roxb.	Lecythidaceae	D,T	13	9	32	54	2.37	12987.7	1.50	3.87
Casearia graveolens Dalz.	Flacourtiaceae	D,T	12	5	12	29	1.27	6347.0	0.73	2.01

Table 1 (continued).

Species	Family	Habit	Abundance				RA (%)	BA (cm^2)	RBA (%)	IV
			Grassland	Edge	Closed-canopy forest	Total				
Castanopsis argyrophylla King *ex* Hk.f.	Fagaceae	E,T	5	1	7	13	0.57	11308.1	1.31	1.88
Castanopsis tribuloides (Sm.) A. DC.	Fagaceae	E,T			1	1	0.04	1434.0	0.17	0.21
Catunaregam spathulifolia Tirv.	Rubiaceae	D,T	8	4	14	26	1.14	1839.0	0.21	1.35
Celastrus monospermus Roxb.	Celastraceae	E,WC		1		1	0.04	32.2	0.00	0.05
Celastrus paniculatus Willd.	Celastraceae	E,WC			1	1	0.04	31.2	0.00	0.05
Cissus repens Lam.	Vitaceae	D,WC			6	6	0.26	523.4	0.06	0.32
Croton roxburghii N. P. Balakr.	Euphorbiaceae	D,T			10	10	0.44	1675.5	0.19	0.63
Cycas pectinata Buch.-Ham.	Cycadaceae	E,Tl	50	27	100	177	7.77	66317.1	7.67	15.45
Dalbergia cana Grah. *ex* Kurz var. *cana*	Leguminosae, Papilionoideae	D,T			1	1	0.04	250.7	0.03	0.07
Dalbergia cultrata Graham *ex* Benth.	Leguminosae, Papilionoideae	D,T	47	19	23	89	3.91	5512.3	0.64	4.55
Dalbergia rimosa Roxb.	Leguminosae, Papilionoideae	D,Sc,Tl	14	9	45	68	2.99	5068.5	0.59	3.57
Dendrocalamus sp.	Gramineae, Bambusoideae	E,H			3	3	0.13			
Dendrocalamns strictus (Roxb.) Nees	Gramineae, Bambusoideae	E,H			2	2	0.09			
Dillenia aurea Sm. var. *aurea*	Dilleniaceae	D,T			18	18	0.79	10405.6	1.20	1.99

Table 1 (continued).

Species	Family	Habit	Abundance				RA (%)	BA (cm²)	RBA (%)	IV
			Grassland	Edge	Closed-canopy forest	Total				
Dillenia parviflora Griff. var *kerrii* (Craib) Hoogland	Dilleniaceae	D,T	36	15	18	69	3.03	19736.5	2.28	5.31
Embelia tsjeriam-cottam (Roem. & Schult.) A. DC. var. *tsjeriam-cottam*	Myrsinaceae	D,Tl,WC			4	4	0.18	154.5	0.02	0.19
Engelhardtia spicata Blume var. *integra* (Kurz) Manning	Juglandaceae	D,T	1	1		2	0.09	607.1	0.07	0.16
Engelhardtia serrata Blume var. *serrata*	Juglandaceae	D,T	2	1	16	19	0.83	2756.5	0.32	1.15
Eriolaena candollei Wall.	Sterculiaceae	D,T	22	9	22	53	2.33	5736.0	0.66	2.99
Eugenia cumini (L.) Druce	Myrtaceae	D,T	3		5	8	0.35	7922.6	0.92	1.27
Fernandoa adenophylla (Wall. *ex* G. Don) Steenis	Bignoniaceae	D,T			2	2	0.09	93.8	0.01	0.10
Ficus rumphii Blume	Moraceae	D,T			1	1	0.04	28.3	0.00	0.05
Firmiana colorata (Roxb.) R. Br.	Sterculiaceae	D,T			1	1	0.04	44.2	0.01	0.05
Flacourtia indica (Burm.f.) Merr.	Flacourtiaceae	D,T	1			1	0.04	845.0	0.10	0.14
Garuga floribunda Decne.	Burseraceae	D,T			1	1	0.04	22.9	0.00	0.05
Garuga pinnata Roxb.	Burseraceae	D,T	3		4	7	0.31	2915.0	0.34	0.64
Glochidion eriocarpum Champ.	Euphorbiaceae	E,Tl	19	2	11	32	1.41	1648.0	0.19	1.60
Glochidion sphaerogynum (Müll.Arg.) Kurz	Euphorbiaceae	E,T	1		1	2	0.09	464.8	0.05	0.14

Table 1 (continued).

Species	Family	Habit	Abundance				RA (%)	BA (cm^2)	RBA (%)	IV
			Grassland	Edge	Closed-canopy forest	Total				
Gmelina arborea Roxb.	Verbenaceae	D,T			5	5	0.22	2135.1	0.25	0.47
Gochnatia decora (Kurz) Cabr.	Compositae	D,Tl		1	1	2	0.09	410.2	0.05	0.14
Grewia eriocarpa Juss.	Malvaceae	D,T	57	16	30	103	4.52	9498.2	1.10	5.62
Heliciopsis terminalis (Kurz) Sleum.	Proteaceae	E,T			3	3	0.13	3001.7	0.35	0.48
Heteropanax fragrans (Roxb. *ex* DC.) Seem.	Araliaceae	D,T	6		4	10	0.44	2791.4	0.32	0.76
Hiptage benghalensis (L.) Kurz ssp. *candicans* (Hk.f.) Sirirugsa	Malphigiaceae	D,T	27	11	22	60	2.64	16783.0	1.94	4.58
Holarrhena pubescens (Buch.-Ham.) Wall. *ex* G. Don	Apocynaceae	D,T		1	6	7	0.31	483.8	0.06	0.36
Hymenodictyon orixense (Roxb.) Mabb.	Rubiaceae	D,T			1	1	0.04	254.5	0.03	0.07
Ilex umbellulata (Wall.) Loesn.	Aquifoliaceae	E,T			3	3	0.13	1634.8	0.19	0.32
Kydia calycina Roxb.	Malvaceae	D,T	1		10	11	0.48	1343.8	0.16	0.64
Lagerstroemia macrocarpa Kurz var. *macrocarpa*	Lythraceae	D,T	6		3	9	0.40	1275.6	0.15	0.54
Lannea coromandelica (Houtt.) Merr.	Anacardiaceae	D,T	7	2	10	19	0.83	4619.5	0.53	1.37
Litsea semecarpifolia Wall. *ex* Nees	Lauraceae	E,T			30	30	1.32	3030.0	0.35	1.67
Magnolia baillonii Pierre	Magnoliaceae	D,T	1			1	0.04	824.5	0.10	0.14

Table 1 (continued).

Species	Family	Habit	Abundance				RA	BA	RBA	IV
			Grassland	Edge	Closed-canopy forest	Total	(%)	(cm^2)	(%)	
Mallotus philippensis (Lam.) Müll.Arg.	Euphorbiaceae	E,T	3			3	0.13	1424.6	0.16	0.30
Mangifera caloneura Kurz	Anacardiaceae	E,T	1			1	0.04	2551.8	0.30	0.34
Melochia umbellata (Houtt.) Stapf.	Sterculiaceae	D,T			1	1	0.04	254.5	0.03	0.07
Mitragyna rotundifolia (Roxb.) Kuntze	Rubiaceae	D,T			2	2	0.09	157.1	0.02	0.11
Oroxylum indicum (L.) Kurz	Bignoniaceae	D,T	3		3	6	0.26	828.6	0.10	0.36
Pavetta fruticosa Craib	Rubiaceae	D,Tl			1	1	0.04	36.3	0.00	0.05
Phoenix loureiroi Kunth. var. *loureiroi*	Palmae	E,Tl	21	11	21	53	2.33	15845.3	1.83	4.16
Phyllanthus emblica L.	Euphorbiaceae	D,T	24	18	45	87	3.82	16861.0	1.95	5.77
Premna flavescens Buch.-Ham. *ex* C.B. Clarke var. *flavescens*	Verbenaceae	D,Tl			2	2	0.09	483.9	0.06	0.14
Premna latifolia Roxb. var. *latifolia*	Verbenaceae	E,Tl			1	1	0.04	46.6	0.01	0.05
Premna sp.	Verbenaceae	D,Tl			4	4	0.18	803.5	0.09	0.27
Pterocarpus macrocarpus Kurz	Leguminosae, Papilionoideae	D,T	1	2	12	15	0.66	8269.7	0.96	1.62
Quercus kerrii Craib var. *kerrii*	Fagaceae	D,T	60	17	41	118	5.18	98816.8	11.44	16.62
Schima wallichii (DC.) Korth.	Theaceae	E,T			11	11	0.48	5961.6	0.69	1.17
Schoepfia fragrans Wall.	Olacaceae	E,Tl			4	4	0.18	1154.0	0.13	0.31

Table 1 (continued).

Species	Family	Habit	Abundance				RA (%)	BA (cm^2)	RBA (%)	IV
			Grassland	Edge	Closed-canopy forest	Total				
Schrebera swietenioides Roxb.	Oleaceae	D,T			2	2	0.09	498.1	0.06	0.15
Shorea siamensis Miq. var. *siamensis*	Dipterocarpaceae	D,T	82	64	169	315	13.83	395404.2	45.76	59.59
Spatholobus parviflorus (Roxb.) Kuntze	Leguminosae, Papilionoideae	D,WC	12	4	26	42	1.84	4984.5	0.58	2.42
Spondias pinnata (L.f.) Kurz	Anacardiaceae	D,T			3	3	0.13	439.5	0.05	0.18
Sterculia pexa Pierre	Sterculiaceae	D,T	2		3	5	0.22	1535.6	0.18	0.40
Sterculia villosa Roxb.	Sterculiaceae	D,T	5		5	10	0.44	4064.8	0.47	0.91
Stereospermum colais (Buch.-Ham. *ex* Dill.) Mabb.	Bignoniaceae	D,T			2	2	0.09	526.0	0.06	0.15
Stereospermum neuranthum Kurz	Bignoniaceae	D,T	40	26	43	109	4.79	12063.0	1.40	6.18
Strychnos nuxvomica L.	Loganiaceae	D,T			1	1	0.04	686.4	0.08	0.12
Styrax benzoides Craib	Styracaceae	E,T			1	1	0.04	716.3	0.08	0.13
Symplocos racemosa Roxb.	Symplocaceae	D,T	4	3	5	12	0.53	1005.1	0.12	0.64
Terminalia bellirica (Gaertn.) Roxb.	Combretaceae	D,T	2		6	8	0.35	2079.2	0.24	0.59
Terminalia chebula Retz. var. *chebula*	Combretaceae	D,T	5	2	12	19	0.83	2262.8	0.26	1.10
Ternstroemia gymnanthera (Wight & Arn.) Bedd.	Theaceae	E,T		1	4	5	0.22	5367.8	0.62	0.84
Vitex peduncularis Wall. *ex* Schauer	Verbenaceae	D,T			3	3	0.13	1334.8	0.15	0.29

Table 1 (continued).

Species	Family	Habit	Abundance				RA	BA	RBA	IV
			Grassland	Edge	Closed-canopy forest	Total	(%)	(cm^2)	(%)	
Wendlandia tinctoria (Roxb.) DC. subsp. *floribunda* (Craib) Cowan	Rubiaceae	E,T			5	5	0.22	1678.9	0.19	0.41
Xantolis cambodiana (Pierre *ex* Dub.) P. Royen	Sapotaceae	E,T			6	6	0.26	2755.2	0.32	0.58
Ziziphus rugosa Lam. var. *rugosa*	Rhamnaceae	D,T	54	21	63	138	6.06	12520.0	1.45	7.51
Total			**769**	**363**	**1145**	**2277**		**864143.4**		
Total per ha			**549.3**	**648.2**	**561.3**	**569.3**				
Basal area per ha (m^2)			**11.7**	**18.4**	**29.3**	**21.6**				
Number of species			**44**	**33**	**79**	**85**				

From a one-time collection in December 2005, we recorded 12 graminoid species: *Apluda mutica* L., *Arundinella setosa* Trin. var. *setosa*, *Capillipedium parviflorum* (R. Br.) Stapf, *Eulalia speciosa* (Debeaux) Kuntze, *Eulalia trispicata* (Schult.) Henrard, *Microstegium fasciculatum* (L.) Henrard, *Mnesithea striata* (Nees ex Steud.) de Konig & Sosef, *Hyparrhenia rufa* (Nees) Stapf var. *siamensis* Clayton, *Oplismenus compositus* (L.) P. Beauv., *Panicum notatum* Retz., *Sorghum nitidum* (Vahl) Pers., and *Themeda triandra* Forssk.

Canopy openness ranged from 13% to 95% among subplots, with a median of 34%. The light-level map allowed us to subdivide the plot into open-canopy grassland (1.40 ha) and closed-canopy forest (2.04 ha) sections, along with an edge (0.56 ha) (Fig. 4). In the grassland section large trees were scattered and interspersed with a dense graminoid layer (Fig. 2). The closed-canopy forest had a fairly continuous canopy, simple vertical stratification, and less graminoid cover and more perennial understory shrubs and tree seedlings (Fig. 2). As expected, after normalizing the canopy-openness values with *ln*-transformation, a one-way ANOVA with post-hoc Bonferroni pairwise comparisons revealed that canopy openness in the grassland was significantly higher than in forest and edge plots (one-way ANOVA $df = 99$, $F = 62.96$, $p < 0.0001$) (Fig. 4). Moreover, there was a significant, positive nonlinear relationship between canopy openness and graminoid height ($y = a(1 - e^{-bx})$, $r^2 = 0.51$, $p < 0.0001$; Fig. 5), with graminoids reaching their maximum height at about 50% canopy openness.

The closed-canopy forest had 79 tree species, compared with 33 along the edge and 44 in the grassland (Table 1). Rarefaction curves indicated that closed-canopy forest was intrinsically the most species-rich when controlling for differences in stem density, while edge and grassland sections exhibited comparatively lower diversities (Fig. 6).

Stem densities were highest along the edge (648 individuals/ha; Table 1), and there was a significant difference across the three sections when analyzed at the subplot level (Table 2). Trees 5–9.9 cm dbh were more than twice as dense in the edge and grassland as in closed-canopy forest. However, basal area in closed-canopy forest was nearly three times higher than under open-canopy conditions, because of higher densities of trees ≥20 cm dbh (Table 1).

Of 19 tested species, three (*Aporosa villosa*, *Litsea semecarpifolia* Wall. ex Nees, *Shorea siamensis*) exhibited higher stem densities in closed forest, while three (*Bridelia retusa*, *Dillenia parviflora*, *Grewia eriocarpa*) had higher densities in grassland, one (*Stereospermum neuranthum*) had highest density along the forest edge, and nine showed no spatial pattern across the three habitat types (Fig. 7. Table 3). *Shorea siamensis* trees ≥10 cm dbh were more common in closed-canopy forest, whereas trees 5–9.9 cm dbh were most common in grassland and edge sections. Seven species showed significantly higher densities of trees 5–9.9 cm dbh in grassland than closed-canopy forest, whereas adult trees of these species (≥10 cm dbh) did not follow that pattern. *Litsea semecarpifolia* was the only species found exclusively in the closed-canopy forest (Fig. 7).

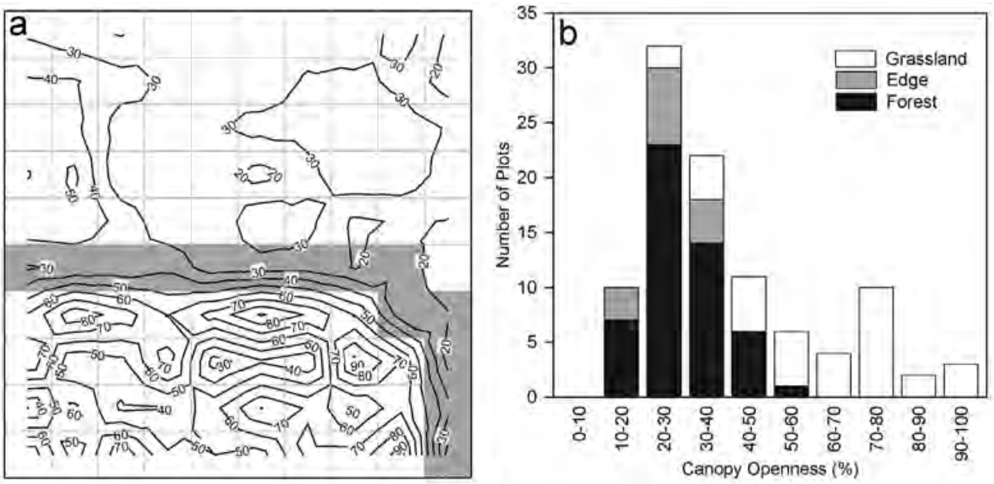

Figure 4. (a): Canopy openness contour map for a 4-ha (200 × 200 m) plot in a mixed deciduous dipterocarp-oak forest with grassland, Thung Yai Naresuan. Contours represent interpolated 10% light level changes. Scale of contours ranges from 10% to 90%. Grey subplots are those classified as 'edge', with forested section in the upper (north) section of the plot and the grassland in the lower (southern) section. (b): Histogram of canopy openness values for the three habitat types.

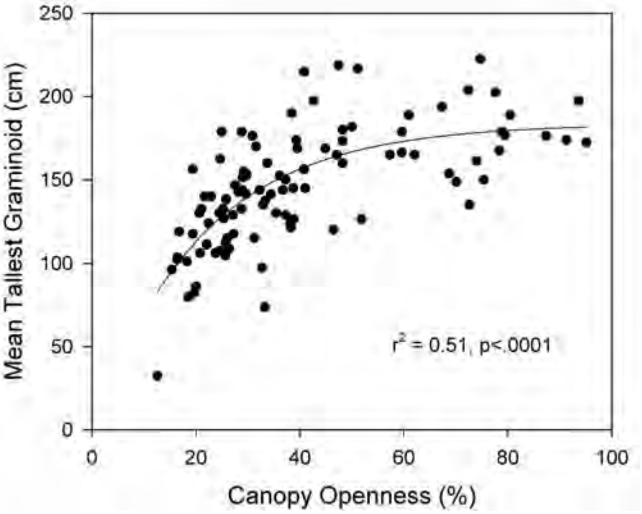

Figure 5. Scatterplot and results of a nonlinear regression on the relationship between canopy openness measured by canopy photographs and the mean height of the tallest graminoids in the center of each subplot.

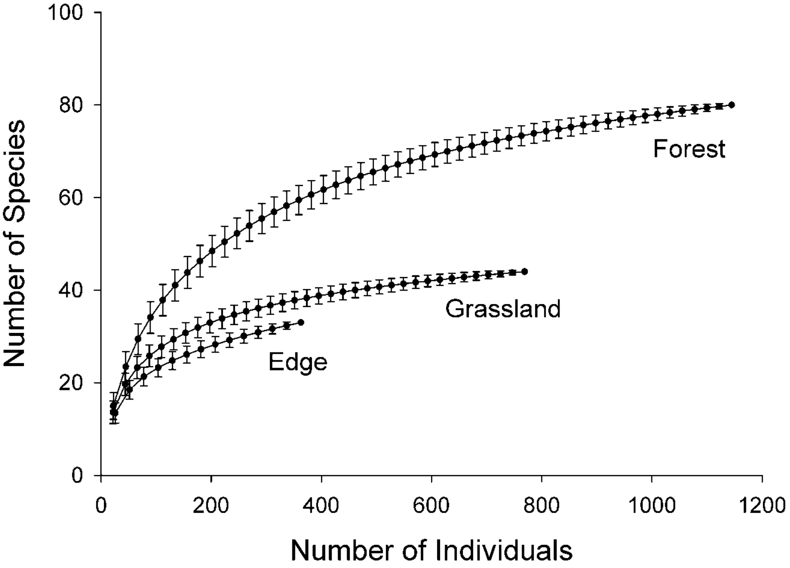

Figure 6. Individual-based species accumulation (rarefaction) curves and 95% confidence intervals for three habitat types in the plot.

Table 2. Mean stem density per 400 m^2 subplot (SD in parentheses; 95% confidence interval for small trees) for all trees, trees ≥10 cm dbh and trees 5–9.9 cm dbh aggregated across all species, in grassland, edge and closed-canopy forest habitats. Small tree densities were *ln*-transformed and then back-transformed to calculate distribution mean and 95% confidence intervals, so no pairwise comparisons were made (Sokal & Rohlf, 1981). P values are the level of significance from a one-way ANOVA across habitat types; letters refer to groupings formed by post-hoc LSD pairwise comparisons. Assumptions of normality were met for all tests.

	Category			P
	Grassland	Edge	Closed-canopy forest	
All trees	19.3 (7.2)^b	23.2 (8.3)^b	17 (5.7)^a	0.009
Trees ≥10 cm dbh	6.6 (3.8)^b	9.2 (4.8)^{a,b}	9.7 (4.0)^a	0.002
Trees 5–9.9 cm dbh	10.6 (8.0–11.4)	10.1 (5.4–14.7)	4.3 (3.5–5.1)	0.000

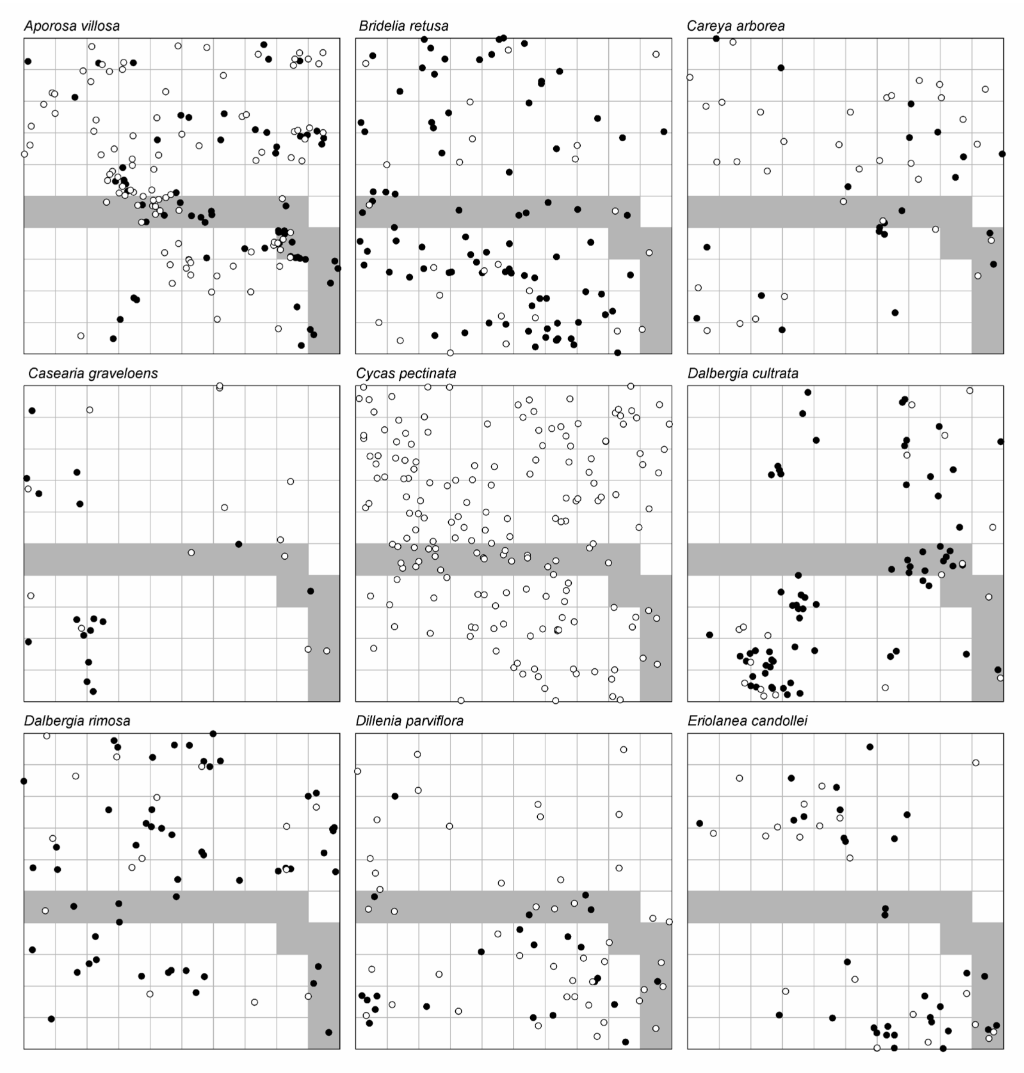

Figure 7. Maps of tree species in 4 ha of mixed deciduous dipterocarp-oak forest with grassland, western Thailand. Open circles are trees ≥10 cm dbh, closed circles are trees <10 cm dbh. Grey subplots are those classified as ‘edge’ with closed forest above the edge and grassland below the edge.

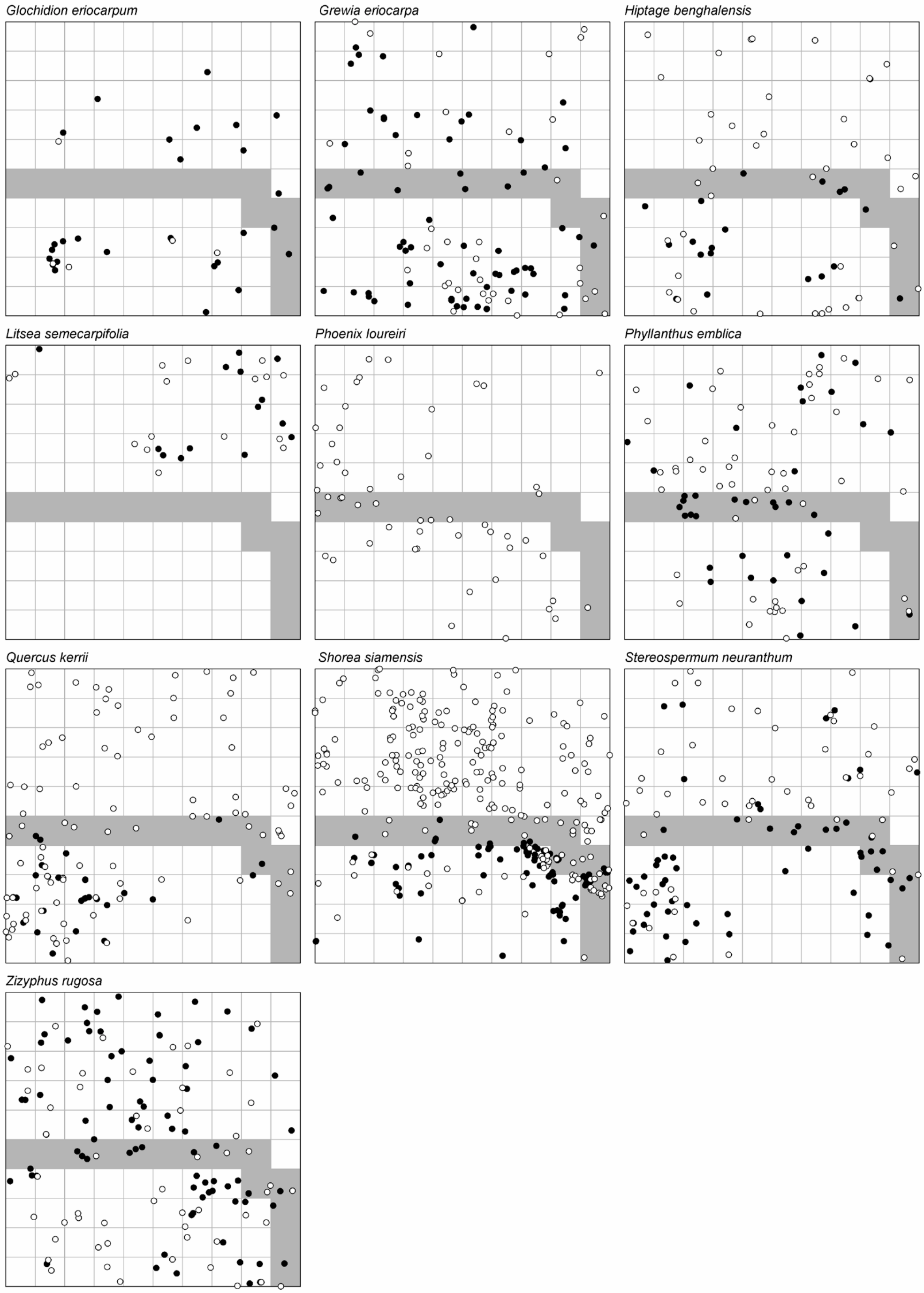

Fig. 7 (continued).

Table 3. Spatial patterns of tree species at the interface of grassland and closed-canopy forest, Thung Yai Naresuan Wildlife Sanctuary, western Thailand. Significant differences between habitat types (“F” = forest, “E” = edge, “G” = grassland) are designated in the “Pattern” column. Significance levels from a Kruskal-Wallis ANOVA across habitat types are indicated with * (p < 0.05), ** (p < 0.01) and *** (p < 0.001). Sample sizes were G = 35 (20 × 20 m) plots, E = 14 plots and F = 51 plots. Empty cells indicate no significant trend. *C. pectinata* and *P. loureiroi* were not broken down into size classes because there was no regeneration.

Species	All Trees		Trees ≥10 cm dbh		Trees 5–9.9 cm dbh	
	N	Pattern	N	Pattern	N	Pattern
Aporosa villosa	163	F, E > G*	98	F > E > G*	65	
Bridelia retusa	111	G > E, F**	25		86	G > E, F**
Careya arborea	54		33	F > E > G (p = 0.052)*	21	
Casearia graveolens	29		13		16	
Cycas pectinata	177			n/a		n/a
Dalbergia cultrata	89		19		70	
Dalbergia rimosa	68		15		53	
Dillenia parviflora var. *kerrii*	69	E > G > F**	46		23	G, E > F***
Eriolaena candollei	53		20		33	
Grewia eriocarpa	103	G > E > F**	36		67	G > E > F**
Hiptage benghalensis subsp. *candicans*	60		40		20	E > G > F**
Litsea semecarpifolia	30	F > E, G***	16	F > E, G**	14	F > E, G**
Phoenix loureiroi var. *loureiroi*	53			n/a		n/a
Phyllanthus emblica	87		50		37	
Quercus kerri var. *kerrii*	118		89		29	G > E > F***
Shorea siamensis var. *siamensis*	315	F, E > G*	235	F > E > G***	80	G, E > F***
Spatholobus parviflorus	42		15		27	
Stereospermum neuranthum	109	E > F, G (p = 0.05)*	51	F, E > G**	58	E > G > F***
Zizyphus rugosa var. *rugosa*	138		56		82	

DISCUSSION

To our knowledge this is the first quantitative description of fire-influenced deciduous dipterocarp-oak forest with grassland in Thailand (and SE Asia). As a result, few comparative data exist. Density of trees ≥5 cm dbh in this plot was substantially lower than reports from fire-influenced, degraded deciduous dipterocarp forest in NE Thailand, which lacked the graminoid layer seen in our plot (569.3/ha in this study versus 1290/ha in NE Thailand, Kabir & Webb, 2006). However, basal area in the Thung Yai plot was twice as high as in the NE Thailand study (21.6/ha versus 9.60/ha, Kabir & Webb, 2006). The plot was also species rich: as a comparison, Vidal's (1965-60, cited in Rundel, 1999) explorations of five different formations of deciduous dipterocarp forest in southern Lao (including forest dominated by *S. siamensis*) revealed only 56 tree species. Although the total area surveyed by Vidal (1965-60) was not recorded, given the large spatial extent of his work it is certain that his species list represents far more than 4 ha of survey area.

This plot was dominated by a single dipterocarp species, *S. siamensis*. Most dipterocarp-oak forests in SE Asia are co-dominated by more than one dipterocarp species, (Rundel, 1999). Therefore, this plot may represent a distinctive variant of deciduous dipterocarp-oak forest. The *thung* also supports a significant population of *Cycas pectinata*, a species with declining populations that is vulnerable to extinction (Hill, 2003). Given the rapid rate of habitat loss and degradation in continental SE Asia, it is critical to locate large, intact populations of threatened species; the deciduous dipterocarp-oak forest and grassland mosaic of western Thailand clearly serves this purpose for some species. Thus, our results highlight the unique ecological, botanical and conservation value of the *thung*.

Fire is the predominant disturbance type in the *thung*, occurring annually or semi-annually, and thus is likely to be the overriding determinant of the spatial patterns in trees we observed. Fire has been shown to control the spatial distribution of tree species, and tree cover overall, in savanna ecosystems (Lehmann *et al.*, 2008, 2009). Research in southern Africa found that total tree densities in savanna were unresponsive to fire, but fire skewed the size-class distribution toward smaller trees (Higgins *et al.*, 2007). Our study accords with that finding, with total stem densities higher in grassland than closed-canopy forest, but basal area showing the opposite trend (much greater in closed-canopy forest). Specifically, small individuals of *Dillenia parviflora, Hiptage benghalensis, Quercus kerrii, Stereospermum neuranthum* and *Shorea siamensis* were significantly more common in the grassland than in closed-canopy forest.

Two main processes may contribute to the variation in spatial patterns observed. First, higher light levels in grassland could support higher seedling survival and growth, leading to higher small tree densities (Hoffmann, 2000; Hoffmann *et al.*, 2004). Second is fire. On the one hand, fire may be a barrier to seedling establishment or tree persistence in the grassland, as fire intensity (mean temperature, maximum temperature, and scorch height) is a function of fuel load (Stott, 1986; Van Langvelde *et al.*, 2003; Thaxton & Platt, 2006), which we have shown is positively correlated with canopy openness. In this regard, seeds or seedlings of fire-sensitive species may be killed, and small trees able to persist may nevertheless be caught in a "fire trap", whereby fires repeatedly kill or damage the aboveground stem, leading to a cycle of basal resprouting (Hoffmann *et al.*, 2009), or stunted tree growth, causing trees to remain small even at advanced ages (Higgins *et al.*, 2007). On the other hand, some species might sustain higher germination and establishment rates in grassland due precisely to the higher fire intensity there. For example, the preponderance of small *S. siamensis* trees (5 – 9.9 cm dbh) in the grassland agrees with other research in western Thailand showing massive recruitment of this species following fire (MAROD *ET AL.*, 2002). In the case of the *thung*, it is most likely that all three factors affect, to varying degrees, the distributions of species in grassland and closed-canopy forest, depending on species-specific light requirements and fire resistances. Further research on the tree species ecology would help to partition the positive and negative effects of fire on the tree populations in the *thung*.

The extent of grassland versus closed-canopy forest patches in dry forest mosaics at local scales in Southeast Asia is controlled proximally by fire (STOTT, 1988). Specific to our plot, if grassland were encroaching into the forest, one would expect to see a 'dying edge', with at least some dead, decaying, or burnt trees in the edge section of the plot. Over the course of this study, however, we only observed one standing, dead burned tree in the grassland, and an uprooted tree in the closed-canopy forest section that appeared to have burned after it toppled over. Moreover, tree density was 13–15% higher at the forest edge than in forest or grassland (Table 1), suggesting low levels of mortality along the grassland-forest edge. These observations suggest that the grassland was probably not encroaching on the forest in our plot. Although our data represent a single point in time, the presence of significantly higher densities of trees 5–9.9 cm dbh in grassland, and the near-absence of fire-killed trees in the plot, suggests that the closed-canopy forest may instead have been expanding into the grassland. This agrees with observations by long-term local inhabitants of the sanctuary, who reported that, over the past 50 years, Thung Yai's grasslands had become smaller and less open, and tree density in the grasslands had increased (M. Tu-U, personal communication). Long-term monitoring using remote sensing and field work would be needed to test whether these observations were really attributed to forest expansion. Additionally, long-term monitoring using remote sensing, ecological surveys, and local knowledge should be used to further our understanding of the origins and future of this important ecosystem, keeping in mind that the processes governing the dynamics of the grassland-forest mosaic operate on a longer timescale than typical conservation horizons (WILLIS & BIRKS, 2006).

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