Species Composition and Spatial Distribution of Dominant Trees in the Forest Ecotone of a Mountain Ecosystem, Northern Thailand

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ABSTRACT

Plants' ecological niches are important to study, particularly for applying the knowledge to restoration programs. This study clarified the relationships of tree species composition and spatial distribution to environmental factors in a mountain ecosystem. A 3 ha permanent plot was established across the forest ecotone at Doi Suthep-Pui National Park, Chiang Mai Province, Thailand. The spatial distributions of the 20 dominant tree species were analyzed using a generalized linear model (GLM) combined with geographic information system (GIS) techniques. High species diversity was found, including 165 species representing 118 genera and 59 families. Elevation strongly influenced tree distribution, which could be divided into three groups: low-altitude species in deciduous dipterocarp forest (DDF), high-altitude species in lower montane forest (LMF) and coexisting DDF and LMF species. The GLM analysis revealed that soil texture, which ranged from sandy to clayey, influenced tree distribution. The results suggest that restoration programs should select suitable species based on their niches.

1. INTRODUCTION

Environmental factors control plant regeneration processes, including plant establishment, reproduction and distribution (Guisan and Zimmermann, 2000; Turner, 2001). Many researchers have defined two types of ecological gradient affecting plant distributions. The first includes direct factors that govern physiological processes (nutrients and climatic factors) and the second comprises indirect factors (such as topographic factors, habitat type and geology) that have no direct physiological relevance to species performance or survival strategies (Guisan et al., 1999; Austin, 2002; Bacaro et al., 2008). Indirect factors can be measured in the field and are often used because they are correlated with the observed tree spatial distributions.

Studies based on long-term ecological research have reported that large permanent plots can be used to predict plant distribution (Bunyavejchewin et al.,

2003; Valencia et al., 2004). Such plots not only provide information about the forest dynamics but can also be used to study species distribution (Dallmeier, 1992; Condit et al., 1999). Statistical approaches such as canonical correspondence analysis or logistic regression are used to analyze species distribution as a function of environmental factors (Guisan and Zimmermann, 2000; Lan et al., 2011; Asanok et al., 2017). For instance, the dominant species is determined based on the total number of trees (Li et al., 2009; Lan et al., 2011; Asanok et al., 2017; Walthert and Meier, 2017) and quantitative values such as the importance value index (Campos et al., 2000) and total basal area (Homeier et al., 2010; Höfle et al., 2014) are used as dependent variables. The results reflect the appearance of a niche or the suitability of a species in a particular area (Lan et al., 2011). A tree distribution map often needs to be coupled with geographic information systems (GIS), which have become popular in recent forest ecology

studies (Caillaud et al., 2010; Walthert and Meier, 2017), particularly in tropical forests, where high plant species diversity is associated with environmental conditions (Condit et al., 1999; Harms et al., 2001; Lan et al., 2011). Although studies have covered almost all forest types, few have documented the forest ecotone (FE) between lowland and upland forest along altitudinal gradients.

The mountain ecosystem in the upper reaches of the Ping River at Doi Suthep-Pui, Chiang Mai Province, Northern Thailand, is an important area for plant conservation (Fukushima et al., 2008). The environmental factors responsible for plant distribution can vary in the FE located between lowland and upland forest (Tang and Ohsawa, 1997), especially the topographic and climatic factors (Martin et al., 2007). In addition, soil properties in this area also vary due to the soil parent material, which is related to topographical and geological gradients (Rhodes et al., 2005; Weill and Munkholm, 2015) or vegetation cover (Ueda et al., 2017). Deciduous and evergreen species coexist in the FE located at altitudes between deciduous dipterocarp forest (DDF) and lower montane forest (LMF) (Marod et al., 2015). The plants in this FE are very sensitive to environmental changes (Odum, 1959; Frelich, 2002; Marchand and Houle, 2006), especially increases in temperature and drought (Ameztegui and Coll, 2011). Marod et al. (2015) reported that deciduous species, which mostly occupy the DDF and are highly adapted to drought, can occur at higher altitudes. By contrast, evergreen species are susceptible to environmental changes. Therefore, rapid environmental changes may influence their regeneration and distribution (Ruiz et al., 2008). However, little long-term ecological research has examined the adaptation and migration of tree species in a LMF in relation to changes in environmental variables. Consequently, this study clarified the species composition and examined correlations between spatial tree distribution and environmental factors (topographic and soil properties) in a 3 ha permanent plot in Doi Suthep-Pui National Park, Northern Thailand. The results of this research should support natural resources management, especially the selection of trees for restoration programs in mountain ecosystems.

2. METHODOLOGY
2.1 Study area

The study area in Doi Suthep-Pui National Park is located at latitude 18° 43'3" - 19° 7'30" N and longitude 98° 48'20" - 98° 57'10" E in Chiang Mai Province, Thailand (Figure 1). About 85% of the land cover is forest and 15% consists of agricultural land and urban areas (Charnsungnern and Tantanasarit, 2017). The area is characterized by a subtropical climate, with a long dry season alternating with a short, wet season; the annual precipitation is 1,139 mm and mean temperature is 24°C. The altitude ranges from 312 to 1,656 m. a. s. l. Geologically, the area contains steep hills and valleys consisting of high-grade metamorphic complex rocks and sandstone (Rhodes et al., 2005). The soil texture varies along altitudinal gradients from sandy soil and sandy clay loam at lower elevations to mostly sandy clay loam and clay soil at higher elevations (above 1,000 m.a.s.l.) (Marod et al., 2014). Complex environmental factors are found in the Doi Suthep-Pui mountain ecosystem, especially elevation gradients, which influence the distribution of forest types; these can be classified into deciduous forest (mixed deciduous forest and deciduous dipterocarp forest), mostly found in low elevations <1,000 m.a.s.l. and evergreen forest (lower montane forest and pine forest), mostly found at higher elevations (≥1,000 m.a.s.l.) (Marod et al., 2014).

2.2 Plot establishment and investigation

In 2016, a 3 ha permanent transect (50×600 m²) was established in the FE between DDF and LMF (latitude 18°47'4"N, longitude 98°54'58"E), where the elevation ranged from 900 to 1,100 m.a.s.l. (Figure 1). According to Hermhuk (2014) and Marod et al. (2015), three forest zones were identified based on stand clustering and canonical correspondence analysis (CCA) related to their elevation: a DDF zone from 900-940 m. a. s. l., a FE zone from 941-980 m. a. s. l. and a LMF zone above 980 m. a. s. l. The transect plot was divided into 300 subplots (10×10 m²). Trees with a diameter at breast height (DBH) larger than 1 cm were tagged; then, DBH was measured, positions were recorded as (x, y) coordinates, and the species were identified based on Smitinand (2014).
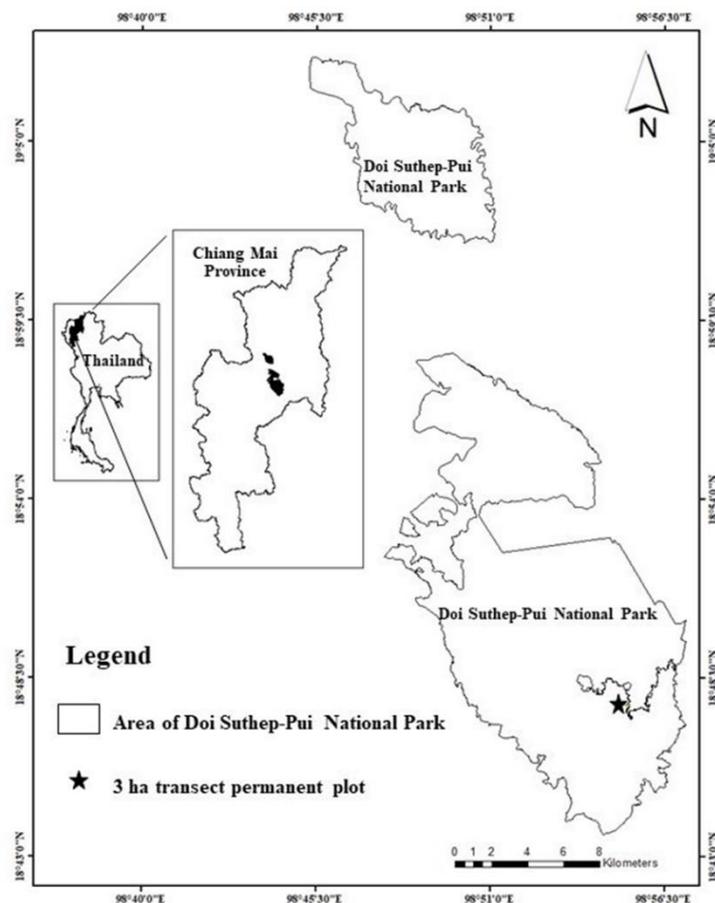
Figure 1. The location of the study site and permanent plot in Doi Suthep-Pui National Park, Chiang Mai Province, Thailand.

2.3 Environmental data collection

2.3.1 Topographic factors

The topographic factors (elevation, slope and aspect) of the subplots were characterized using a digital elevation model (DEM) developed by the Geo-Informatics and Space Technology Development Agency (GISTDA), Bangkok, Thailand, with a raster surface of 30 m resolution.

2.3.2 Soil properties

Samples were collected from the surface soil 0-15 cm depths in 20×50 m^2 subplots in the 3 ha permanent plot. In each subplot, 36 samples were collected for soil property analysis. The physical and chemical properties of the soil were analyzed at the Laboratory of Soil Science, Faculty of Agriculture, Kasetsart University, using standard methods (National Soil Survey Center, 1996). The soil texture (percentages of sand, silt and clay), soil moisture content (SMC), soil pH and amount of organic matter were determined to examine the trees' spatial distribution as a function of these properties.

2.4 Data analysis

2.4.1 Forest structure and species composition

The forest structure and species composition are described in terms of the number of individual stems, the basal area (BA) and the dominant species (Berhanu et al., 2017). The dominant species were defined using the relative frequency (RF), relative dominance (RDo), relative density (RD) and importance value index (IVI), which were estimated following Whittaker (1975) for all tree species with DBH$\geq$4.5 cm.

2.4.2 Environmental factors

Topographic factors in this study were derived by resampling the DEM to 10 m resolution using the bilinear interpolation technique to create a more continuous surface corresponding to the spatial resolution of the field data. Estimates of topographic factors were exported for each sample. The mean elevation of a subplot was defined as the mean of the elevations of its four corners (Tarboton, 1997) and the steepest slope was the mean angular deviation from

the horizontal for each of the four triangular planes formed by connecting three of the corners of a subplot (Harms et al., 2001). Aspect in degrees relative to north was calculated using the formula:

$$\text{Aspect} = 180 - \arctan(f_y/f_x) \times (180/3.14) + 90(f_x/|f_x|),$$

where f_x and f_y are the changes in elevation when going from east to west and from north to south, respectively.

The kriging interpolation technique was use for mapping of the topographic factors and soil properties. All maps were analyzed using ArcMap ver. 10.1 (Jirakajohnkool, 2009; Walthert and Meier, 2017).

The spatial distribution of tree species was considered to identify the top 20 dominant species based on IVI, combining deciduous and evergreen species. A GLM technique was applied to determine the relationships of environmental factors with tree species distribution. The dependent variable in each plot was the total basal area of each species, and the independent variables were the environmental factors. Independent variables, selected by calculating Pearson's correlation coefficients ($r \geq 0.80$ or $r \leq -0.80$) (Lan et al., 2011; Dormann et al., 2013), included nine factors: elevation, slope, aspect, soil texture (%sand, %silt and %clay), soil pH, organic matter and soil moisture content. The model omitted three factors, %silt, organic matter (SOM) and soil moisture content (SMC), because these factors were highly dependent on other selected environmental features. Consequently, six factors were used for modeling the tree spatial distributions. The model with the lowest Akaike information criterion (AIC) was chosen using the MASS package (Ripley et al., 2017) available in R version 3.2.2 according to the equation.

$$Y(I) = <-\text{glm (total BA (species I)} \sim x1 + x2 + \dots$$
$$x6, \text{family=gaussian (link=identity))},$$

where x1-x6 are independent variables: x1 is elevation, x2 is aspect, x3 is slope, x4 is %sand, x5 is %clay and x6 is soil pH.

3. RESULTS AND DISCUSSION
3.1 Forest structure and species composition

Within the 3 ha permanent plot, there were 11,384 tagged trees (DBH $\geq$ 1 cm) across the FE, including DDF and LMF, representing 212 species,

140 genera and 67 families. Considering the trees with DBH $\geq$ 4.5 cm, there were 165 species, 118 genera and 59 families. The tree density was 1,190 individual/ha and the basal area was 29.56 m^2/ha. The dominant families based on species number were Fagaceae, Phyllanthaceae and Fabaceae, with 15, 12 and 10 species, respectively. These dominant families also had high total BA (m^2), particularly Fagaceae and Dipterocarpaceae (Figure 2 (A)). The Fagaceae, Rubiaceae and Lauraceae had high total stem densities in the FE zone (Figure 2 (B)). *Quercus brandisiana* (32.34%) was the dominant species (based on IVI), followed by *Dipterocarpus obtusifolius* (17.73%), *Wendlandia paniculata* (17.34%), *Litsea martabanica* (17.05%), *Schima wallichii* (15.86%), *Lithocarpus garrettianus* (12.20%), *Castanopsis acuminatissima* (11.40%), *Castanopsis tribuloides* (8.90%), *Shorea obtusa* (7.96%), *Dipterocarpus tuberculatus* (6.96%), *Myrsine seguinii* (6.88%), *Tarennoidea wallichii* (6.54%), *Syzygium claviflorum* (5.24%), *Rothmannia sootepensis* (5.10%), *Persea gamblei* (5.08%), *Aporosa nigricans* (4.61%), *Lithocarpus dealbatus* (4.56%), *Scleropyrum pentandrum* (4.32%), *Aporosa villosa* (4.14%) and *Anneslea fragrans* (3.88%). These include both deciduous and evergreen species, with some species being distributed in all three zones, i.e., the DDF, FE and LMF zones, such as *Quercus brandisiana*, *Dipterocarpus obtusifolius, Schima wallichii, Wendlandia paniculata, Litsea martabanica* and *Anneslea fragrans* (Table 1). This indicates a high degree of success in their establishment. The species in Fagaceae, the dominant family, showed a different distribution across DDF to LMF and could be divided into two groups. The first group, consisting of *Castanopsis acuminatissima*, *Castanopsis tribuloides* and *Lithocarpus garrettianus,* was distributed mostly in the montane forest, with cooler climate conditions (Hara et al., 2002; Khamyong et al., 2003; Marod et al., 2014). The second group, consisting of *Quercus brandisiana* and *Lithocarpus dealbatus*, was found in the deciduous forest, particularly the DDF undergoing high drought conditions (Hermhuk, 2014; Marod et al., 2015). By contrast, the deciduous species in the Dipterocarpaceae (*Dipterocarpus tuberculatus* and *Shorea obtusa*) mostly occupied the DDF, with only *Dipterocarpus obtusifolius* found at elevations higher than 940 m.a.s.l., where it coexisted with evergreen species, albeit only in a narrow zone where environmental factors were similar to those of the FE (Ohsawa, 1993; Ashton, 2003).

Table 1. GLM analysis of the relationships between species distribution and environmental factors for the top 20 dominant species in the permanent plot. The values in the various columns are model regression coefficients. The coefficients with the lowest AIC were selected.

Species	Family	Type	Zonation	Environmental factors					
				Elevation	Aspect	Slope	%Sand	%Clay	Soil pH
Dipterocarpus obtusifolius	Dipterocarpaceae	D	All zones	-0.01***			2.16**	-1.56**	
Lithocarpus dealbatus	Fagaceae	D	DDF-FE	-1.24**		-1.61*		-3.37***	-1.22*
Aporosa nigricans	Phyllanthaceae	D	DDF-FE	-1.04*	2.23			-5.35*	-9.69**
Aporosa villosa	Phyllanthaceae	D	DDF-FE	-1.94**		5.57**	4.67*	-1.11*	
Dipterocarpus tuberculatus	Dipterocarpaceae	D	DDF	-0.01***		-0.01***	0.01**	-3.48**	-0.11**
Litsea martabarnica	Lauraceae	E	All zones	2.32***	5.74**		-1.72***	2.44***	0.02*
Castanopsis acuminatissima	Fagaceae	E	LMF	1.96***		2.54**		1.21***	
Persea gamblei	Lauraceae	E	LMF-FE	1.46**			-1.28**	2.01*	2.01**
Scleropyrum pentandrum	Santalaceae	E	LMF-FE	3.04*			-1.56*		
Syzygium claviflorum	Myrtaceae	E	LMF-FE	0.01***		0.01*	0.02*		
Myrsine seguinii	Primulaceae	E	All zones				-1.41**	1.71**	
Lithocarpus garrettianus	Fagaceae	E	LMF-FE		-0.9***			0.01***	-0.01*
Schima wallichii	Theaceae	E	All zones			3.11***		1.10***	
Tarennoidea wallichii	Rubiaceae	E	All zones		-7.82**	1.91**		1.21*	2.15***
Castanopsis tribuloides	Fagaceae	E	LMF			1.48***	-4.98**	0.15**	
Anneslea fragrans	Pentaphylacaceae	E	All zones			0.01*	0.15*		
Wendlandia paniculata	Rubiaceae	D	All zones		0.04**		0.01*		
Quercus brandisiana	Fagaceae	D	All zones			0.01**	0.01**	-0.02**	-0.07*
Shorea obtusa	Dipterocarpaceae	D	DDF-FE				3.81***	-1.25**	
Rothmannia sootepensis	Rubiaceae	D	DDF-FE			2.43**			

Type: D=deciduous species; E=evergreen species
Zone: LMF=lower montane forest; DDF=deciduous dipterocarp forest; FE=forest ecotone between DDF and LMF
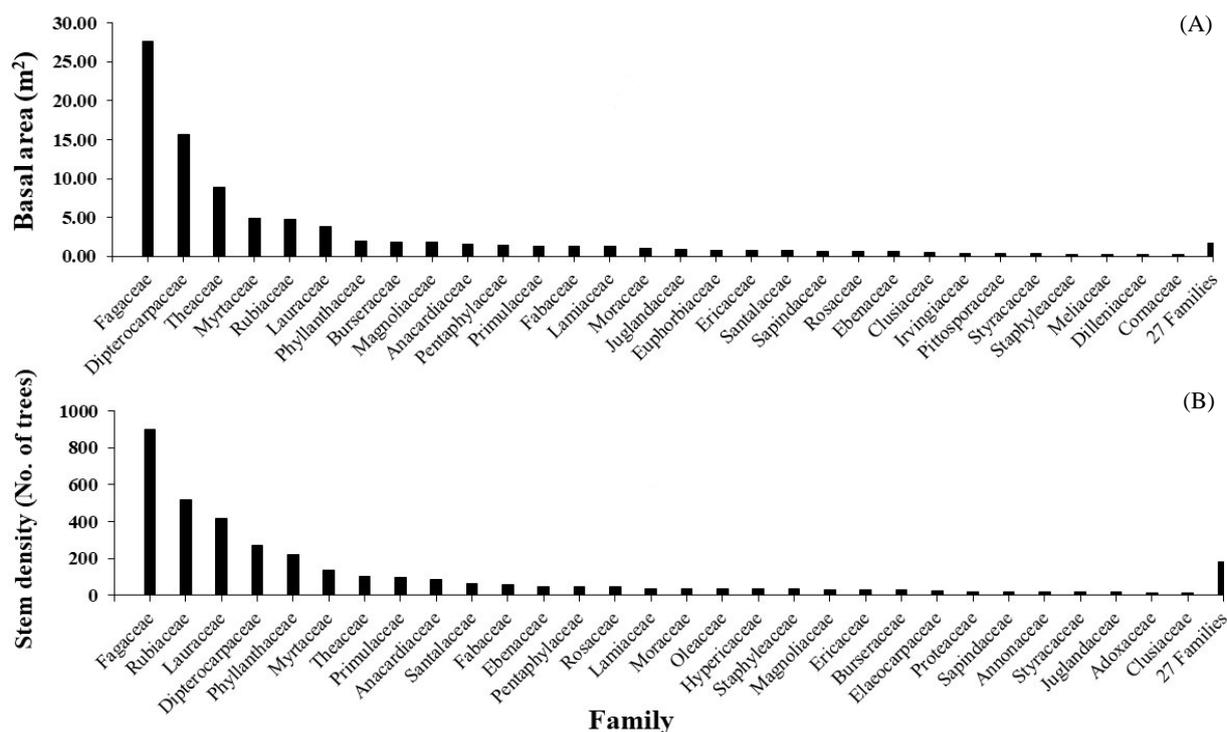*=p<0.05, **=p<0.01, ***=p<0.001

Figure 2. Basal area (A) and stem density (B) of each family across the DDF and LMF in Doi Suthep-Pui National Park.

3.2 Relationships of environmental factors and spatial distribution of the dominant tree species

The soil properties, especially soil texture, varied among the zones in the 3 ha permanent plot. There was a lowland-to-upland gradient in soil texture ranging from sandy to clayey types. Sandy soil was mostly distributed in the DDF and clayey soil mostly in the LMF, with a sandy clayey soil or mixed soil texture found in the FE. The soil was acidic, with a pH of 4.5-6.2 and SOM of 3.5-10% and increasing with elevation. In the FE, in addition to high pH and SOM, the SMC was high, suggesting that the observed highest tree density is due to these factors.

The spatial distribution of the 20 selected tree species reflected environmental factors, particularly elevation, although soil texture and other soil properties also influenced the distributions. The tree spatial distribution could be divided into three groups based on elevation, i.e., species found at low, intermediate and high altitudes. The distributions of the first and second groups were significantly correlated with elevation (10 species), although the correlations differed between the groups and were negative for some factors and positive for others (Table 1). By contrast, the distribution of the third group of 10 species was not significantly correlated with elevation, although slope factors strongly influenced its distribution. The details of the spatial distributions of each group are discussed below.

The distribution of the first group was negatively associated with elevation, comprising low-altitude species, including five deciduous species: *Dipterocarpus obtusifolius*, *Dipterocarpus tuberculatus* (Figure 3(A)-(B)), *Aporosa nigricans*, *Aporosa villosa* and *Lithocarpus dealbatus*. The distribution was positively associated with sandy soil texture and acidic soil (pH≤4.5) and negatively associated with clay soil (Table 1). These findings were consistent with the species' distribution in the DDF, with its fertile soils (Teejuntuk, 2003; Sahunalu, 2009; Ueda et al., 2017) . This species group can shift to higher elevation as drought or low SMC increase with climate change (Marod et al., 2002; Sahunalu, 2009; Trisurat et al., 2009).

The distribution of the second group increased with higher elevation, where the soil was mostly clayey. This group of high-altitude species included five evergreen species from the LMF: *Castanopsis acuminatissima*, *Litsea martabarnica* (Figure 3(C)-(D)), *Persea gamblei*, *Scleropyrum pentandrum* and *Syzygium claviflorum* (Table 1). In addition, distributions of *Persea gamblei* and *Litsea martabarnica* showed negative correlations with sandy soil, indicating that the families Fagaceae

(*Castanopsis acuminatissima*) and Lauraceae (*Litsea martabarnica* and *Persea gamblei*) prefer clay soil, which has good fertility based on its high organic content, as reported previously (Khamyong et al., 2003; Santisuk, 2003; Sri-Ngernyuang et al., 2003). Clay soil texture is very important for LMF

species distribution and is a common characteristic of topical montane forest (Williams-Linera, 1993; Gradstein et al., 2008; Marod et al., 2014). *Castanopsis acuminatissima* and *Syzygium claviflorum* distributions showed positive association with steep slopes (Table 1).
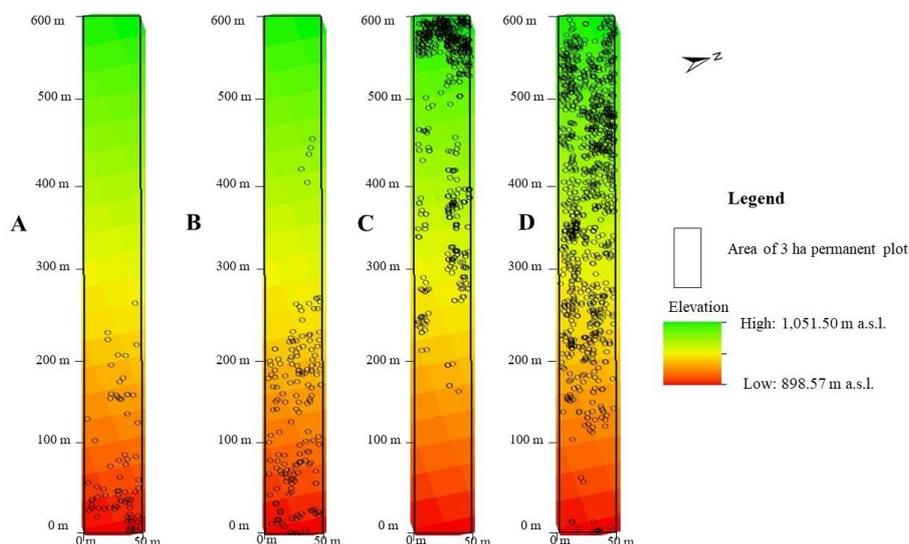

Figure 3. Spatial distributions of the dominant tree species in the 3 ha permanent plot as a function of elevation. The low-altitude species group includes (A) *Dipterocarpus tuberculatus* and (B) *Dipterocarpus obtusifolius*. The high-altitude species group includes (C) *Castanopsis acuminatissima* and (D) *Litsea martabarnica*.

The third group's distribution showed no significant correlation with elevation and consisted of intermediate-altitude species. Most were found in the FE and their distribution was highly dependent on soil texture and steep slopes. The group included 10 species (Table 1), with coexisting species from DDF and LMF. The distribution of the DDF species (*Quercus brandisiana*, *Shorea obtusa* (Figure 4(A)-(B)) and *Wendlandia paniculata*) were highly significantly associated with sandy soil texture (Table 1), whereas those of the LMF species (*Lithocarpus garrettianus, Schima wallichii* (Figure 4(C)-(D)), *Myrsine seguinii, Castanopsis tribuloides* and *Tarennoidea wallichii*) were associated with clayey soil. The LMF species *Schima wallichii* and *Anneslea fragrans* were distributed in all three zones (DDF, FE and LMF), indicating that they can establish in areas of drought and less fertile soil. These are light-demanding species (Asanok et al., 2013; Marod et al., 2015). The DDF species *Quercus brandisiana* and *Shorea obtusa* also had wider distributions, ranging from DDF to LMF, indicating that they have high potential to invade and establish at higher elevations when drought conditions increase and are suitable for

their regeneration (Gardner et al., 2000; Sungpalee, 2002; Santisuk, 2003; Rueangruea, 2009). By contrast, the distribution of the DDF species *Rothmannia sootepensis* was significantly correlated only with steep slopes and mostly occurred in the FE and DDF. Compared with the other species, *Rothmannia sootepensis* has larger fruit, 4.5-5 cm (Puff et al., 2005) and steep slopes may assist in seed dispersal based on gravity (Foster and Janson, 1985).

4. CONCLUSIONS

High tree species diversity was found in the FE between DDF and LMF in Doi Suthep-Pui National Park. The spatial distributions varied among species, and their ecological niches were based on environmental factors. Elevation strongly influenced the tree spatial distribution. Using elevation, the dominant species could be divided into three groups: low-altitude species (deciduous species); high-altitude species (evergreen species); and forest ecotone species (coexisting DDF and LMF species). Soil texture, which ranged from sandy to clayey, also strongly influenced on tree density. The GLM analysis also revealed that soil texture strongly

influenced the tree spatial distribution. The relationship between plant establishment and environmental factors is very important for decision makers who establish restoration management plans. The selection of suitable species based on their niches is needed to promote successful restoration programs.
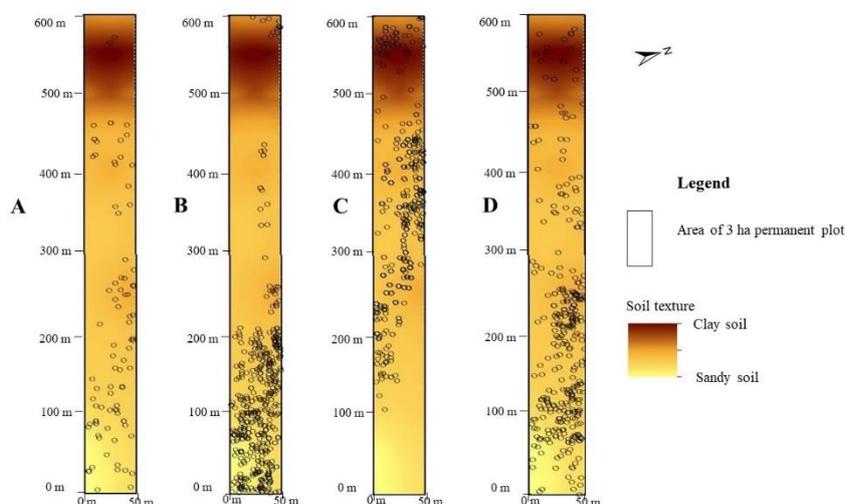

Figure 4. Spatial distribution of the intermediate-altitude species group in the 3 ha permanent plot as a function of soil texture. The distribution of the deciduous species was associated with sandy soil, including (A) *Shorea obtusa* and (B) *Quercus brandisiana*. The distribution of the evergreen group species was associated with clay texture, including (C) *Lithocarpus garrettianus* and (D) *Schima wallichii*.

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