



Research article

Effect of environmental gradients on tree distribution in lowland dry evergreen forest, northeastern Thailand

Dokrak Marod^{a,†}, Wongsatorn Phumphuang^{a,*,†}, Chongrak Wachrinrat^b^a Department of Forest Biology, Faculty of Forestry, Kasetsart University, Bangkok 10900, Thailand^b Department of Silviculture, Faculty of Forestry, Kasetsart University, Bangkok 10900, Thailand

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Abstract

Understanding tree distributions in the context of ecological niches is critical to conserving and restoring sensitive forest communities, such as dry evergreen forest (DEF). This study determined the distributions of dominant tree species in relation to environmental factors in a recovering DEF. In 2016, a 3 ha permanent plot (150 m × 200 m) was set up in lowland DEF on the Wang Nam Khiao Forestry Research and Training Station, northeastern Thailand. Each tree with diameter at breast height (DBH) ≥ 2 cm was tagged and identified, and its DBH and position (X, Y) were recorded. Topographic factors and soil properties were selected as important environmental variables. The tree distribution in the plot was analyzed using detrended correspondence analysis (DCA) and generalized linear model (GLM) methods. DCA indicated that tree distribution was strongly influenced by the topographic gradient, which affected the soil bulk density ($p < 0.05$). Using the DCA diagram, two forest communities were identified; the first was distributed in areas of high elevation and steep slopes, while the second was characterized by high soil bulk density, which was mostly found in low-lying plateau areas, particularly near the stream bank. The GLM results showed that the native species, *Walsura pinnata*, was mostly in low-relief areas along the stream ($p < 0.05$), likely to minimize water stress. In contrast, *Hydnocarpus ilicifolia* and *Streblus ilicifolius* generally occupied ridge areas ($p < 0.05$). The results indicated that ecological niches varied among species, following environmental patterns. These findings can be applied to restoration programs, allowing suitable species to be selected for planting based on their niches.

* Corresponding author.

† Equal contribution.

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Introduction

The structure and composition of tropical forests can be shaped by environmental factors (Mathew et al., 2016). The heterogeneity of environments in tropical forests strongly influences the distribution of tree species and can vary substantially on very small spatial scales (John et al., 2007). Understanding tree species distributions and their relationships with environmental factors is essential for a range of forest management activities, including management of threatened species stand composition and forecasting how tropical forests will respond to global environmental changes (Zare and Zare, 2010; Jucker et al., 2018).

A key factor in maintaining heterogeneity in a tropical forest is topography (Werner and Homeier, 2015). Topographic factors such as elevation, slope and convexity drive local-scale variation in soil properties, hydrology and microclimate (Jucker et al., 2018). In this way, they restrict the growth of trees and affect demographic characteristics of populations, such that growth and mortality rates can differ among habitats based on edaphic associations (Russo et al., 2008). These factors also drive environmental filtering; differences in physiological adaptations to light, nutrient, and water availability have been linked to topographic and edaphic variations (Baltzer et al., 2005). They also shape community structure and the distribution of trees; for example, topographic factors have been shown to influence size structure and distribution in *Dipterocarp* species (Bunyavejchewin et al., 2003).

Analyses of tree distributions in relation to their environments have always been a central topic in forest ecology. The suitability of tree species in an environment depends primarily on environmental variables, as revealed by ecological niche modeling (Warren and Seifert, 2011). However, the use of such models is often inadequate due to the lack of regional datasets, poor predictive performance and inconsistent model projections under future climatic conditions (Bedia et al., 2013). Alternatively, a combination of niche modeling and ordination has been used to evaluate the synergy of these two methods (Asanok et al., 2017a). Niche modeling combined with regression analyses and multiple ordination has been used to assess tree distribution (Guisan and Zimmermann, 2000). The choice of environmental variables has a critical impact on results, requiring key environmental parameters, such as topography (elevation and slope) and soil properties (Dalle et al., 2014; Mathew et al., 2016), to be included.

In Thailand, dry evergreen forest (DEF) covers approximately 20% of protected areas, which is more than other evergreen forest types (Pongpattananurak, 2014). DEF contains a large number of timber species and distinctive biotic communities (Bunyavejchewin, 1999). Such areas have been disturbed not only by natural disasters but also anthropogenic activities such as the conversion of forest into agricultural land, due to their distribution on flat sites and soil that is suitable for agriculture (Marod and Kutintara, 2009; Phumphueng et al., 2018). Therefore, understanding the tree distribution in DEF based on ecological niches is necessary to protect and restore this forest community. The current study assessed the influences of topographic factors and soil properties on the spatial distribution of trees in a permanent plot in DEF.

Materials and Methods

Study site

The study was conducted in DEF on the Wang Nam Khiao Forestry Research and Training Station, Wang Nam Khiao district ($14^{\circ}30'N$ $101^{\circ}55'E$), Nakhon Ratchasima province, northeastern Thailand (Fig. 1). The study site is located along Highway Number 304 about 250 km from Bangkok. The altitudinal range of the site is from 250 to 762 m above sea level (asl) (Niamrat, 2003). The climate is tropical, with rainfall occurring mainly from July to October and low rainfall in the other 8 mth. The mean annual rainfall is approximately 1,100 mm per year and the mean monthly temperature is $27.3^{\circ}C$ (Sakaerat Environmental Research Station, 2015).

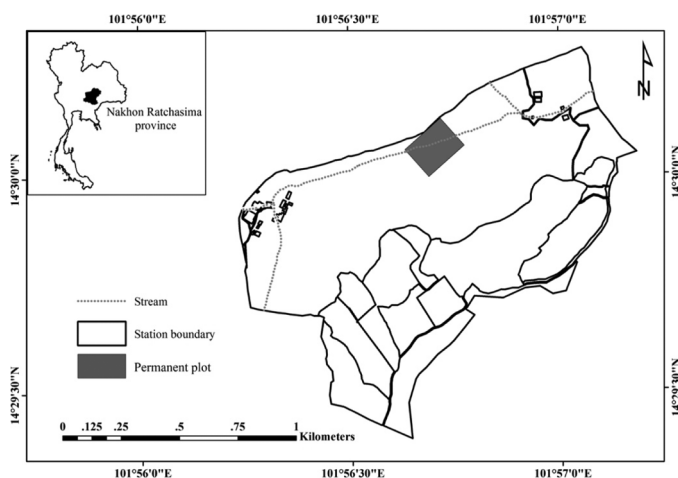


Fig. 1 The study site and 3 ha plot location at Wang Nam Khiao Forestry Research and Training Station, Nakhon Ratchasima province, Thailand

The dominant forests in the study area are DEF, mixed deciduous forest (MDF) and deciduous dipterocarp forest (DDF). Of these, DEF covers the largest area, distributed from lowlands adjacent to streams to the highest altitudes in the study area (Niamrat, 2003). This site was disturbed by road construction for Highway Number 304, particularly in lowland areas. Today, the forest is undergoing a natural recovery process.

Plot establishment and investigation

In 2016, a 3 ha permanent plot (200 m × 150 m) was established in lowland DEF, which was divided into 300 subplots (10 m × 10 m). All trees with a diameter at breast height over bark (DBH, at 1.30 m) ≥ 2 cm were tagged, measured, mapped in grid coordinates (X, Y), and identified to the species level. This plot contained 4,810 individuals representing 46 families, 119 genera and 150 species. For trees with DBH ≥ 5 cm, the tree density and basal area were 806 individuals/ha and 24.18 m²/ha, respectively (Phumphuang et al., 2018). Subplots of 30 m × 30 m were used to study tree spatial distributions and environments (Fig. 2).

Environmental data collection

Topographic factors (elevation and slope) of the permanent plot were characterized using a digital elevation model (DEM) from the Geo-Informatics and Space Technology Development Agency, Bangkok, Thailand, based on a raster surface at 30 m resolution. Vector data for distances from a water resource were obtained from a shape file of the stream in the study site and

transformed into a continuous raster layer using the Euclidean distance method (Gigović et al., 2019) in the QGIS software (version 3.10; QGIS Development Team, 2020).

To collect soil data, 30 sampling plots were established within the permanent plot at a plot size of 30 m × 30 m (Pongpattananurak et al., 2012). In each plot, five soil samples (one from each corner and one from the center) were collected from the topsoil layer (0–15 cm depth) and then combined into one composite soil sample. The soil data were analyzed for physical and chemical properties in the Laboratory of Soil Science, Faculty of Agriculture, Kasetsart University, Bangkok, Thailand. In particular, soil texture and soil bulk density were compared to tree spatial distributions. These properties were analyzed following the methods of the National Soil Survey Center (1996).

Data analyses

Linear correlations among seven environmental factors (elevation, slope, percentages of sand, silt and clay, soil bulk density and stream distance) were determined using Pearson correlation analysis to detect correlations within environmental variables. To determine the distribution gradients of the tree community across the 30 subplots, a 30 m × 30 m spatial scale was selected (Fig. 2) and detrended correspondence analysis (DCA) was used (Hill and Gauch, 1980). DCA is an indirect gradient analysis technique that detects gradients in species composition using species abundance data; the DCA ordination was performed using the function *decorana* in the vegan package (Oksanen et al., 2020)

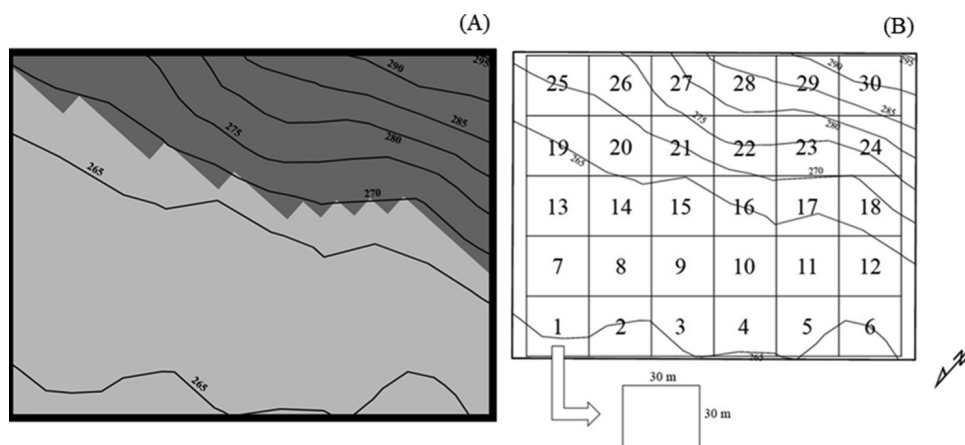


Fig. 2 Information for the 3 ha permanent plot: (A) topographic map with 5 m contour intervals, with flat terrain (light gray) and ridge (dark gray); (B) layout of subplots (30 m × 30 m)

of the R software (version 3.3.3; R Core Team, 2017). DCA was coupled with *a posteriori* interpretation (explanation using measured environmental variables) of ordination because it can identify patterns solely due to species, without interference from environmental variables, as occurs in some joint analyses of direct ordinations (Kent, 2011). The tree species matrix contained tree abundance data based on the total basal area of each species using individuals with a DBH ≥ 5 cm in each subplot. The seven environmental factors were fitted to the DCA ordination. Significant variables ($p < 0.05$) were identified using the *envfit* test (environmental fit) of the *vegan* package. In addition, Pearson correlation coefficients between these significant environmental variables and the ordination scores of the area along each DCA axis were obtained. Furthermore, the DCA and Pearson correlation analyses were used to classify the differences in plant communities in the study area.

To clarify the spatial distribution of tree regeneration, a generalized linear model (GLM) was employed with a Gaussian distribution identity link function to investigate the relationships between environmental factors and tree species. The GLM analysis only considered 20 dominant sapling species ($2 \leq \text{DBH} < 5$ cm), based on total basal area (see Table 1). However, *Leucaena leucocephala*, one of the 20 selected species, is classified as an invasive species. This

species was planted along mountain ridges at the site for a restoration program. Today, it shows strong regeneration in the study area and has expanded into lowland areas, particularly in openings (Marod et al., 2012). As a result, *L. leucocephala* was excluded from further analysis, leaving 19 species. The dependent and independent variables used in the GLM analysis were the total basal area of the 19 selected species in each subplot and the environmental variables (elevation, slope, percentages of sand, silt and clay, soil bulk density and stream distance), respectively. Based on a preliminary analysis, log-transformation was applied to standardize the distributions of the dependent variables. Finally, the model with the lowest Akaike information criterion (AIC) was chosen (Akaike, 1974) using the step AIC function of the MASS package (Venables and Ripley, 2002) in R version 3.3.3. Distribution maps for the selected species were then created using the QGIS software.

Results and Discussion

Environmental factors

Environmental factors in the study area are summarized in Table 2. The mean ($\pm$ SD) altitude and slope were 268.83 ± 7.15 m asl and 18.02 ± 10.04 %, respectively. The stream was

Table 1 Top-20 dominant sapling species by basal area in dry evergreen forest permanent plot

Rank	Species	Family	Number of stems	Basal area (m ²)
1	<i>Cleistanthus papyraceus</i> Airy Shaw	Phyllanthaceae	321	0.205
2	<i>Streblus asper</i> Lour	Moraceae	171	0.144
3	<i>Hydnocarpus ilicifolia</i> King	Achariaceae	126	0.100
4	<i>Aphanamixis polystachya</i> (Wall.) R. Parker	Meliaceae	99	0.077
5	<i>Micromelum minutum</i> (G. Forst.) Wight & Arn.	Rutaceae	75	0.066
6	<i>Streblus ilicifolius</i> (S. Vidal) Corner	Moraceae	87	0.063
7	<i>Memecylon ovatum</i> Sm.	Melastomataceae	62	0.061
8	<i>Antidesma sootepense</i> Craib	Phyllanthaceae	67	0.060
9	<i>Markhamia stipulata</i> (Wall.) Seem. var. <i>stipulata</i>	Bignoniaceae	66	0.058
10	<i>Diospyros variegata</i> Kurz	Ebenaceae	60	0.055
11	<i>Cinnamomum iners</i> Reinw. ex Blume	Lauraceae	62	0.054
12	<i>Dipterocarpus alatus</i> Roxb. ex G. Don	Dipterocarpaceae	54	0.051
13	<i>Glochidion wallichianum</i> Müll. Arg.	Phyllanthaceae	53	0.047
14	<i>Mallotus philippensis</i> (Lam.) Müll. Arg.	Euphorbiaceae	63	0.045
15	<i>Aglaia lawii</i> (Wight) C. J. Saldanha	Meliaceae	57	0.039
16	<i>Walsura pinnata</i> Hassk.	Meliaceae	41	0.033
17	<i>Leucaena leucocephala</i> (Lam.) de Wit	Fabaceae	38	0.033
18	<i>Mitrephora tomentosa</i> Hook. f. & Thomson	Annonaceae	40	0.032
19	<i>Millettia xylocarpa</i> Miq.	Fabaceae	31	0.031
20	<i>Suregada multiflora</i> (A. Juss.) Baill.	Euphorbiaceae	33	0.024

located in the lower-lying portion of the plot with an average distance to the sub-plots of 36.74 ± 24.07 m. The soil texture was sandy loam, dominated by sand (66.46 ± 1.82 %) followed by silt (20.73 ± 0.77 %) and clay (13.24 ± 1.24 %). These results were similar to those of previous reports emphasizing that sandy loam is the characteristic soil type of the Korat series in northeastern Thailand (Treloges and Sriboonlue, 2002; Islam et al., 2014; Arunrat et al., 2020). In addition, the plot had a low soil bulk density (0.63 ± 0.01 g/cm³). Soil bulk density is recognized as an indicator of plant growth, where plants are considered to be capable of good growth at values < 1.6 g/cm³ for sandy soils (Miller and Donahue, 1995). Therefore, the plot soil bulk density values implied appropriate conditions for the establishment of plants in this area.

Based on the Pearson correlation test, among the seven environmental variables, there were 12 significant correlations among the 21 combinations (57%, see Table 3). Elevation and slope were significantly positively correlated, indicating they tended to increase simultaneously. Low-lying areas with gentle slopes were found in the lower and middle sections of the plot. Stream distance was also significantly positively

correlated with these factors because it was located on flat terrain with high soil moisture conditions. These two variables are among the most important factors in the establishment of forest communities (Luizão et al., 2004; Zhang et al., 2016). The sand percentage was negatively correlated with the silt and clay percentage; the sand percentage was also significantly positively correlated with elevation and stream distance. Sandy and sandy loam soils are the most common soil types in DEF (Marod and Kutintara, 2009) and are characterized by good drainage. Increasing distance from stream was significantly negatively correlated with silty and clayey soils. Silty and clayey soil textures indicate fertile soils (Wang et al., 2018) and were mostly found along the stream bank. Soil bulk density had a significant negative relationship with elevation, slope and stream distance; therefore, it was highest in the lowest-lying areas in the plot. High soil bulk density can be the result of both anthropogenic disturbances and natural disasters. Critical-level flooding occurred in the plot during the rainy seasons in 2003 and 2011, leading to high sediment accumulation, which typically promotes high soil bulk densities (Przewoźna, 2014).

Table 2 Environmental factors in the permanent plot

Environmental factor	Maximum	Minimum	Mean $\pm$ SD
Elevation (m above sea level)	288.10	260.20	268.83 $\pm$ 7.15
Slope (%)	39.75	2.68	18.02 $\pm$ 10.04
Percentage sand (%)	72.29	62.76	66.46 $\pm$ 1.82
Percentage silt (%)	22.05	18.73	20.73 $\pm$ 0.77
Percentage clay (%)	16.55	10.94	13.24 $\pm$ 1.24
Soil bulk density (g/cm ³)	0.65	0.60	0.63 $\pm$ 0.01
Stream distance (m)	97.30	5.55	36.74 $\pm$ 24.07

Table 3 Summary table of Pearson correlation coefficients among environments, results of *envfit* test used to select environmental variables for detrended correspondence analysis (DCA) and eigenvalues and correlation matrix of relationships between environmental factors and two axes of DCA

Environmental factor	Pearson correlation analysis							<i>envfit</i> Test	Correlation between environment and ordination score	
	Elevation	Slope	% Sand	% Silt	% Clay	Soil bulk density	Stream distance	<i>p</i> -Value	DCA axis 1	DCA axis 2
Elevation	1.000	–	–	–	–	–	–	0.001	0.796***	0.329
Slope	0.782***	1.000	–	–	–	–	–	0.001	0.779***	0.522**
% Sand	0.391*	0.174	1.000	–	–	–	–	0.716	0.060	0.168
% Silt	-0.239	0.010	-0.722***	1.000	–	–	–	0.834	-0.017	-0.095
% Clay	-0.248	-0.240	-0.708***	0.079	1.000	–	–	0.884	-0.081	-0.167
Soil bulk density	-0.790***	-0.840***	-0.225	0.078	0.309	1.000	–	0.001	-0.813***	-0.379*
Stream distance	0.888***	0.623***	0.704***	-0.534**	-0.378*	-0.578***	1.000	0.229	0.556**	0.307

Ordination of tree community

Differences in the composition of the 30 subplots of the lowland DEF and their relationships with environmental variables are summarized in a spider plot of DCA ordination (Fig. 3). The eigenvalues of axis 1 and axis 2 were 0.646 and 0.352, respectively. These eigenvalues are relatively high (> 0.3), indicating that there is significant species turnover along the gradients described by the first two axes (ter Braak, 1995; Oliveira-Filho et al., 2006). The first DCA ordination axis had a 0.646 eigenvalue, implying that plant communities were widely dispersed along the axis. Significant variables, as determined using *envfit*, were elevation, slope and soil bulk density (Table 3). The correlations between environmental variables and DCA axes are provided in Table 3. Elevation and stream distance were positively correlated with DCA axis 1. Slope was positively correlated with both axes. By contrast, soil bulk density was negatively correlated with both axes.

The first DCA ordination axis was mainly correlated with elevation, slope, soil bulk density and stream distance, while the second axis was also correlated with slope and soil bulk density. This indicated that the data structure was summarized by the first axis, which primarily reflected an environmental

gradient. Ridge (elevation ≥ 268 m asl and slope ≥ 20 %) and flat terrain along the stream bank (elevation < 268 m asl and slope < 20 %) groups could be classified based on this structure (Figs. 2 and 3). In particular, the correlation between the first axis and the environmental variables clearly classified the plateau groups (Fig. 4), which corresponded well with the findings of other studies (Zhang et al., 2013; Thammanu et al., 2021). The flat terrain communities showed a significant negative correlation with elevation ($r = -0.59$, $p < 0.05$) and soil bulk density ($r = -0.76$, $p < 0.001$), whereas the ridge communities had a significantly positive association with elevation ($r = 0.91$, $p < 0.001$) and slope ($r = 0.72$, $p < 0.01$). The areas of flat terrain along the stream bank in the plot were associated with high values of soil bulk density. The tree community in these areas, represented by subplots 1–15 (P1–P15), indicated the most abundant species were: *Dipterocarpus alatus* (dipala), *Aphanamixis polystachya* (aphpol), *Holoptelea integrifolia* (holint) and *Adenanthera pavonina* (adejav) as the most abundant species. The ridge areas consisting of subplots 16–30 (P16–P30) were linked to high elevation and slope. The major tree species in this group were: *Aglaia lawii* (agllaw), *Hydnocarpus ilicifolia* (hydili), *Mallotus philippensis* (malphi) and *Vitex scabra* (vitsca).

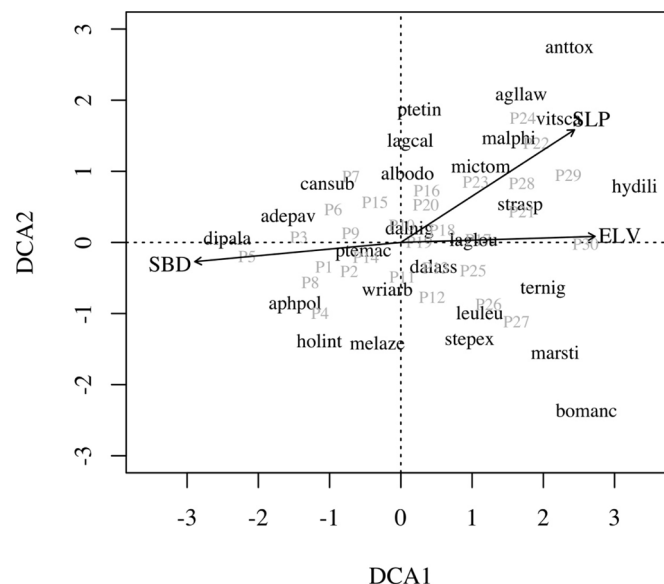


Fig. 3 Diagram of detrended correspondence analysis (DCA) results for (ELV) elevation, (SLP) slope and (SBD) soil bulk density, where P followed by a number represents each subplot. only the top 20% of dominant tree species based on the total basal area are shown and dipala = *Dipterocarpus alatus*, aphpol = *Aphanamixis polystachya*, adejav = *Adenanthera pavonina*, cansub = *Canarium subulatum*, wriarb = *Wrightia arborea*, dalnig = *Dalbergia nigrescens*, dalass = *Dalbergia assamica*, holint = *Holoptelea integrifolia*, melaze = *Melia azedarach*, ptetin = *Pterocymbium tinctorium*, lagcal = *Lagerstroemia calyculata*, albodo = *Albizia odoratissima*, laglou = *Lagerstroemia loudonii*, ptemac = *Pterocarpus macrocarpus*, ternig = *Terminalia nigrovenulosa*, leuleu = *Leucaena leucocephala*, marsti = *Markhamia stipulata* var. *stipulata*, bomanc = *Bombax anceps*, strasp = *Streblus asper* hydili = *Hydnocarpus ilicifolia*, mictom = *Microcos tomentosa*, malphi = *Mallotus philippensis*, vitsca = *Vitex scabra*, agllaw = *Aglaia lawii* and anttox = *Antiaris toxicaria*

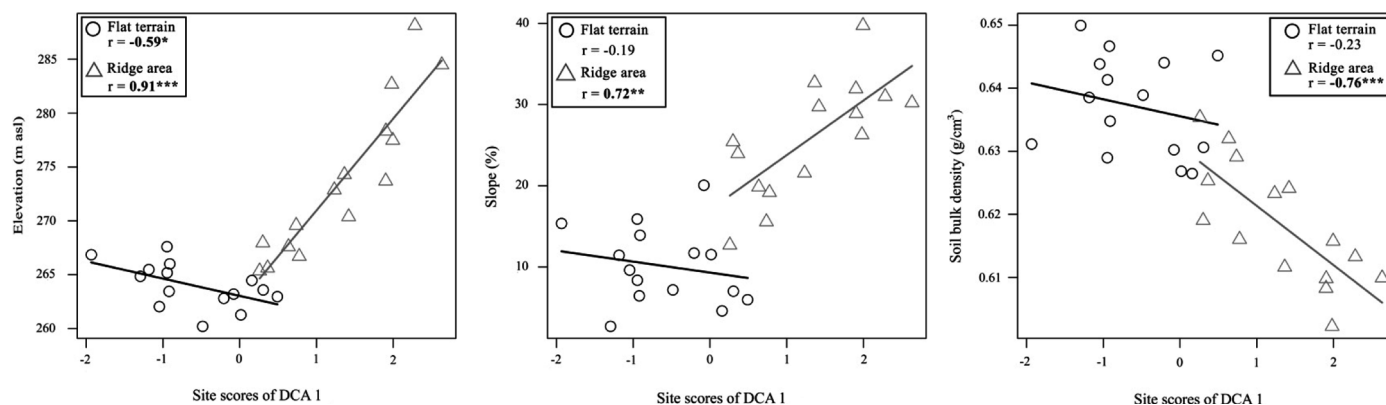


Fig. 4 Pearson correlation coefficients between environmental factors (elevation, slope, and soil bulk density) and first axis of detrended correspondence analysis and significance of correlations is indicated in bold (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$)

Relationships between the plant community and environmental factors based on the DCA analysis revealed that the most important environmental factors driving tree species composition were related to topographic factors and soil properties. The ridge plant community had high positive loadings along axis 1, while the flat terrain plant community had negative loadings on that axis. Elevation and slope had positive correlations, whereas soil bulk density had a negative correlation with ridge tree species. This indicated that the amplitude tolerance to topographic and edaphic factors differed among tree species. Increased elevation and slope have been associated with increased distance from the water resource and reduced soil moisture (Pérez, 1987; Qiu et al., 2001), indicating that the ecological niche of ridge tree species such as *Hydnocarpus ilicifolia* and *Aglaia lawii* consisted of dry conditions found at high elevations and on steep slopes in the plot. By contrast, soil bulk density, which has been reported to increase with decreasing elevation (Saeed et al., 2014), had a negative correlation with flat terrain tree species such as *Dipterocarpus alatus* and *Aphanamixis polystachya* that were mostly found near the stream. Other studies have reported similar results, as these species prefer high soil moisture during their establishment (Saldanha and Nicolson, 1976; Bunyavejchewin et al., 2003; Kumar et al., 2014).

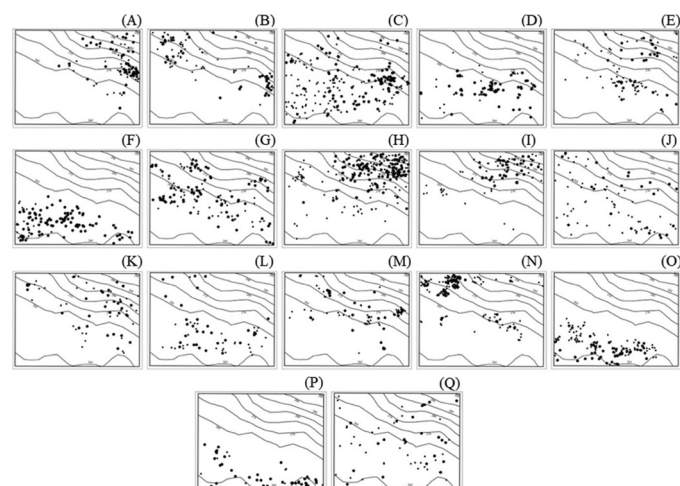
Tree spatial distribution

Only 17 species could be fitted to the GLM model for saplings, as there were insufficient data for *Glochidion wallichianum* and *Millettia xylocarpa* had. The relationships between species and environmental factors varied among species (Table 4 and Fig. 5). Only 13 species showed significant correlations with environmental factors; *Cleistanthus papyraceus*, *Aphanamixis*

polystachya, *Cinnamomum iners* and *Mitrephora tomentosa* did not. GLM models indicated that one to three environmental factors had a significant effect on the spatial distribution of 10 species. For example, *Walsura pinnata* was only associated with stream distance, being significantly negatively associated with this variable. *Diospyros variegata* was negatively related to elevation and positively related to slope. However, three middle-canopy species (*Memecylon ovatum*, *Micromelum minutum* and *Streblus asper*) were highly correlated with more than four environmental variables. Elevation and soil texture (percentages of sand, silt and clay) were strongly correlated with *Memecylon ovatum* and *Micromelum minutum*. This indicated that the spatial distributions of these species were strongly regulated by their ecological niches during establishment and suggested a potential causal relationship between environmental factors and plant abundance (Bautista-Santiago et al., 2018). The species had high correlations for a variety of factors, indicating that their distribution was not biased by habitat conditions (Harms et al., 2001) or that they were generalist species (Cannon and Leighton, 2004; Asanok et al., 2017b). Understanding species niches is important for predicting species abundance and regeneration in a given area (Antúnez et al., 2017). Among the four species that did not have a significant impact on all environments (Table 4), *Aphanamixis polystachya* and *Cinnamomum iners* likely should have been correlated with some factor, given that they were mainly distributed in the lower area of the plot (Fig. 5), suggesting that the suite of factors considered here may have been insufficient to detect their spatial distribution. Future efforts regarding GLM modeling may benefit from the inclusion of soil pH (Marod et al., 2019), soil nutrient status (Zare and Zare, 2010) and vegetation structure (tree density and basal area) (Asanok et al., 2017a).

Table 4 Results of generalized linear model analyses, where values are model regression coefficients

Species	Estimated value	Environmental variable					
	Elevation	Slope	% Sand	% Silt	% Clay	Soil bulk density	Stream distance
<i>Memecylon ovatum</i>	-5.788***	—	7.850**	4.200**	6.073**	-1.403	-3.584*
<i>Micromelum minutum</i>	-5.231***	—	6.902**	3.811**	4.045**	—	—
<i>Streblus asper</i>	-5.844***	—	—	—	0.391*	-0.631*	1.200**
<i>Antidesma sootense</i>	-6.586***	—	—	—	—	-1.119**	—
<i>Aglaia lawii</i>	-6.827***	—	-2.170**	-1.338*	-1.726**	—	—
<i>Dipterocarpus alatus</i>	-6.095***	—	2.611*	1.899*	1.479	—	—
<i>Hydnocarpus ilicifolia</i>	-6.230***	1.710*	0.824	—	0.455	—	-1.358
<i>Streblus ilicifolius</i>	-6.850***	1.309**	-2.797	-1.672	-1.408	—	—
<i>Mallotus philippensis</i>	-6.428***	—	1.649	1.032	1.025	-0.629*	-0.610
<i>Walsura pinnata</i>	-6.564***	—	3.469	1.408	1.5874	-0.782	-1.312*
<i>Suregada multiflora</i>	-6.978***	—	-0.616	-0.453	-0.662	—	—
<i>Diospyros variegata</i>	-6.520***	1.333**	—	—	—	—	—
<i>Markhamia stipulata</i> var. <i>stipulata</i>	-6.266***	—	-1.990*	-0.910	-0.980	—	—
<i>Cleistanthus papyraceus</i>	-5.481***	—	-1.079	—	—	—	1.093
<i>Aphanamixis polystachya</i>	-4.920***	—	-1.563	-1.730	-1.464	1.417	—
<i>Cinnamomum iners</i>	-3.886**	27.356	-11.311	—	-10.478	8.558	—
<i>Mitrephora tomentosa</i>	-6.737***	—	—	—	—	—	—

Significant coefficients based on Akaike information criterion; * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$ **Fig. 5** Spatial distributions of 17 tree species in the 3 ha permanent plot: (A) *Memecylon ovatum*; (B) *Micromelum minutum*; (C) *Streblus asper*; (D) *Antidesma sootense*; (E) *Aglaia lawii*; (F) *Dipterocarpus alatus*; (G) *Markhamia stipulata* var. *stipulata*; (H) *Hydnocarpus ilicifolia*; (I) *Streblus ilicifolius*; (J) *Mallotus philippensis*; (K) *Walsura pinnata*; (L) *Suregada multiflora*; (M) *Diospyros variegata*; (N) *Cleistanthus papyraceus*; (O) *Aphanamixis polystachya*; (P) *Cinnamomum iners*; (Q) *Mitrephora tomentosa*, where large and small circles represent tree and sapling stages, respectively.

A group of species was detected that was strongly associated with topographic factors (elevation, slope and stream distance), consisting of *Hydnocarpus ilicifolia*, *Streblus ilicifolius*, *Walsura pinnata*, *Suregada multiflora* and *Diospyros variegata*. Among these, *H. ilicifolia* and *S. ilicifolius* were positively correlated with elevation. This finding was similar to other reports (Niamrat and Marod, 2005; Panichsuay, 2012) and the regeneration of these species was concentrated on ridges where the soil bulk density was low. In contrast, *D. variegata* and *S. multiflora* preferred flat areas. Stream distance was significantly negatively correlated with *W. pinnata*, indicating that this species regenerates on flat terrain along the stream bank. *W. pinnata* is a native species (Marod and Kutintara, 2009) and thus may be more vulnerable to water stress than fast-growing non-native species (Cabin et al., 2002), which may have explained its distribution in the plot.

A second group of species was strongly associated with soil properties (soil texture and bulk density), consisting of *Mallotus philippensis*, *Aglaia lawii*, *Dipterocarpus alatus* and *Markhamia stipulata* var. *stipulata*. Only *M. philippensis* was significantly negatively associated with soil bulk density; the remaining species were significantly correlated with soil texture. *D. alatus* had a significantly positive correlation with

the percentages of sand and silt and was mostly distributed on flat terrain or along the stream bank in the plot because it requires high soil moisture and fertile soil conditions (Asanok et al., 2017a). The percentage of sand had a significantly negative relationship with *M. stipulata* var. *stipulata*, which had a low distribution across the sandy loam soils in the plot. This species typically occurs in mixed deciduous forests up to 1,000 m asl in the lower montane region (Santisuk, 1974) where soils are primarily clay (Marod et al., 2019).

The distribution of tree species was influenced by environmental gradients. Based on the DCA analysis, two distinct groups of tree species were detected, representing ridges and flat terrain along stream banks. The sapling analysis indicated that variation in the spatial distribution of species was mostly related to environmental conditions. This is known as a species' ecological niche, which is critical for plant establishment. These findings are relevant for forest management in DEF, particularly for forest restoration programs. Similar studies are recommended to improve species selection, boost local population acceptance and interest in woody species for restoration, and to provide practical management guidelines. Restoration programs must evaluate species suitability based on their niches and in accordance with the environmental conditions of restoration sites, as well as their successional stage associations, to increase the likelihood of succession leading toward the climax stage, in terms of both structure and species composition.

Conflict of Interests

The authors declare that there are no conflicts of interests.

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