

# Environmental Factors Influencing Tree Species Regeneration in Different Forest Stands Growing on a Limestone Hill in Phrae Province, Northern Thailand

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## Abstract

Improved knowledge of the environmental factors affecting the natural regeneration of tree species in limestone forest is urgently required for species conservation. We examined the environmental factors and tree species characteristics that are important for colonization in diverse forest stands growing on a limestone hill in northern Thailand. Our analysis estimated the relative influence of forest structure and environmental factors on the regeneration traits of tree species. We established sixty-four 100-m<sup>2</sup> plots in four forest stands on the limestone hill. We determined the species composition of canopy trees, regenerating seedlings, and saplings in relation to the physical environment. The relationships between environmental variables and tree species abundance were assessed by canonical correspondence analysis (CCA), and we used generalized linear mixed models to examine data on seedling/sapling abundances. The CCA ordination indicated that the abundance of tree species within the mixed deciduous forest was closely related to soil depth. The abundances of tree species growing within the sink-hole and hill-slope stands were positively related to the extent of rocky outcropping; light and soil moisture positively influenced the abundance of tree species in the hill-cliff stand. Physical factors had a greater effect on tree regeneration than did factors related to forest structure. Tree species, such as *Ficus macleilandii*, *Dracaena cochinchinensis*, and *Phyllanthus mirabilis* within the hill-cliff or sink-hole stand, colonized well on large rocky outcroppings that were well illuminated and had soft soils. These species regenerated well under conditions prevailing on the limestone hill. The colonization of several species in other stands was negatively influenced by environmental conditions at these sites. We found that natural regeneration of tree species on the limestone hill was difficult because of the prevailing combination of physical and biological factors. The influence of these factors was species dependent, and the magnitude of effects varied across forest stands.

**Key Words:** environmental factors, limestone hill, Northern Thailand, tree species regeneration, tropical limestone forest

## Introduction

Limestone hills are elements of karst landscapes, which are characterized by a distinctive topography that develops

as water dissolves soluble calcareous rock. Karst landscapes are characterized by fluted and pitted rock surfaces, vertical shafts, sinkholes, sinking streams, springs, subsurface drainage channels, and caves (Ford and Williams 2007; De

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Waele et al. 2009; Liu 2009). Tropical forests growing on limestone occupy ca. 40% of the total area of tropical Asian landscapes (Tang et al. 2012). Limestone karst habitats are highly heterogeneous. They are characterized by extremely slow soil formation from the underlying limestone, very shallow and patchy soils with low water-retention capacity, and highly porous underlying limestone rock (Liu 2009; Liu et al. 2012). Limestone outcroppings support tropical forest biodiversity at low latitudes around the globe (Felfili et al. 2007). Tropical forests on limestone are viewed as relict communities, with many endemic and new species (Musser et al. 2005; Crottini et al. 2011; Bogutskaya et al. 2012; Chen et al. 2014; Peng et al. 2015). Natural environmental factors and human activities have complex negative and positive effects on the biodiversity of these unique environments. The effects of socioeconomic factors have been well documented in Thailand (Niskanen 1998; Westera and Yongvanit 2005; Duangjai et al. 2015) and neighboring countries, such as Vietnam (Nguyen et al. 2010, 2014). However, the effects of environmental factors are not well known. The climax configuration of tall vegetation growing on limestone is evergreen/deciduous broadleaf mixed forest (Lu et al. 2014). The tree species are extremely sensitive to environmental disturbance. A strong artificial perturbation can reverse their natural succession, and restoration is very difficult (Li et al. 2013).

Comprehensive information on the environmental factors affecting tree species is required to fully understand limestone forest ecology (Wei et al. 2011; Liu et al. 2012; Li et al. 2013; Lu et al. 2014; Yang et al. 2015). Forest regeneration patterns are related mostly to environmental factors, including physical (e.g., soil and light availability) and topographic factors (Asanok et al. 2013; Han et al. 2015; Nguyen et al. 2015). Light availability, soil conditions, elevation, proportion of rocky outcroppings, and slope are the most significant factors affecting the species diversity of woody vegetation in limestone forests (Csergo et al. 2014; Liu et al. 2015; Nguyen et al. 2015). Rocky outcrops generally provide heterogeneous habitat conditions that support species with physiological requirements that differ from those of species living in the surrounding landscape (Speziale and Ezcurra 2012). Light and soil moisture variables are important for tree species regeneration in tropical forests (Marques and Oliveira 2008). Soil moisture avail-

ability is a key factor influencing the growth and survival of plant communities in tropical dry forests (Khurana and Singh 2001). This factor is often the most important among those affecting plant establishment and growth following a disturbance (Yang et al. 2011). Light is a key environmental driver of tree growth and survival in tropical rainforests, and it is often the primary limiting factor for seedling regeneration in tropical lowland stands (Gaviria and Engelbrecht 2015). Light is the most important abiotic factor for seedling survival in closed-canopy forests, and soil moisture is the most important factor in open, better illuminated areas (McLaren and McDonald 2003; Guarino and Scariot 2012).

The tropical evergreen/deciduous forest cover and vegetation types on limestone hills in Thailand vary with topography and geomorphology (Nangngam et al. 2011). The limestone in this complex ecosystem is quarried and used in the industrial production of cement for housing construction. The Thai Government has promoted limestone cutting, particularly in northern and central regions of the country (Office of Industrial Economics 2014). Quarries are often located in ecologically sensitive areas, where the large disturbances contribute to habitat fragmentation and to the loss of habitat and species diversity in forest interiors due to edge effects. These disturbances involve removal of vegetation and soil, drilling, and blasting to reach the mineral ore (Cohen-Fernandez and Naeth 2013).

Many studies suggest that limestone hills in Thailand provide critical habitat for endemic and rare species of plants and animals, e.g., the plants *Wrightia siamensis*, *Thepparatia thailandica*, and *Adiantum phanomensis*, the rodents *Leopoldamys neilli* and *Niviventer hinpoon*, the bird *Napothera crispifrons calcicola*, and at least seven fish and dozens of snail species (World Bank 2004; Waengsothorn et al. 2007; Latinne et al. 2011; Nangngam et al. 2011; Pooma 2011). However, the ecology of forests growing on limestone hills in Thailand remains poorly understood, despite great scientific interest (Koh and Kettle 2010; Sodhi et al. 2010). Thus, we investigated environmental factors and tree species characteristics that are important for colonization in the different forest types on the limestone hills in Phrae Province, northern Thailand; our objective was to improve karst ecosystem management. We focused on the following questions: 1) what are the most important factors affecting tree distribution in the different forest stands on

limestone hills; and 2) which factor(s), i.e., physical variables or factors related to forest structure, prevent regeneration of limestone forest species?

## Materials and Methods

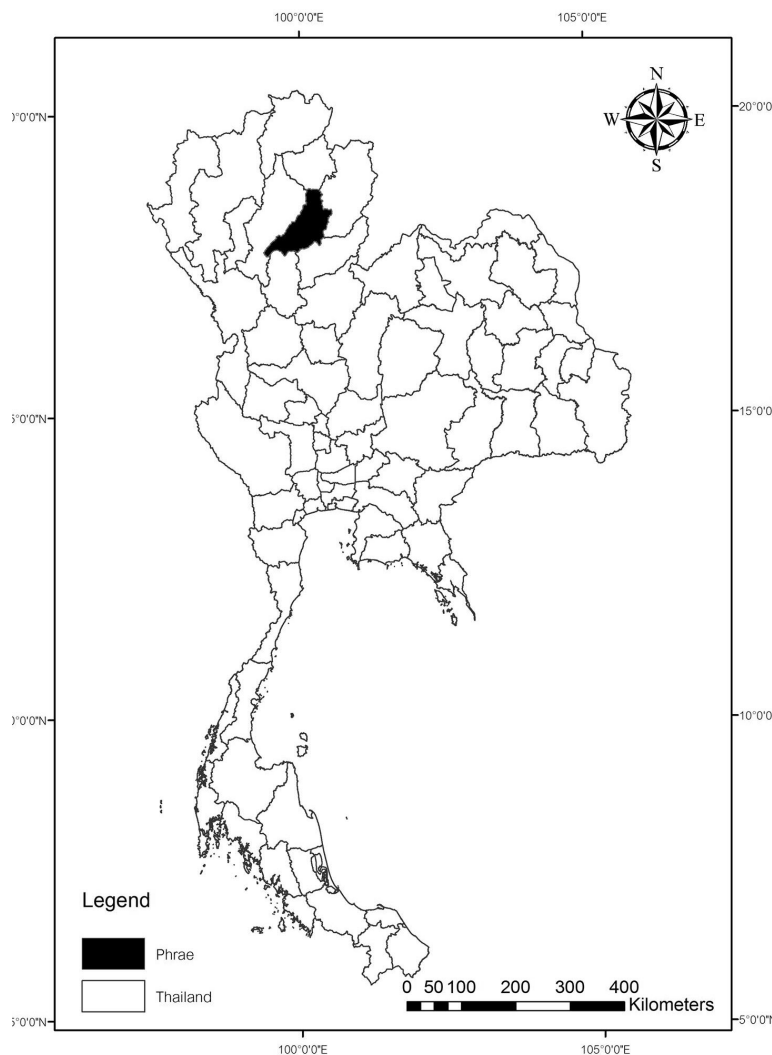
### Study site

The study site was on a limestone hill in the Rong Kwang District (northern sector of Phrae Province, northern Thailand) ca. 550 km from Bangkok (17°70'-18°84'N, 99°58'-100°32'E) (Fig. 1). The site spanned elevations of 320-460 m above mean sea level. The mean annual temperature and rainfall were 35.87°C and 1400 mm, respectively. The area has two main seasons: (i) a wet season (May-

October; the mean rainfall and temperature were 1460 mm and 35.42°C) and (ii) a dry season (November-April; the mean rainfall and temperature were 406 mm and 35.42°C). The dry season is subdivided into cool-dry (November-January) and hot-dry sub-seasons (February-April) (Phrae Information Department 2013; Thai Meteorological Department 2015). Limestone hills occupy 318 km<sup>2</sup> or 4.8% of the total landscape area in Phrae Province (Geology Bureau 2012).

### Sampling plot selection and species composition

The field study period extended from October 2014 until December 2015. Four forest stands on a limestone hill were selected: a mixed deciduous forest stand (MDS), a



**Fig. 1.** Location of the study sites on a limestone hill in the Rong Kwang District (northern sector of Phrae Province, Thailand).

hill-slope stand (HSS), a sink-hole stand (SHS), and a hill-cliff stand (HCS). The stands were differentiated by the topography and geomorphology of the limestone hill (Table 1).

We established a 10×10-m permanent plot in each forest stand. At each corner of each plot, we established a 4×4-m sub-quadrat, thereby generating a total of 64 sub-quadrats (Table 1). We counted adult trees (diameter at breast height [DBH]  $\geq 4.5$  cm) in each 10×10-m quadrat, and saplings (DBH  $< 4.5$  cm; height  $> 1.30$  m) and seedlings (height  $< 1.30$  m) in each 4×4-m sub-quadrat. All of the trees, saplings, and seedlings were tagged and identified to species. We identified species by collecting leaf specimens and comparing them with standard specimens in the herbarium at the Department of National Park, Wildlife and Plant Conservation. The nomenclature followed the Flora of Thailand (The Forest Herbarium 2014). We measured the DBH values (1.30 m above ground level) of all trees (but not those of saplings and seedlings) of each species.

#### *Physical environment measurements*

Five physical environmental variables were measured: photosynthetically active radiation (PAR), soil moisture content (SMC), soil bulk density (SDB), soil depth (SoD), and percentage cover of rock outcroppings (RC). Light and soil moisture jointly regulate seed germination, seedling establishment, and seedling survival in tropical forests (Khurana and Singh 2001). Soil moisture availability is influenced directly by rainfall, which is highly seasonal in dry tropical forest ecosystems (McLaren and McDonald 2003). This pronounced seasonality affects the patterns of seed production, germination, and seedling survival and development (Khurana and Singh 2001). Light is often the pri-

mary limiting factor for seedling regeneration in tropical lowland rainforests (Gustafsson et al. 2016). Improved light conditions after a large-scale canopy disturbance can promote the growth of seedlings in some tropical species (Dupuy and Chazdon 2008).

Soil bulk density and soil water content are linked closely to substratum penetration resistance, which increases with increasing bulk density and decreasing water content (Alameda et al. 2012). High organic matter content is also associated with low soil bulk density and affects tree root activities (Quero et al. 2011). Soil depth is also related directly to soil moisture and tree root systems (de Graaff et al. 2014; Gevaert et al. 2015). Rocky outcrops in karst landscapes produce extremely harsh microenvironments wherever large limestone rocks are abundant and cover much of the ground surface (Felfili et al. 2007). The number of plant species growing in the communities colonizing these environments is limited (Tang et al. 2010).

We measured light and soil moisture variables in each 10×10-m plot and within 64 sub-quadrats. To measure SMC, we collected 100-cm<sup>3</sup> soil samples from the topsoil layer (0-15 cm) in October 2015 using a soil core sampler inserted in the center of each 4×4-m sub-quadrat. All samples were collected on the same day, 10 days after the last rainfall and close to the onset of the dry season, when rain was infrequent. The soil was relatively damp. More variations in soil conditions were observed among the quadrats during this season than during the mid-wet and mid-dry seasons. SDB (g cm<sup>-3</sup>) was estimated for each soil sample as the proportion of oven-dried soil mass in the total volume (Brahim et al. 2012). SMC (%) was determined from the ratio of fresh weight to dry weight (Anctil et al. 2008). We measured SoD (cm) from the surface soil to the bedrock in

**Table 1.** Sampling plot numbers and descriptions of the four forest stands selected on a limestone hill; the selection was based on the topographic and geomorphological features of the hill

Forest stand	Definition	Number of plots
Mixed deciduous forest stand (MDS)	A mixed deciduous forest located at the base of the limestone hill, with rock outcroppings covering $> 50\%$ of the area	28
Hill-slope stand (HSS)	A forest stand located on a long narrow ridge on the high, steep slope of the limestone hill	10
Sink-hole stand (SHS)	A forest stand established in a sink hole on the limestone hill; the sink hole was surrounded by rocky limestone terrain	15
Hill-cliff stand (HCS)	A forest stand established on a rocky cliff located at the summit of the limestone hill	11

a pit soil sampler located at the center of each 4×4-m sub-quadrat.

We measured PAR ( $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ), which is the photon fluence within the 400-700-nm spectral band of solar radiation. Photons in the PAR range drive the light reactions of the photosynthetic process in plants, and are therefore important for plant growth, biomass production, and CO<sub>2</sub> exchange between plants and the atmosphere (Olofsson et al. 2007). We measured PAR at the center and in each of the four corners of each 10×10-m plot (five points per plot) using a Spectrum 3415FX LightScout External Sensor device. Each measurement was made 1.3 m above ground level on a sunny day (08:00-10:00) in November 2015.

We determined RC (%) from the proportions of rock

and soil in each 10×10-m plot. The physical factor measurements were used to represent environmental conditions for our analyses of adult tree and/or seedling/sapling abundances in each forest stand.

### Data analyses

We compared the physical environmental conditions among forest stands (MDS, HSS, SHS, and HCS) using the Kruskal-Wallis test (Ruxton and Beauchamp 2008). We calculated the means of the sample measurements made in the 10×10-m plots and identified significant differences among the forest stands.

For each 10×10-m plot, we calculated the following biological variables: species richness, tree density (TD, stems ha<sup>-1</sup>), tree basal area (BA, m<sup>2</sup> ha<sup>-1</sup>), and the importance val-

**Table 2.** Counts of 28 species with four or more stems per plot in at least one of the mixed deciduous forest (MDS), hill-slope (HSS), sink-hole (SHS), and hill-cliff (HCS) stands

No.	Species	Code	MDS	HSS	SHS	HCS	Total
1	<i>Dracaena cochinchinensis</i>	DRCO	0	5	23	118	146
2	<i>Sreblus taxoides</i>	STTA	1	140	0	0	141
3	<i>Alphonsea elliptica</i>	ALEL	3	39	41	6	89
4	<i>Memecylon caeruleum</i>	MECA	0	5	49	0	54
5	<i>Phyllanthus mirabilis</i>	PHMI	1	0	44	0	45
6	<i>Sterculia</i> sp.	STSP	2	9	10	11	32
7	<i>Santisukia kerrii</i>	SAKE	7	7	1	16	31
8	<i>Ficus macleilandii</i>	FIMA	1	4	10	12	27
9	<i>Diospyros castanea</i>	DICA	0	0	22	2	24
10	<i>Schleichera oleosa</i>	SCOL	16	0	0	0	16
11	<i>Diospyros mollis</i>	DIMO	13	1	0	0	14
12	<i>Lannea coromandelica</i>	LACO	8	0	2	0	10
13	<i>Aglaiia edulis</i>	AGED	0	1	4	4	9
14	<i>Ficus tinctoria</i>	FITI	9	0	0	0	9
15	<i>Millettia brandisiana</i>	MIBR	9	0	0	0	9
16	<i>Phanera bracteata</i>	PHBR	8	0	0	0	8
17	<i>Sterculia lanceolata</i>	STLA	0	2	2	4	8
18	<i>Alangium salviifolium</i>	ALSA	7	0	0	0	7
19	<i>Diospyros malabarica</i>	DIMA	7	0	0	0	7
20	<i>Chukrasia tabularis</i>	CHTA	5	0	0	0	5
21	<i>Lagerstroemia villosa</i>	LAVI	5	0	0	0	5
22	<i>Melientha suavis</i>	MESU	0	0	5	0	5
23	<i>Tarennia hoensis</i>	TAHO	0	5	0	0	5
24	<i>Cordia cochinchinensis</i>	COCO	4	0	0	0	4
25	<i>Falconeria insignis</i>	FAIN	4	0	0	0	4
26	<i>Lepisanthes tetraphylla</i>	LETE	4	0	0	0	4
27	<i>Terminalia nigrovenulosa</i>	TENI	2	0	2	0	4
28	<i>Vitex canescens</i>	VICA	4	0	0	0	4

ue index (IVI). The IVI value was calculated as the sum of the relative densities and relative basal areas of each species in each stand. We used this index to identify dominant species at each site (Koonkhunthod et al. 2007; Juwarkar et al. 2014; Tripathi and Shankar 2014). The seedling/sapling ratios of species with high IVI values were used as measures of regeneration among the dominant species in each forest stand. The Shannon-Wiener index ( $H'$ ) was also calculated as a measure of tree species diversity in each forest stand (Hill 1973; Gotelli and Chao 2013).

To investigate the physical factors affecting adult tree distributions in each forest stand, we analyzed the matrices of (i) adult tree stem densities in the 10×10-m plots and (ii) the physical environmental variables using canonical correspondence analysis (CCA) ordination; the ordinations were performed with PC-ORD for Windows version 6 software (McCune and Mefford 2011). Our tree species matrix contained counts of individual tree species in the plots; species with fewer than four individuals/plot in all of the stands were excluded from the analysis (De Souza et al. 2007; Magnago et al. 2012; Nguyen et al. 2015). Thus, our matrix included 28 species (Table 2) and 64 samples. The environmental data matrix initially included RC (%), SoD (cm), SMC (%), and PAR ( $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ).

We used generalized linear mixed models (GLMMs) constructed with R v 2.11.1 software (R Core Development Team, Vienna, Austria) to determine the environmental factors affecting the regeneration of tree species. We performed a stepwise regression analysis of seedling/sapling densities;

this analysis included species density data that were adequate for statistical analyses (species with  $\geq 30$  stems across the 64 4×4-m sub-quadrats). The independent environmental variables were PAR, SDb, SMC, and RC. The forest structure response variables were BA and TD measurements obtained in each of the 10×10-m plots. We calculated a matrix of pairwise correlation coefficients across all of the environmental factors and selected those with coefficients  $< 0.7$ . Forest stand was included as a random factor, and the model with the lowest Akaike's information criterion (AIC) was selected as the best for each species (Ing et al. 2012).

## Results and Discussion

### Physical environmental factors

All of the physical environment factor variables (PAR, RC, SoD, SDb, and SMC) differed significantly among stands ( $p < 0.001$ , Table 3). The HCS had the highest PAR, followed in rank order by the HSS, MDS, and SHS. The SMC was highest in the HCS, followed in rank order by the HSS, SHS, and MDS. In contrast, SDb was highest in the MDS, lowest in the HCS, and intermediate in the HSS and SHS. Trends in SoD were similar to those of SDb. The SHS had the highest proportion of rock outcroppings, followed in rank order by the HCS, HSS, and MDS (Table 3). Among environmental factors, light and soil conditions most strongly affect species diversity, woody vegetation structure, and tree regeneration in a given local-

**Table 3.** Physical factor measures in each forest stand type: photosynthetically active radiation (PAR,  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) at 1.3 m above the ground, proportion of rock outcroppings (RC, %), soil depth (SoD, cm), soil bulk density (SDb,  $\text{g cm}^{-3}$ ), and soil moisture content (SMC, %)

Environmental factors	Forest stand				p value
	MDS	HSS	SHS	HCS	
PAR	77.60 <sup>bc</sup> ± 61.95	205.15 <sup>ab</sup> ± 229.82	29.60 <sup>c</sup> ± 25.71	275.73 <sup>a</sup> ± 161.33	< 0.001
RC	71.86 <sup>b</sup> ± 16.27	85.53 <sup>bc</sup> ± 9.30	92.60 <sup>a</sup> ± 2.84	89.18 <sup>bc</sup> ± 7.00	< 0.001
SoD	60 <sup>a</sup> ± 11.48	39 <sup>ab</sup> ± 9.72	30 <sup>ab</sup> ± 5.76	17 <sup>c</sup> ± 3.29	< 0.001
SDb	0.57 <sup>a</sup> ± 0.20	0.38 <sup>ab</sup> ± 0.12	0.33 <sup>ab</sup> ± 0.13	0.21 <sup>b</sup> ± 0.42	< 0.001
SMC	51.21 <sup>c</sup> ± 21.46	72.80 <sup>b</sup> ± 47.50	65.45 <sup>bc</sup> ± 19.75	83.49 <sup>a</sup> ± 34.89	< 0.001

Values are mean ± SD.

The forest stand types on a limestone hill in northern Thailand were mixed deciduous forest stand (MDS), hill-slope stand (HSS), sink-hole stand (SHS), and hill-cliff stand (HCS). Different lower case letters in rows indicate significantly different means (Kruskal-Wallis test,  $p < 0.05$ ,  $n = 64$ ).

ity (Zhang et al. 2012; Asanok et al. 2013). The distribution of vegetation patterns is generally controlled by physical factors, such as light and soil conditions (McLaren and McDonald 2003; Guarino and Scariot 2012). Rocky outcrops, also referred to as edaphic islands (Williamson and Balkwill 2015), support species with physiological requirements that differ from those of species living in the surrounding landscape (Speziale and Ezcurra 2012).

**Species composition**

We assembled data on 776 tree stems belonging to 76 species 56 genera and 36 families (data not provided). The MDS had highest species richness and species diversity index, but its basal area and stems density values were the lowest among the stands (Table 4). The HSS had an intermediate species richness value and a low diversity index. Although the stem density at this site was highest among stands, its basal area was low, indicating that the site was populated by a large number of small trees. All of the ecological measures for the SHS had intermediate values. Species richness at the site was similar to that at the HSS, but the SHS had a higher diversity index. The HCS had the lowest species richness and diversity index values, but had the highest total BA; TD at this site was also high, indicating that large trees of a few species were dominant in the stand (Table 4). The dominant five species ranked by IVI values are listed in Table 5. *Dracaena cochinchinensis* and *Alphonsea elliptica* were the first and second most dominant species at the HCS and HSS, respectively. Both species appeared at the HSS, SHS, and HCS. The domi-

nant species at the MDS contrasted with those at the other stands (Table 5). The species diversity of tropical forests growing on limestone outcrops is low compared with that of a range of other forest types (Speziale and Ezcurra 2012). The low diversity on this carbonate substratum is likely produced by the extremely harsh microenvironments in sites where large limestone rocks are abundant, protrude from the soil, and cover the ground surface. The combination of this landform structure and steep topography produces dry habitats, shallow soils, and strong seasonality. Some species are restricted to this rocky environment, while others may also occur in more mesic environments, and even in other vegetation types (Felfili et al. 2007).

**Table 4.** Ecological characteristics of four forest stands on a limestone hill in northern Thailand

Ecological characteristics	Forest stand			
	MDS	HSS	SHS	HCS
1. Number of species	49	13	13	9
2. Number of genera	36	11	12	7
3. Number of families	26	9	11	6
4. Species diversity index ( $H'$ )	3.52	1.31	2.5	1.21
5. Basal area ( $m^2 ha^{-1}$ )	10.79	14.45	11.72	21.11
6. Density (stems $ha^{-1}$ )	597	2,200	1,434	1,582

The forest stand types were mixed deciduous forest (MDS), hill slope (HSS), sink hole (SHS), and hill cliff (HCS).

**Table 5.** The five dominant species in each stand ranked by the importance value index [IVI, sum of the relative densities (RD) and relative basal areas (RDo)] of each species

Forest stand /Ranking	Species	RD	RDo	IVI
<b>Mixed deciduous forest (MDS)</b>				
1	<i>Schleichera oleosa</i>	9.58	12.52	22.10
2	<i>Diospyros mollis</i>	7.78	9.25	17.04
3	<i>Millettia brandisiana</i>	5.39	6.32	11.71
4	<i>Ficus tinctoria</i>	4.79	6.00	10.79
5	<i>Phanera bracteata</i>	4.79	3.78	8.57
<b>Hill-slope stand (HSS)</b>				
1	<i>Streblus taxoides</i>	63.64	66.99	130.62
2	<i>Alphonsea elliptica</i>	17.73	10.30	28.03
3	<i>Sterculia</i> sp	4.09	5.59	9.68
4	<i>Santisukia kerrii</i>	3.18	6.39	9.57
5	<i>Dracaena cochinchinensis</i>	2.27	4.70	6.97
<b>Sink-hole stand (SHS)</b>				
1	<i>Memecylon caeruleum</i>	22.79	16.09	38.88
2	<i>Phyllanthus mirabilis</i>	20.47	16.93	37.40
3	<i>Alphonsea elliptica</i>	19.07	16.78	35.85
4	<i>Diospyros castanea</i>	10.23	20.71	30.95
5	<i>Dracaena cochinchinensis</i>	10.70	10.26	20.95
<b>Hill-cliff stand (HCS)</b>				
1	<i>Dracaena cochinchinensis</i>	67.82	54.85	122.66
2	<i>Santisukia kerrii</i>	9.20	11.02	20.22
3	<i>Sterculia</i> sp.	6.32	6.14	12.46
4	<i>Ficus macleilandii</i>	6.90	4.93	11.83
5	<i>Alphonsea elliptica</i>	3.45	3.29	6.74

The forest stand types were mixed deciduous forest (MDS), hill slope (HSS), sink hole (SHS), and hill cliff (HCS).

*Physical factors influencing tree species composition*

The CCA ordination identified strong correlations between species abundance and the environmental variables measured. The eigenvalues for axis 1 and axis 2 were very high and accounted for substantial proportions of the variation in species composition (Table 6). Therefore, these axes were good predictors of species distribution and abundance. However, the eigenvalue for axis 3 was low, and the proportions of variation explained by this axis were also small. Axis 1 was the most powerful predictor of changes in species composition. The species-environment correlations between (i) the sample scores for the axis derived from the species data and (ii) the sample scores that were linear combinations of the environmental variables for the first two axes of the CCA were high (significant Pearson and Kendall correlation coefficients; Table 6). Thus, the species-environment

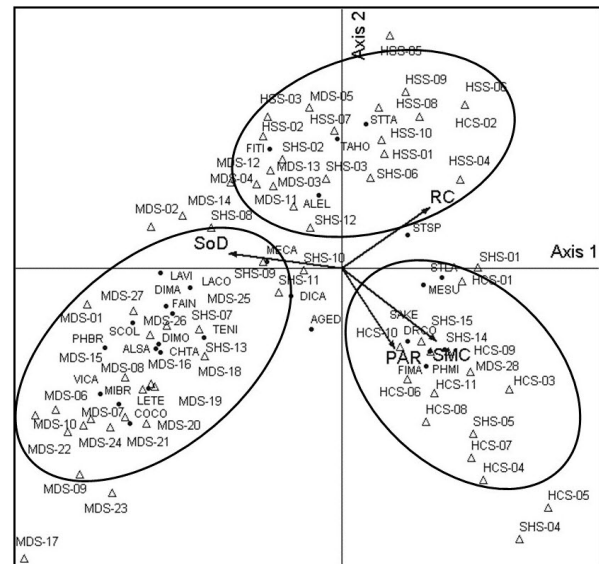
relationship was well explained by the CCA. Correlations between the environmental variables and the CCA axes are listed in Table 7. RC and SMC correlated positively with the first axis, but SoD correlated negatively with it. PAR correlated negatively with the second axis. Only SoD was significantly negatively correlated with SMC (Table 7).

The CCA ordination plot (Fig. 2) graphically depicts the relationship between the distribution of abundant tree species and environmental factor variables across the four for-

**Table 6.** Eigenvalues and the proportions of variance explained by the species/species-environment correlations on the three canonical correspondence analysis (CCA) axes used to examine the distribution of tree species in four forest stands on a limestone hill in northern Thailand

CCA results	Axis1	Axis2	Axis3
<b>Eigenvalue</b>	0.601	0.492	0.192
<b>Variance in species data</b>			
Percentage of variance explained	20.3	11.2	8.1
Cumulative percentage of variance explained	18.1	11.1	13
<b>Species-Environment Correlations</b>			
Pearson correlation	0.856	0.817	0.615
Kendall (rank order) correlation	0.675	0.563	0.445

All of the correlation coefficients are significant ( $p < 0.05$ ).



**Fig. 2.** Canonical correspondence analysis (CCA) ordination plot of physical environmental variables (soil depth [SoD], soil moisture content [SMC], photosynthetically active radiation [PAR], and proportion of rocky outcroppings [RC]) affecting the dominant tree species distribution (●) in four forest stands growing on a limestone hill (△): mixed deciduous forest stand (MDS), hill-slope stand (HSS), sink-hole stand (SHS), and hill-cliff stand (HCS). The species codes are listed in Table 2.

**Table 7.** Correlation matrix (Spearman rank order correlation coefficients) for the relationships between the environmental factor variables (proportion of rocky outcroppings [RC], photosynthetically active radiation [PAR], soil depth [SoD], soil moisture content [SMC]) and the three axes of the canonical correspondence analysis of four forest stands growing on a limestone hill in northern Thailand

Factor	Axis1	Axis2	Axis3	RC	PAR	SoD	SMC
RC	0.714*	0.461	0.486	1			
PAR	0.433	-0.615*	0.09	0.238	1		
SoD	-0.932**	0.112	0.152	-0.518	-0.424	1	
SMC	0.772*	-0.558	0.152	0.448	-0.543	-0.715*	1

\* $p < 0.05$ , \*\* $p < 0.01$ .



est stands (Fig. 2). The plot clearly shows the distribution patterns of the dominant species within the forest stands. The SoD trend affected adult tree abundance in the MDS. Several abundant species in this stand, e.g., *Lagerstroemia villosa* (LAVI), *Lanmea coromandelica* (LACO), *Diospyros malabarica* (DIMA), and *Falconeria insignis* (FAIN), were associated strongly with deep soil. This suggests that these species have rooting depths controlled by soil depth (de Graaff et al. 2014). Roots provide resources for plant growth by accessing water and mineral nutrients (Hashemian et al. 2015). Limestone rock outcrops extend up to the vegetation/soil interface, and the bedrock makes direct contact with plant roots and the soil; little soil occurs in the main body of limestone (Crowther 1989; Nie et al. 2012). The structure of plant root systems, including root diameters and depths of penetration, has direct effects on the soil aggregation state (Han et al. 2015). Roots of smaller diameter turn over faster than thicker roots; small-root mortality decreases as soil depth increase (Chimento and Amaducci 2015). Due to the thin soil layer, plants growing on karst landforms usually have extensive root systems (Huang et al. 2011).

Adult tree abundances in the HSS and SHS were related to RC. The abundances of *Sterculia* sp. (STSP), *Sterculia lanceolata* (STLA), *Melientha suavis* (MESU), and *Streblus taxoides* (STTA) were limited by this factor. The species in these two stands were likely high tolerant of extreme environmental stress. The rocky outcrops provided islands of suitable habitat within a matrix of unsuitable habitat, such as forested land. These islands and their unique environment provide habitat for specialist plant species (Csergo et al. 2014; Gao et al. 2015). Rocky outcrops are often referred to as edaphic islands due to their sharp boundaries and patchy distribution (Williamson and Balkwill 2015). Vegetation cover on thin soils overlying limestone is extremely vulnerable to soil degradation, water loss, and erosion (Zhang et al. 2011; Thomas et al. 2016). Soils derived from serpentine rocks are regarded as harsh environments for plants due to their low nutrient levels and poor water-retention capacity (Chen et al. 2009; Zhou et al. 2015).

PAR and SMC trends positively influenced tree abundances in the HCS and SHS. These two factors were linked strongly to the abundances of the dominant species at the HCS (*Dracaena cochinchinensis* [DRCO], *Ficus macleilandii* [FIMA], and *Santisukia kerrii* [SAKE]) and SHS

(*Phyllanthus mirabilis* [PHMI]). The abundances of these trees were related strongly to bright light, suggesting that they are light-demanding, fast-growing species (Engone Obiang et al. 2014). Their populations were likely in conditions of demographic imbalance, with past peaks of recruitment and current deficits of regeneration (Zhang et al. 2013). Light availability interacts directly with the canopy structure, which is determined by the vertical profile of the vegetation and the foliage traits of local species (Flores et al. 2006). Light quality and quantity are heterogeneous in time and space at various scales in dense vegetation (Kelly et al. 2015). These species are also related strongly to humid soil. Soil moisture plays an important role in the ecological processes of the surface soil in the epikarst (Bakalowicz 2005; Aquilina et al. 2006; Zhang et al. 2011). The epikarst has rich, non-uniform fracture and porosity characteristics that produce high hydraulic conductivity, which in turn confers particular hydrological properties to karst aquifers (Bakalowicz 2013; Hu et al. 2015). The characteristics of rocky cliffs and the diffuse flow systems of karst aquifers contribute to the rapid penetration of rainwater through the thin soil layer and connected fissures in the bedrock layer into the groundwater at such sites (Butscher and Huggenberger 2009), which are subject to frequent flood/drought events (Nie et al. 2012). An understanding of the hill-cliff ecosystem requires information on soil and epikarst water and on its contribution to the vegetation system (Bakalowicz 2005). The encroachment of woody plants into semiarid karst ecosystems is likely to increase the contribution of bare-soil evaporation relative to evapotranspiration, as most water taken up by plants is absorbed by roots (Huang et al. 2011).

Thus, variability in physical environmental factors determined the species composition of the forest growing on the limestone hill we studied. These factors differed among the four forest stands.

#### *Environmental factors affecting tree regeneration*

We analyzed 10 species with seedling/sapling densities that were adequate for statistical analyses ( $\geq 30$  stems from each species): three, two, three, and two species in the MDS, HSS, SHS, and HCS, respectively (Table 8). The regeneration of seedlings/saplings of the tree species in our study area was affected by many factors and varied among species. Many distribution patterns were associated with

**Table 8.** Generalized linear mixed model (GLMM) analyses of the relationships of the abundances of the dominant species ( $\geq 30$  stems for each species) in each forest stand with (i) forest structure and (ii) physical factors

Forest stand/Species	Forest structure			Physical environment		
	TD	BA	RC	PAR	SDB	SMC
<b>Mixed deciduous forest stand (MDS)</b>						
1. <i>Millettia brandisiana</i>	0.173*	10.969*	0.075***	0.046***	6.561***	
2. <i>Schleichera oleosa</i>	0.203***		0.085***			
3. <i>Diospyros mollis</i>	0.159***			0.009*		
<b>Hill-slope stand (HSS)</b>						
1. <i>Alphonsea elliptica</i>	0.065***	4.959*	0.072***	2.511*	0.019***	
2. <i>Streblus taxoides</i>	0.068**	19.118***		0.018***	3.247**	
<b>Sink-hole stand (SHS)</b>						
1. <i>Memecylon caeruleum</i>		33.761***	0.117***		37.948***	0.074***
2. <i>Diospyros castanea</i>	0.220**					0.024***
3. <i>Phyllanthus mirabilis</i>		1.157**	1.025**	1.081**	5.499***	
<b>Hill-cliff stand (HCS)</b>						
1. <i>Ficus macleilandii</i>		1.472***	5.992***	2.042*		
2. <i>Dracaena cochinchinensis</i>			0.053*	0.078*	8.037***	

\* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

The values in the cells are model regression coefficients; only significant coefficients selected to minimize the Akaike's information criterion (AIC) are included. TD, BA, RC, PAR, SDB, and SMC indicate tree density (stems  $\text{ha}^{-1}$ ), basal area ( $\text{m}^2 \text{ha}^{-1}$ ), proportion of rocky outcropping (%), photosynthetically active radiation ( $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ), soil bulk density ( $\text{g cm}^{-3}$ ), and soil moisture content (%), respectively.

physical factors (RC, PAR, SDB, and SMC) and factors related to forest structure (BA and TD). The physical environmental factors influenced the regeneration of more species than did factors related to forest structure. Both types of factor had effects on regeneration. Factors related to forest structure were more important for the dominant species in the MDS and HSS than for the dominant species in the SHS and HCS (Table 8). The magnitude of the effect of each factor on establishment ability was species dependent in each forest stand. The regeneration of seedlings/saplings in the tropics is related to forest type, stand developmental stage (which may be represented by BA and TD), and a range of environmental factors, such as soil moisture and light (Asanok et al. 2013).

The regeneration of the three species at the MDS included in the analysis was affected by factors related to both forest structure and the physical environment. TD had significant, negative effects on all three species, and only one species was affected by BA (significant positive effect). The regeneration values of two of the three MDS species were affected negatively by RC and/or PAR. Only one species was affected positively by SDB (Table 8). The regeneration

of *Millettia brandisiana* was influenced positively or negatively by both forest structure factors and most of the physical factors (RC, PAR, and SDB). The regeneration levels of *Schleichera oleosa* and *Diospyros mollis* were determined by one forest structure factor and one physical factor each. The regeneration of the species dominating the MDS tended to be influenced by forest structure factors (negative relationship with TD) and physical factors. The emergent species of mixed deciduous forests have closed canopies in the growing (wet) season and open canopies in the dry season; this seasonal variation influences seedling dormancy and makes establishment under the canopy difficult (Marod et al. 1999). Areas with low tree stem densities have canopy breaks through which direct sunlight may reach the ground surface and promote seedling establishment (De Govenain et al. 2007; Ediriweera et al. 2008). The survival of juveniles varies by canopy openness; it is elevated in sites where more sunlight is available (Dupuy and Chazdon 2008).

The regeneration levels of the two species from the HSS included in the analysis were influenced significantly by most of the forest structure and physical environmental

factors. Regeneration levels of both species were influenced significantly by TD and BA (positively and negatively, respectively). PAR and SDb had significant negative effects on the regeneration levels of both species (Table 8). RC had no significant influence on the regeneration of *S. taxoides*, but this factor positively affected the regeneration of *Alphonsea elliptica*. All other factors influenced the regeneration of both species (Table 8). The regeneration of the dominant species in the HSS tended to be influenced by dense, small-stemmed trees under low light, and by soft soil texture. Restricted tree regeneration in this site was determined by most environmental factors. The densely packed stems of adult trees and the shade cast by their canopy strongly reduced illumination. Species growing at such sites are likely shade demanding, rather than shade tolerant (Yang et al. 2011). The low light regime of the forest understory favors seedling growth in more shade-tolerant species (Palomaki et al. 2006; Read et al. 2015). A steep light gradient without canopy gaps or a moisture gradient across a uniform topography may affect juvenile survival (Aiba and Nakashizuka 2007). Soft soil texture likely regulates both seedling establishment and survival (Uselman et al. 2015).

The regeneration levels of the three species from the SHS included in the analysis were influenced more by physical environmental than by forest structure factors. Only one forest structure factor had a significant effect. The effects of the physical and forest structure factors varied among the three species (Table 8). The regeneration values of two of the three SHS species were affected negatively by BA. Only one species was affected positively by TD (Table 8). SMC had significant positive effects on the regeneration levels of *Memecylon caeruleum* and *Diospyros castanea*, which varied among other physical factor levels and factors related to forest structure. On the steep slopes of limestone hills, rainwater penetrates rapidly through the thin soil layer and connected fissures in the bedrock layer to layers below the rooting zone (Butscher and Huggenberger 2009). However, dense bedrock in karst landforms enhances the surface soil moisture in the epikarst, thereby contributing positively to the colonization process of tree species and vegetation development in the area (Li et al. 2014). Soil moisture likely regulates both seedling establishment and survival, and is a key factor in the initial process of seedling recruitment (Khurana and Singh 2001; McLaren and McDonald 2003).

Trejo-torres and Ackerman (2002) indicated that the soil humidity regime, which is related to topography, was more important than geography in promoting floristic links among limestone vegetation communities of the Caribbean. Dry communities on single islands had stronger floristic affinities with dry communities on other islands than with more humid vegetation on the same islands (Felfili et al. 2007). The regeneration values of *Phyllanthus mirabilis*, one of three dominant species in the SHS, had significant positive relationships with RC and PAR, but were related negatively to SDb (Table 8). This suggests that this species established well in limestone outcroppings, illuminated sites, and thin soil sites. Tree species that regenerate on rocky outcrops usually have specialized root systems that are able to thread through the rocky substratum and extract nutrients from the thin soil/humus layer (Denk et al. 2014; Duarte et al. 2015). The roots commonly grow deep into the rock fissures of the epikarst substratum (Huang et al. 2011). This species also occurred at illuminated sites, suggesting that it requires high light conditions and has rapid growth rates (Carreño-Rocabado et al. 2012; Lusk et al. 2013).

The regeneration levels of the two species from the HCS included in the analysis were influenced more by physical environmental than by forest structure factors (Table 8). The regeneration levels of both species included in the analysis had significant positive relationships with RC and PAR. The regeneration of *Ficus macleilandii* was determined by BA, RC, and PAR (positive or negative effects). The regeneration value of *Dracaena cochinchinensis* was affected positively by RC and PAR, but negatively by SDb (Table 8). Physical factors, especially RC and PAR, had greater significant positive effects on the regeneration of the dominant species at the HCS than did factors related to forest structure. This site was relatively dry due to the very shallow soils and relatively high summer temperatures caused by intense solar radiation, which exceeded the levels in surrounding areas. The cliffs are protected as special habitats, but access is allowed to interesting viewpoints at the tops of selected promontories, and rock climbing is allowed in some places (Wezel 2007). The dominant species had strong colonization capabilities under the extreme conditions prevailing at the HCS. The biological assemblages in such cliff environments have limited ecological stability; they readily lose community organization when perturbed by external

agents (Clark and Hessler 2015). Tree species that regenerate on rocky cliffs, such as *Ficus* spp. and *Dracaena* spp., usually have specialized root systems that are able to thread through the rocky substratum and extract nutrients from the thin soil/humus layer (Denk et al. 2014; Duarte et al. 2015). The roots commonly grow deep into the rock fissures of the epikarst substratum (Huang et al. 2011). A classification system is required for tree species based on the degree to which their roots alter nutrient availability and soil organic matter decomposition (Yin et al. 2014).

Among species from the HCS, PAR had significant positive effects on regeneration. Establishment occurred in well-illuminated sites, indicating that the species likely required high light conditions and had rapid growth rates (Carreño-Rocabado et al. 2012; Lusk et al. 2013). Light is the main factor that limits the growth and survival of many species, and variation in light availability affects the regeneration pattern at forest sites (Lusk et al. 2011; Lusk et al. 2013). The heterogeneity of light distribution changes with differences in light availability during the day and among seasons (Dlugos et al. 2015; Tarvainen et al. 2015). Changes in the availability of sunlight resulting from natural or anthropogenic clearances play key roles in the initial development and survival of trees in tropical rainforests (Seidler and Bawa 2000; Edwards et al. 2014; Mao et al. 2014).

#### *Implications for management of the forest cover on limestone hills*

We demonstrated that light, soil conditions, and the extent of rocky outcroppings determined species composition in different forest stands distributed over a limestone hill. These factors variably influenced regeneration among tree species. We found that the regeneration of shade-tolerant species in the HSS, such as *A. elliptica* and *S. taxoides*, was influenced by many factors, suggesting that these species are difficult to replace through natural regeneration processes and that they are sensitive to disturbances. Light-demanding species, such as *F. macleilandii* and *D. cochinchinensis* at the HCS, and *P. mirabilis* at the SHS, grew rapidly (Lusk et al. 2013; De Vasconcellos et al. 2014; Schönbeck et al. 2015). They established well under high light conditions and in the limestone hill environment, where large rocky outcroppings, shallow soils, and relatively high

summer temperatures created by intense solar radiation were prevalent. They are likely good candidate species for the restoration of disused limestone quarries. The prevalence of bare land, rocky outcroppings, and high light would provide suitable habitat for these light-demanding species, especially the relict taxa that are largely endemic to these environments. Improved knowledge of the physical and biological factors of limestone hill environments will help to optimize the use of available funds for restoration and conservation of the special biological communities on karst landforms.

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