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Natural tree regeneration after selective cutting in a dry evergreen forest in Northeastern Thailand

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Abstract. *Marod D, Sungkaew S, Thinkampaeng S, Wachrinrat C, Hermhuk S, Thongsawi J, Phumphuang W, Yarnvudhi A, Yatar C, Cheysawat S, Sawasmongkol C. 2024. Natural tree regeneration after selective cutting in a dry evergreen forest in Northeastern Thailand. Biodiversitas 25: 4074-4085.* Forest degradation is a serious problem caused by anthropogenic disturbance, nevertheless, forest recovery rates vary among forest ecosystems. We investigated forest regeneration after selective cutting in a dry evergreen forest at the Wang Nam Khiao Forestry Research and Training Station (WFRS), Nakhon Ratchasima Province, Thailand. In 2002, a 1-ha permanent plot was established in the forest. All woody plant (sapling and trees) in the plot with Diameter at Breast Height (DBH) >2 cm were identified, and their DBHs and positions were recorded. Data on environmental and topographic factors and soil properties were collected to analyze their relationships with tree spatial distribution. Tree monitoring was conducted in 2004, 2018, and 2020 and forest dynamics were analyzed for the periods 2002-2004, 2004-2018, and 2018-2020. In 2020, we identified 3,669 trees of 91 species, 81 genera, and 36 families. Based on importance index values, the dominant tree species (all with DBH ≥4.5 cm) were *Walsura pinnata* Hassk., *Dialium cochinchinense* Pierre, *Hopea ferrea* Laness., *Hydnocarpus ilicifolius* King and *Vitex scabra* Wall. ex Schauer. Based on the DBH class distribution, the natural regeneration of all woody plants tended toward a reverse J-shaped, indicating a good regeneration condition. The results of forest dynamics analysis showed that the net recruitment rate (2.75±1.70% year^{-1}) was higher than the mortality rate (2.14±0.73% year^{-1}) throughout the study period. Tree spatial distributions varied among species and across environmental factors which were strongly influenced by soil texture followed by topographic and can be divided into generalist and specialist species. This indicates that the forest is going toward a positive regeneration trajectory after the disturbances. Nonetheless, additional information based on forest monitoring is required. Additionally, an understanding of the relationships between species niches and environmental changes is important for tree regeneration research and forest restoration programs; it will allow better matching of tree species to their optimal environmental conditions, thereby increasing the likelihood of plant community success.

Keyword: Ecological niche, forest degradation, forest dynamics plots, long-term ecological research

INTRODUCTION

Tropical forests harbor more than half of the Earth's biodiversity (Lewis et al. 2015). Yet, they experience directional shifts in species composition and structure due to anthropogenic disturbances (Brancalion et al. 2019; Liu et al. 2023). The main driver of biodiversity loss and global environmental changes is forest conversion, or the destruction of natural forests, particularly for agricultural use, while another significant problem is forest degradation, which is an initial step to forest conversion (Raven and Wagner 2021). One of the main causes of forest degradation in tropical forests is illegal logging, which has a wide range of effects on the composition and structure of the forest (Lewis et al. 2015). However, tropical forests can recover from disturbances when given sufficient time (Poorter et al. 2021). Forest recovery is the process of vegetation succession after natural and/or anthropogenic disturbance (Potapov et al. 2017). Forest recovery rates are influenced by many factors, such as land use intensity (Rebola et al. 2021), area size, soils and remnant forest areas. All of this affects plant regeneration seed dispersal to promote the forest recovery process.

In Thailand, Dry Evergreen Forests (DEFs) cover approximately 20% of protected areas, greater in proportion than other evergreen forest types. The DEFs are important both economically and ecologically, due to their large number of timber species and distinctive biotic communities (Phumphuang et al. 2018). In the past, some DEFs within the country were subjected to logging activities in both protected and preserved areas (Phumsathan et al. 2022). However, unregulated logging activities in those areas were then banned due to the occurrence of extreme natural disasters, such as floods and landslides (Sulaiman and Abdul-Rahim 2015). Previously logged areas were left to recover through natural and artificial restoration methods, allowing the forest to regenerate after both human disturbances and natural disasters. However, Phumphuang et al. (2018) reported that flooding occurred on permanent plot established on lowland area in DEF had restricted regeneration and created large gaps, particularly along riverbanks. Subsequently, the increased light condition had an effect on light-demanding species to occupy and grow in the large gap area. In this study site, the permanent plot was flooded in the short rainy season, but only in the lowlands. Therefore, an understanding of tree distributions and forest dynamics in dry evergreen forests based on investigations of ecological niches and environmental factors influencing regeneration is necessary for restoration and sustainability management.

Most knowledge of post-disturbance vegetation in sites older than 10-15 years is based on chrono sequence studies of abandoned disturbed sites, rather than long-term studies of monitored forest dynamics plots. Forest dynamics encompass changes in stand structure, species composition, and species interactions with disturbance and environmental factors over a range of area-based and time scales. Long-term ecological research is crucial for the quantification of ecological responses to natural and anthropogenic disturbances (Gaiser et al. 2020). Long-term research is particularly valuable for efforts to understand the forest dynamics, forest structure and species composition changes, and natural regeneration processes (e.g., growth, mortality, and recruitment) related to environmental changes (e.g., climate, soil, and topographic). Forest dynamics plots can also be used to detect relationships between plant spatial distributions and ecological niches, which are useful for the selection of suitable species for restoration based on their adaptation in various ecosystems. For example, Guisan et al. (1999) used Generalized Linear Models (GLMs) to investigate tree spatial distributions in the Spring Mountains of southern Nevada, USA. This study used GLMs due to their extensive use in detecting tree spatial distributions. The range of habitats inhabited by an organism defines its ecological niche. The elucidation of species coexistence and biodiversity patterns requires an understanding of the mechanisms influencing niche determination. For example, specialist species are closely associated with narrow and specific environmental factors, whereas generalist species can occupy diverse environments (Denelle et al. 2020).

Although ecological studies have been conducted in Thailand for many years, but only a few long-term ecological research programs have been established using forest dynamics plots (Marod et al. 2019). Therefore, this study aimed to investigate natural tree regeneration after selective cutting in a dry evergreen forest at Wang Nam Khiao Forestry Research and Training Station, Nakhon Ratchasima Province, Northeastern Thailand. In this study, we used a 1 ha permanent plot to: (i) study forest structure and species composition; (ii) detect relationships between tree and environmental factors; and (iii) clarify forest dynamics after disturbances from 2002-2020 where the forest is currently undergoing natural regeneration. Based on long-term data, our findings enhance the science and practice of forest regeneration processes and provide insight into the relationships between species and their environments.

MATERIALS AND METHODS

Study area

This study was conducted in a DEF at the Wang Nam Khiao Forestry Research and Training Station (WFRS) in Wang Nam Khiao District, Nakhon Ratchasima Province, Northeastern Thailand (14°30’N, 101°57’E; Figure 1). The elevation ranges from 250 to 762 meters above sea level (m a.s.l.). The study site has a tropical monsoon climate, with rainfall mainly occurring between July and October. Based on climate data collected during 1983-2020, the mean annual rainfall is 1,100 mm year^{-1} and the mean monthly temperature is 26.2°C, reaching a maximum of 29.2°C in April and minimum of 21.9°C in December. Triassic and Cretaceous sandstone found in the study area represents the Khorat group of the Phra Wihan formation.

Forest types in the station comprised Deciduous Dipterocrap Forest (DDF), Mixed Deciduous Forest (MDF) and DEF. Most of the study area is covered by DEF. The dominant tree species were *Dipterocarpus alatus*, *Streblus asper*, *Hydnocarpus ilicifolius* and *Markhamia stipulata*. (Phumphuang et al. 2018). In the past, it has been disturbed by illegal selective logging targeting *Hopea ferrea* and *Dialium cochinchinense* and road construction. Nowadays, the forest is currently undergoing natural regeneration.

Data collection

Establishment of permanent plot and tree investigation

In 2002, a 1 ha permanent plot (40 m × 250 m) was established in the recovering DEF in the Wang Nam Khiao Forestry Research and Training Station (WFRS) (14° 30’ N, 101° 55’ E). Elevation of the plot ranged from 280-320 m a.s.l., spanning from the foothills to the summit of the mountain. The plot was divided into 100 subplots (10 m × 10 m). All woody plant species with a diameter at breast height (DBH; 1.3 m) ≥2 cm (DBH 2-4.5 cm categorized as saplings, and >4.5 cm as trees) were tagged, measured, identified to species level and recorded their position (X, Y). Specimens of unidentified species were collected for comparison with identified specimens in the forest herbarium at the Department of National Parks, Wildlife and Plant Conservation, Bangkok Thailand. The nomenclature used in this study adheres to that of Smitinand (2014). In addition, tree monitoring was done in 2004, 2018, and 2020, in which mortality and any newly recruited trees were recorded. Especially in 2020, 25 subplots (10 m × 250 m) were selected to examine forest stratification and crown cover area following Saiful and Latiff (2017). Although the forest dynamics were taken into account in all census data, the analyses of forest structure, species composition, and species-environment relationships were focused on 2020 data with all woody plants (≥2 cm DBH).

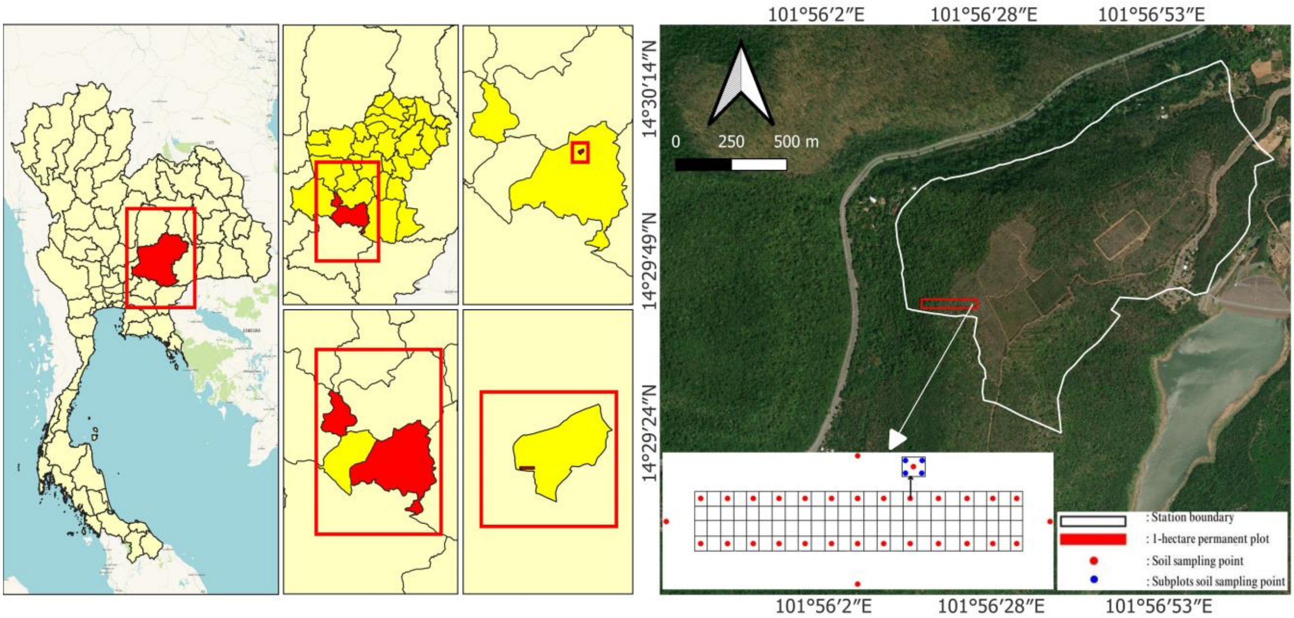

Figure 1. Map of a 1-ha permanent plot in naturally regenerated dry evergreen forest at Wang Nam Khiao Forestry Research and Training Station in Wang Nam Khiao District, Nakhon Ratchasima Province, Northeastern Thailand

Environmental factors collection

For soil collection, soil samples were collected in the subplot within a 20-m distance of the first and fourth lines. Five topsoil samples (depth, 0-15 cm) were collected and combined into a single composite soil sample. Control soil samples were also collected outside of the plot (4 samples) (Figure 2), resulting in a total of 30 soil samples. Then, soil properties, including the soil textures (the percentages of sand, silt, and clay) were measured using a hydrometer (Soil Science Division Staff 2017) following a modified protocol. The Organic Matter (OM) was analyzed based on the wet oxidation method (Allison 1965). The soil pH was analyzed based on a pH meter in a 1:1 soil: water mixture (Beck 1999). All soil properties were done at the Laboratory of Soil Science, Faculty of Agriculture, Kasetsart University.

Topographic factors (elevation and slope) in the 1-ha plot, were characterized using a digital elevation model obtained in 2000 from Earth Explorer, comprising a raster surface with 30-m resolution. A Global Positioning System (GPS) device was used to mark the location of each corner of the subplot using GPS Handhelds by Garmin GPSMAP 64s version, then resampled to a raster resolution data from 30 m into a 10 m grid.

According to the climate, data used in the study were obtained from the Sakaerat Environmental Research Station, including daily maximum temperature (°C), minimum temperature (°C), and total amount of precipitation (mm) data from 2002-2020.

Data analysis

Forest structure and species composition

The number of individual woody plant species, basal area, and frequency of each species were analyzed to determine species dominance based on the Importance Value Index (IVI), which is calculated as the sum of relative frequency, relative dominance, and relative density. The dominant species were determined among saplings and trees. Plant diversity was evaluated using the Shannon-Wiener Index (H'), calculated following Dharmawan et al. (2024).

DBH class distribution was quantified for all identified woody plant species with more than 30 individuals and DBH ≥2 cm. The total number of individuals in each diameter class was recorded to evaluate the DBH distribution (Morgenroth et al. 2020). Then, we visually categorized the species according to the DBH distribution form.

Species-environment relationship

Continuous surface edaphic and topographic factors were used to create a map of topography and soil characteristics (elevation, slope, sand, silt, clay, pH and OM factor) in the permanent plot using the kriging technique in QGIS software version 3.34.

Then, tree spatial distributions were considered only the top woody plant species with more than 10 individuals to evaluate the relationships between environmental factors using a GLM with poisson distribution. The topographic factors (elevation and slope) and soil properties (sand, silt, clay, pH and OM) were independent variables and the total number of individuals per tree species was the dependent variable. The spatial distributions of woody plant species were assumed to be influenced by environmental factors that affected plant establishment and ecological niches. The model with the lowest Akaike Information Criterion (AIC) was chosen by *stepAIC* function from "MASS" package (Ripley 2017) in R program version 4.1.1 (R Core Team, Vienna, Austria).

Forest dynamics

To clarify the drought event, the Standardized Precipitation-Evapotranspiration Index (SPEI), a multiscalar drought index based on climate data (Vicente-Serrano et al. 2010), was used extract dry and wet conditions from air temperature and precipitation data for 2002-2020. The SPEI was calculated for 12-month periods using the SPEI package in R (Beguería et al. 2014). Potential Evapo-Transpiration (PET) was estimated as previously described. To compare climatic conditions between local and global scales, we used the Multivariate El Niño Southern Oscillation (ENSO) Index v2 (MEI.v2) time series data, which include sea level pressure, sea surface temperature, surface zonal winds, surface meridional winds, and outgoing longwave radiation data compiled by the National Oceanic and Atmospheric Administration Physical Sciences Laboratory (https://psl.noaa.gov/enso/mei/).

Then, annualized Mortality (M) and Recruitment (R) rates were used to analyze the forest dynamics in relation to climatic event, based on the method of Sherman et al. (2012) as follows:

$$M\ (\%) = \frac{\ln(N0) - \ln(Ns)}{t} \times 100$$

$$R\ (\%) = \frac{\ln(Nt) - \ln(Ns)}{t} \times 100$$

Where Nt and N0 are the population at time t and time 0, respectively, and Ns is the number of survivors at time t.

RESULTS AND DISCUSSION

Forest structure and species composition

In 2020, the total number of woody plant species with DBH ≥2 cm was 3,669 individuals, including 91 species, 81 genera, and 36 families. The dominant species at the sapling stage (2 cm≤DBH≤4.5 cm) based on IVI values (%) (Table 1) were *Walsura pinnata* (101.34%), *Streblus ilicifolius* (36.08%), *Cleistanthus helferi* (23.28%), *H. ilicifolius* (18.47%), *Streblus taxoides* (12.32%), *Memecylon ovatum* (11.87%), *D. cochinchinense* (9.04%), *Vitex scabra* (7.29%), *Cleistanthus papyraceus* (6.97%), and *Micromelum minutum* (5.22%).

Among tree species with DBH ≥4.5 cm (Table 2), the tree density was 1,552 individuals ha^{-1} and the basal area was 19.12 m^2 ha^{-1}, comprising 75 species, 71 genera, and 32 families. The dominant tree species with DBH ≥4.5 cm with highest IVI values were *W. pinnata* (55.94%), followed by *D. cochinchinense* (53.25%), *H. ferrea* (21.60%), *V. scabra* (13.40%), *H. ilicifolius* (13.26%), *Sterculia pexa* (9.86%), *Leucaena leucocephala* (9.36%), *Microcos tomentosa* (8.17%), *S. ilicifolius* (5.18%), and *Mallotus philippensis* (4.57%).

Table 1. Top 10 dominant sapling species in dry evergreen forest at Wang Nam Khiao Forestry Research and Training Station in Wang Nam Khiao District, Nakhon Ratchasima Province, Northeastern Thailand

Species	Density (individual. ha^{-1})	BA (m^{2}ha^{-1})	IVI (%)	Growth form
Walsura pinnata Hassk.	898	0.74	101.34	T
Streblus ilicifolius (Kurz) Corner	316	0.22	36.08	S/T
Cleistanthus helferi Hook. f.	186	0.14	23.28	S/ST
Hydnocarpus ilicifolius King	120	0.08	18.47	ST
Streblus taxoides (B.Heyne ex Roth) Kurz	98	0.05	12.32	S/T
Memecylon ovatum Sm.	67	0.04	11.87	S/ST
Dialium cochinchinense Pierre	45	0.04	9.04	T
Vitex scabra Wall. ex Schauer	44	0.03	7.29	S/T
Cleistanthus papyraceus Airy Shaw	51	0.03	6.97	S/ST
Micromelum minutum (G.Forst) Wight & Arn.	26	0.02	5.22	S/ST
Other species (55)	296	0.20	68.11	
Total	2,147	19.12	300	

Note: BA: Basal Area; T: Tree; ST: Shrubby Tree, S/ST: Shrub or Shrubby Tree

Table 2. Top 10 dominant tree species in dry evergreen forest at Wang Nam Khiao Forestry Research and Training Station in Wang Nam Khiao District, Nakhon Ratchasima Province, Northeastern Thailand

Species	Density (individual. ha^{-1})	BA (m^{2}ha^{-1})	IVI (%)	Growth form
Walsura pinnata Hassk.	538	1.88	55.94	T
Dialium cochinchinense Pierre	275	4.93	53.25	T
Hopea ferrea Laness.	29	3.15	21.60	T
Vitex scabra Wall. ex Schauer	70	0.92	13.40	ST/T
Hydnocarpus ilicifolius King	62	0.69	13.26	ST
Sterculia pexa Pierre	29	1.01	9.86	ST/T
Leucaena leucocephala (Lam.) de Wit	36	0.94	9.36	S/ST
Microcos tomentosa Sm.	36	0.50	8.17	T
Streblus ilicifolius (Kurz) Corner	33	0.12	5.18	S/T
Mallotus philippensis (Lam.) Müll.Arg	22	0.22	4.57	S/T
other species (65)	422	4.76	105.42	
Total	1,552	19.12	300	

Note: BA: Basal Area; T: Tree; ST: Shrubby Tree, S/ST: Shrub or Shrubby Tree

The species that were dominant in both stages were *W. pinnata*, *D. cochinchinense*, *V. scabra*, *H. ilicifolia* and *S. ilicifolius*, indicating this group of species can maintain a balance of saplings grow into trees stage. However, many of the dominant species were pioneer shrubs, such as *S. pexa*, *M. tomentosa*, and *S. ilicifolius*, or invasive species including *L. leucocephala*. Thus, many species exhibited good regeneration after disturbance.

Within the same size class, the dominant families based on species numbers were Fabaceae (n = 8), followed by Annonaceae (n = 6), Malvaceae (n = 6), Moraceae (n = 6), Ebenaceae (n = 5), and Meliaceae (n = 5). Family Fabaceae also had the highest basal area, at 6.81 m^2 ha^{-1}, followed by Dipterocarpaceae (3.15 m^2 ha^{-1}), Meliaceae (2.24 m^2 ha^{-1}), Malvaceae (1.93 m^2 ha^{-1}), Lamiaceae (0.92 m^2 ha^{-1}), and Achariaceae (0.68 m^2 ha^{-1}). Family Meliaceae had the highest tree density (575 individuals ha^{-1}), followed by Fabaceae (345 individuals ha^{-1}), Malvaceae (88 individuals ha^{-1}), Lamiaceae (72 individuals ha^{-1}), Achariaceae (63 individuals ha^{-1}), and Phyllanthaceae (47 individuals ha^{-1}), due to their large sapling numbers (Figure 2).

The dry evergreen forest examined in this study had a lower tree density and basal area than reported in previous tropical forest studies (Memiaghe et al. 2016; Joshi and Dhyani 2019). However, the high density of saplings was consistent with the findings of Phumphuang et al. (2024). These results indicate that the plant community is in the regeneration process after disturbance. Saplings were abundant in the canopy gap, particularly among pioneer species when large gaps were created. The *H. ferrea* (Dipterocarpaceae), a remnant tree species, had the second highest IVI value but the largest basal area (15.29% of the total basal area; Table 1), demonstrating its significant contribution to the overall forest structure. According to the Shannon-Wiener index, the forest had intermediate species diversity (H' = 2.66).

Stratification of trees with DBH ≥4.5 cm showed that the forest has three vertical stratification and a closed canopy with 72% coverage, particularly on the high elevation (Figure 3). The top canopy layer (height ca. 20-30 m) is mainly dominated by remnant climax species such as *H. ferrea* and *D. cochinchinense*, whereas the middle layer (10-20 m) dominated by *H. ilicifolius*, *M. ovatum*, *S. pexa*, *M. tomentosa*, and *W. pinnata*. The lower canopy (<10 m) dominated by pioneer shrub species such as *S. taxoides*, *M. minutum*, and *Clausena wallichii*. The pioneer species also established under the mid-canopy gap after disturbance. Thus, gaps created through selective cutting provided sufficient light intensity to support the establishment of pioneer species, particularly early in the forest recovery process (Goodale et al. 2014; Furtado et al. 2017; Velázquez and Wiegand 2020).

Our analysis of DBH class distribution included a total of 18 tree species with populations of ≥30 individuals. The results showed two types of DBH class distribution with regular form or reverse J-shaped (13 species) and irregular form (5 species). In both forms, most individual trees belonged to the low-size classes, and tree density rapidly decreased as DBH increased (Figures 4 and 5).

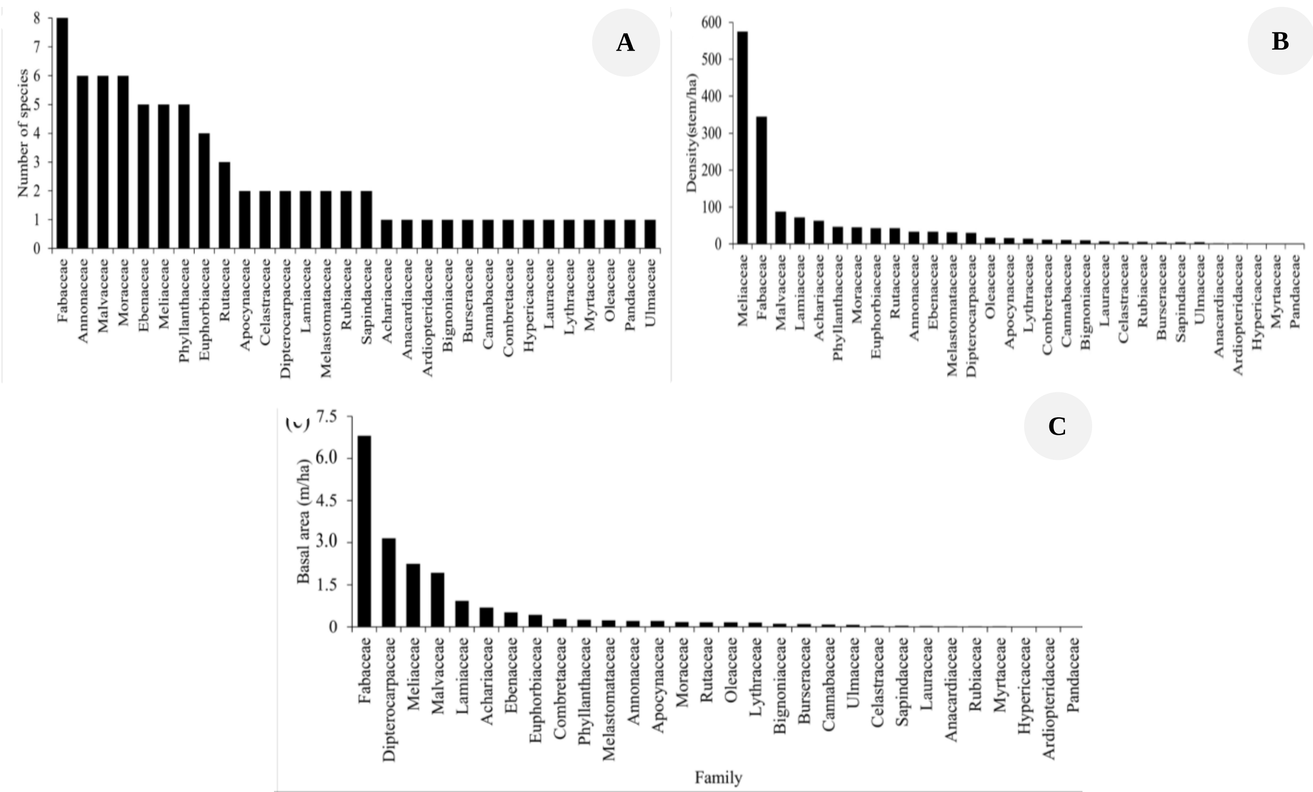

Figure 2. A. Number of species; B. Tree density; and C. Basal area of families in the permanent plot, trees with Diameter at Breast Height (DBH) ≥4.5 cm are included

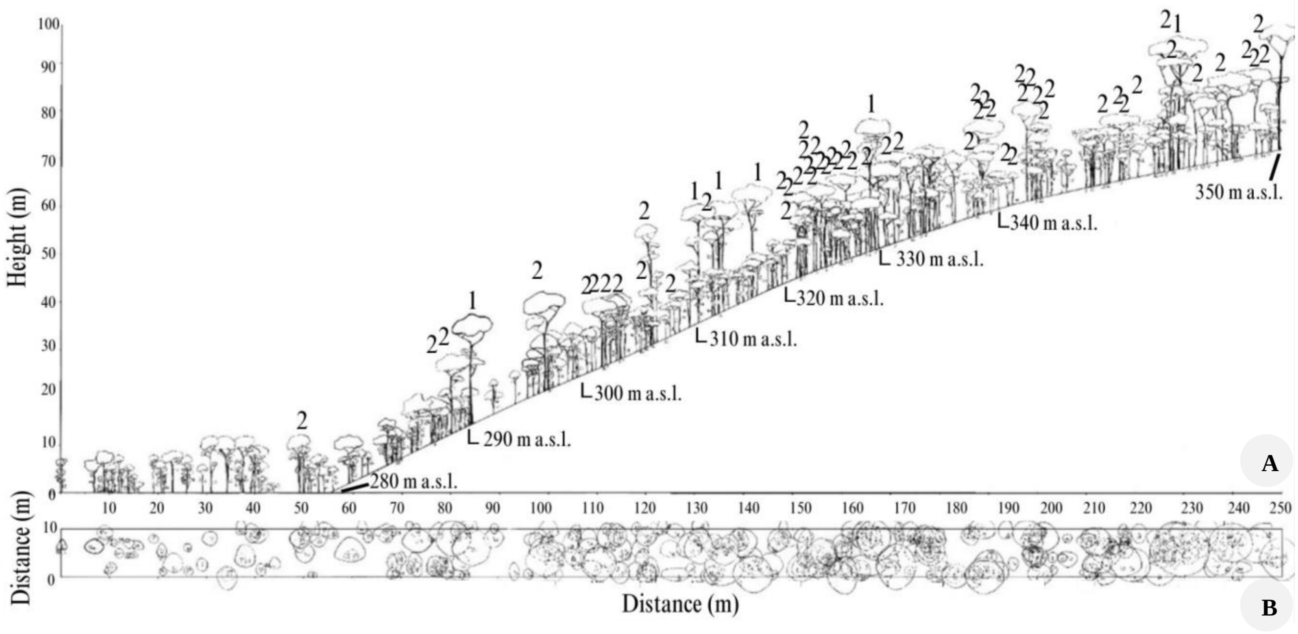

Figure 3. A. Profile diagram; and B. Crown cover diagram in a 1-ha dry evergreen forest at Wang Nam Khiao Forestry Research and Training Station in Wang Nam Khiao District, Nakhon Ratchasima Province, Northeastern Thailand. The numbers indicated the species of 1. *Hopea ferrea* and 2. *Dialium cochinchinense*, respectively

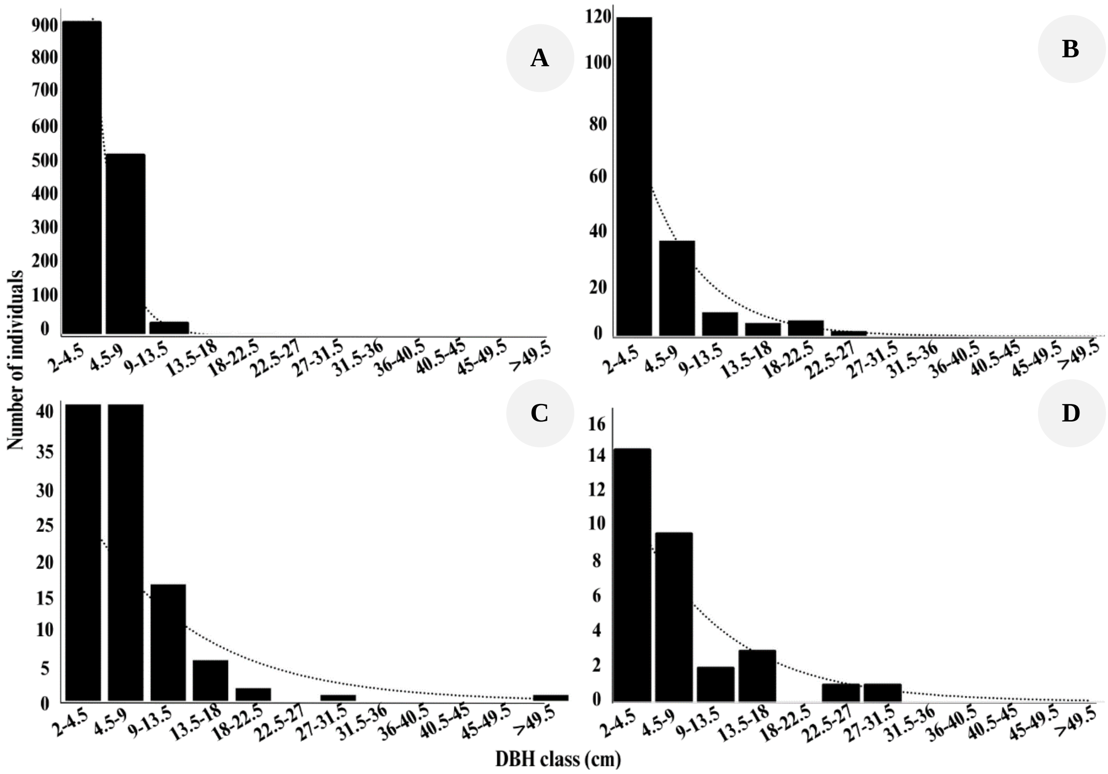

Figure 4. Diameter class distribution of reverse J-shaped form; A. *W. pinnata*; B. *H. ilicifolius*; C. *V. scabra*; and D. *A. lawii*

The negative exponential DBH class distribution form were *W. pinnata*, *H. ilicifolius*, *V. scabra*, and *Aglaia lawii* (Figure 4). This group of species can maintain their population structure by replacing larger trees with those in smaller size classes (Marod et al. 2022). This result is consistent with a study of tropical rainforests that generally consist of large proportions of small-diameter trees (negative exponential distribution form) (Picard 2019).

In contrast, remnant dominant tree species (the upper canopy) such as *H. ferrea* and *D. cochinchinense*, exhibited an irregular DBH class distribution form after selective cutting (Figure 5), indicating discontinued regeneration, particularly within the intermediate DBH size classes. On the other hand, *M. philippensis* and *L. leucocephala*, which had many trees in intermediate DBH also exhibited an irregular DBH class distribution form (Figures 4.C and 4.D). This group was a pioneer species, exhibited rapid establishment after gap canopy creation (Revilla et al. 2024), and reduced growth under a closed canopy with low light intensity. The light-demanding species will be lost from the permanent plot because of environmental factors was changes (low-light Intensity from a closed canopy) (Marod et al. 2012; Swinfield et al. 2016; Saikhammoon et al. 2023).

Species-environment relationship

Our correlation analysis of various environmental factors, such as elevation; slope; sand, silt, clay, pH and OM contents are presented as gradient plots (Figure 6). Slopes were highest in the center of the plot (range, 0-86.6%), and elevations were highest on hilltops (ranges 280-350 m a.s.l.). Sand and clay contents were highest in lowlands due to stream proximity, whereas silt and OM were high at high elevations. The OM was significantly positively correlated with elevation and slope because the permanent plot in the lowlands was near the stream, which caused om runoff during the rainy season. The pH was high on lower slopes (ranges 4.9-5.5).

The spatial distributions of the 19 woody plant species with DBH ≥2 cm and the highest IVI values (more than 10 individuals) varied according to environmental factors. Our GLM analysis revealed that soil texture (silt, clay, and sand contents), slope, and pH had the greatest influence on tree spatial distribution (Table 2). According to these results, we divided the 19 tree species into two groups, such as generalist and specialist species groups.

The first group included generalist group, consisting of *S. ilicifolius*, *W. pinnata*, *D. cochinchinense*, *H. ferrea*, *M. tomentosa*, *M. minutum*, *V. scabra*, *S. lefevrei*, *C. papyraceus* and *L. leucocephala*, which were generally distributed throughout the permanent plot (Figure 7). The distributions of these species were strongly correlated with 4-7 environmental factors (>50% of all factors). Remnant climax species in DEF (*D. cochinchinense* and *H. ferrea)* were correlated with soil texture factors ($p<0.01$ and $p<0.001$, respectively) and topographic factors ($p<0.05$ and $p<0.01$, respectively) (Figures 7.A and 7.B). The spatial distributions of mid-canopy species such as *W. pinnata*, *S. lefevrei*, *M. tomentosa*, and *M. minutum* showed the same trends. Notably, *W. pinnata* had the highest abundance and was distributed across the entire plot (Figure 7.C). The *L. leucocephala* correlated with soil (sand, $p<0.01$; silt clay and pH, $p<0.001$) (Figure 7.F). Thus, this group of species can survive in a wide range of environments and utilize a diverse range of resources, grouping them as a generalist species (Denelle et al. 2020).

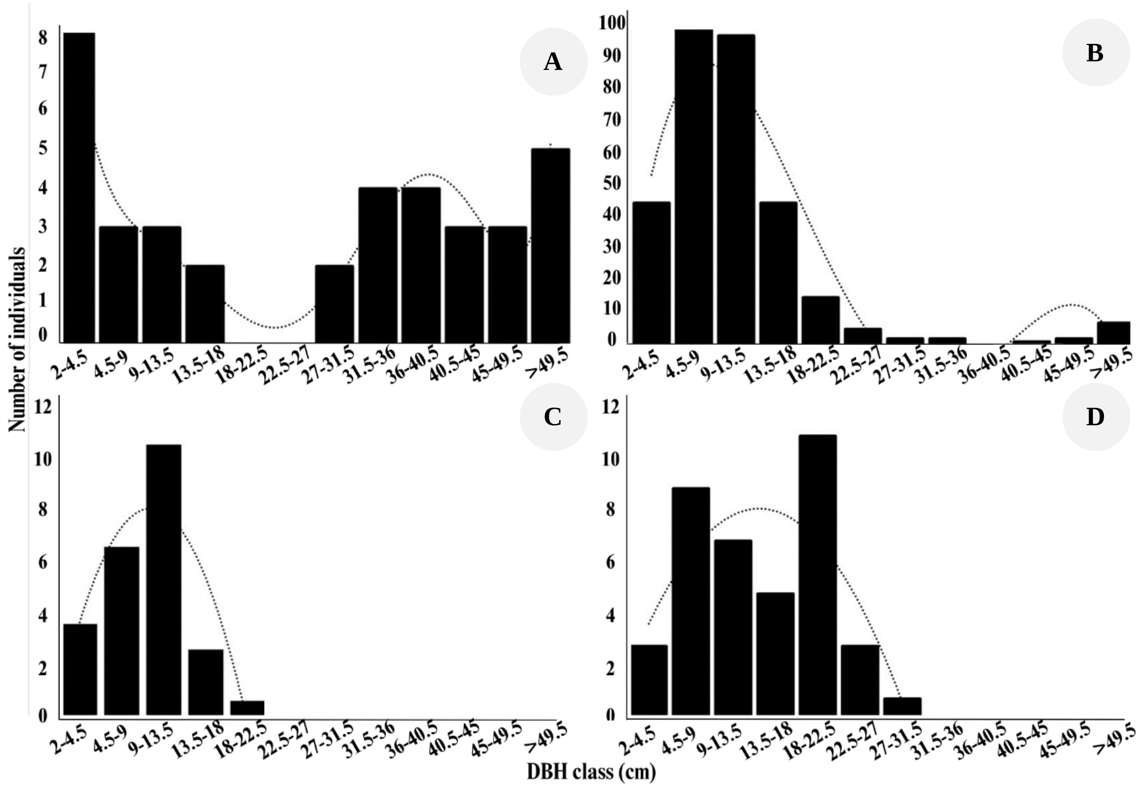

Figure 5. Diameter class distribution of irregular form; A. *H. ferrea*; B. *D. Cochinchinense*; C. *M. philipinensis*; and D. *L. leucocephala*

Table 3. Result of GLM analysis show the relationship between selected dominant species and environmental factors, elevation, slope, sand, silt, clay, OM and pH. The values represented the model regression coefficients which selected form the lowest AIC

Species	Environmental factor								
	Intercept	**Elevation**	**Slope**	**Sand**	**Silt**	**Clay**	**pH**	**OM**	**AIC**
Memecylon ovatum Sm.	-122.94**	0.05***		1.45**	0.69.				277.26
Dialium cochinchinense Pierre	0.94***	-0.64*		-3.21**	-3.00**	-0.76**	-0.45***		566.87
Cleistanthus helferi Hook. f.	4.58	-0.03***	0.019			-1.32	4.92***		521.24
Cleistanthus papyraceus Airy Shaw	-1837***	0.29***	0.14***	18.37***	13.68***	18.69***			151.15
Microcos tomentosa Sm.	-768.31***	0.05*	-0.07**	7.54***	6.98***	9.97***	-5.62.		182.05
Sterculia pexa Pierre	-9.22**	0.11**	0.06*		-1.37*				143.27
Streblus ilicifolius (Kurz) Corner	63.31***	-0.12***	0.06***		-0.70**	-3.36***	4.42***	5.35***	452.78
Walsura pinnata Hassk.	-154.8***		0.02***	1.49**	1.67***	1.91***	-1.14**	0.62	777.35
Hopea ferrea Laness.	-351.38***		0.06**	3.77***	3.60***		6.52***		143.6
Sphaerocoryne lefevrei (Baill.) D.M.Johnson & N.A.Murray	-58.24		-0.13**		-2.06***	10.91***	-21.25***		149.31
Vitex scabra Wall. ex Schauer	-46.72***		-0.04**		0.56***	4.37***	-6.37***		353.92
Hydnocarpus ilicifolius King	2.3		0.01*			-0.87**	2.21**		385.55
Micromelum minutum (G.Forst) Wight & Arn.	-994.34***		0.03*	10.76***	7.59***	7.05***		11.38***	184.81
Murraya paniculata (L.) Jacq.	-38.99***		0.07***		-0.21		7.53***		147.07
Streblus taxoides (B.Heyne ex Roth) Kurz	17.00***		0.05***				-3.72***		273.97
Suregada multiflora (A.Juss.) Baill.	-44.72**				0.23	2.41**			150.36
Wrightia arborea (Dennst.) Mabb.	-491.717**			4.504*	5.048*	6.286***			124.43
Leucaena leucocephala (Lam.) de Wit	-1552.75***			12.05**	12.56***	23.50***	27.72***		89.65
Mallotus philippensis (Lam.) Müll.Arg	95.1914		-0.2007		4.7086*	-12.6826	21.9778	-29.7083*	81.22

Note: Significant level: ***** p<0.05; ****** p<0.01; ******* p<0.001

The second group (Figure 8) included a specialist species group, consisting of 9 species: *H. ilicifolius*, *W. arborea*, *C. papyraceus*, *S. taxoides*, *M. paniculata*, *C. helferi*, *M. ovatum*, *S. multiflora*, *S. pexa*, and *M. philippensis*. This group species was correlated with only three environmental factors (<50% of all factors). The topographic and soil texture factors also influenced the spatial distributions of species in this group, but these factors differed among species. For example, the *H. ilicifolius* was positively correlated with slope and soil pH. The *C. helferi* correlated with soil pH and elevation (Table 2). Almost all species, excluding *H. ilicifolius*, were pioneer species; many were dominant in open lowland areas, such as *M. paniculata* and *C. helferi* (Figures 8.A and 8.B), whereas *S. taxoides* were distributed between remnant trees (Figure 8.A). Thus, species in this group can endure limited environmental factors and utilize a narrow range of resources, particularly under high light intensity, making them specialist species (Denelle et al. 2020). By strategically incorporating both pioneer and climax species as framework species in restoration efforts (Elliott et al. 2022), forest managers can encourage more natural progression of plant communities over time, leading to greater biodiversity and ecosystem resilience. For example, we found that the pioneer species *M. minutum* and the climax species *M. ovatum, W. pinnata*, and *D. cochinchinense* were suitable for promoting restoration in this degraded dry evergreen forest. Considering the ecological niches of this group that can be applied to forest restoration projects, selected species for specific environmental factors promote the chance of success.

Forest dynamics

SPEI index values ≥1 and ≤-1 were used to extract wet and dry periods (Figure 9.A), respectively, from the ENSO data. Similarly, MEI.v2 index values ≥0.5 and ≤-0.5 were used to extract warm and cold phases (Figure 9.B), respectively. The forest structure in the study area was significantly impacted by ENSO occurrences and drought conditions, although they showed different patterns. For example, drought conditions were observed during 2002-2008 despite a La Niña event. An extreme El Niño event occurred during 2015-2016, followed by increasingly moderate conditions in 2009-2010, 2002-2003, 2007, 2004-2005, and 2018-2020 (Figure 9).

Our analysis of forest dynamics from 2002 to 2020 showed that the net average recruitment rate (RR) (2.75 ± 1.70% year^{-1}) was higher than the net average mortality rate (MR) (2.14 ± 0.73% year^{-1}) and varied among periods; notably, the RR rates during 2018-2020 increased almost twofold (Table 2). This change led to an overall increase in basal area, from 16.76 to 20.60 m^2 ha^{-1}, although basal area had been reduced during 2002-2004 due to greater losses than gains (Table 3). Species diversity was almost balanced throughout the study period.

However, pioneer or light-demanding species, such as *Trema orientalis* and *Grewia eriocarpa*, disappeared and were replaced by shade-tolerant shrubby dry evergreen species including *Garcinia speciosa* and *Glycosmis pentaphylla*. The establishment of evergreen species, particularly under the extremely wet conditions during 2018-2020 (Figure 9.A), indicate highly successful natural recovery from disturbance, supported by high recruitment rates. The opposite trend observed under the dry conditions during 2002-2005 (Figure 9.B), which indicated that low light intensity and high moisture content were strongly influential factors for dry evergreen species establishment (Phumphuang et al. 2024).

The overall relationships between mortality and recruitment rates (Figure 10, Table 4) for individual tree species with DBH ≥2 cm and more than 10 individuals varied among species throughout the study period (black dot), these species were divided into three groups, considering the balance line (dashed line). The first group consisted of species with higher recruitment rates than mortality rates, among which *S. taxoides* (approximately 9.8% year^{-1}) had the highest recruitment rate, followed by *M. ovatum*, *S. ilicifolius*, *H. ilicifolius*, *S. lefevrei*, and *W. pinnata*. The second group consisted of species with higher mortality rates than recruitment rates, among which *M. minutum* had the highest mortality rate (11.25% year^{-1}), followed by *L. leucocephala*, *C. timorensis*, and *H. ferrea*. The third group exhibited almost balanced recruitment and mortality rates; this group contained only *W. arborea* and *D. cochinchinense*.

Relationships between MR and RR in 3 periods indicated that the patterns differed among periods and species (Figure 11). Deciduous light-demanding species, such as *L. leucocephala* demonstrated increased mortality rates in each period (Figure 11) and were invasive species (Diaz-Soltero 2022). Invasive species grow and rapidly expand through high tolerance of nutrient-poor soils, high temperatures, and drought, which allow quick regeneration (Bageel et al. 2020; Bageel and Borthakur 2022). These species inhibit light transmittance to the forest floor due to excessively broad and bushy growth, interrupting natural forest regeneration within their shade (Marod et al. 2012).

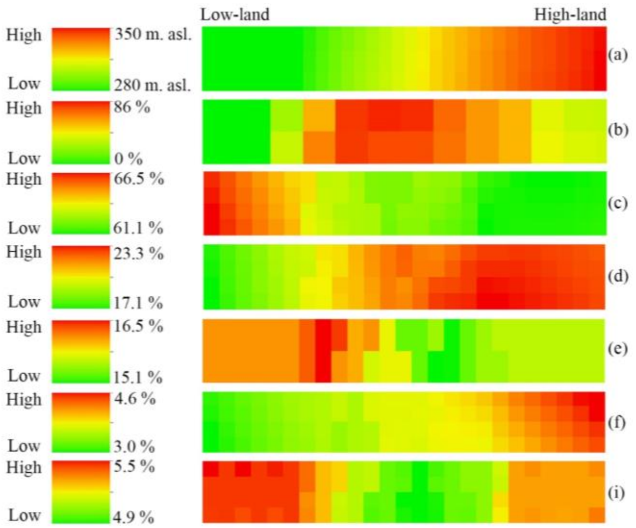

Figure 6. Environmental factor mapping characteristics in the dry evergreen forest at Wang Nam Khiao Forestry Research and Training Station in Wang Nam Khiao District, Nakhon Ratchasima Province, Northeastern Thailand; (a) elevation; (b) slope, (c) sand, (d) silt; (e) clay, (f) organic matter (OM), and (i) soil pH, respectively

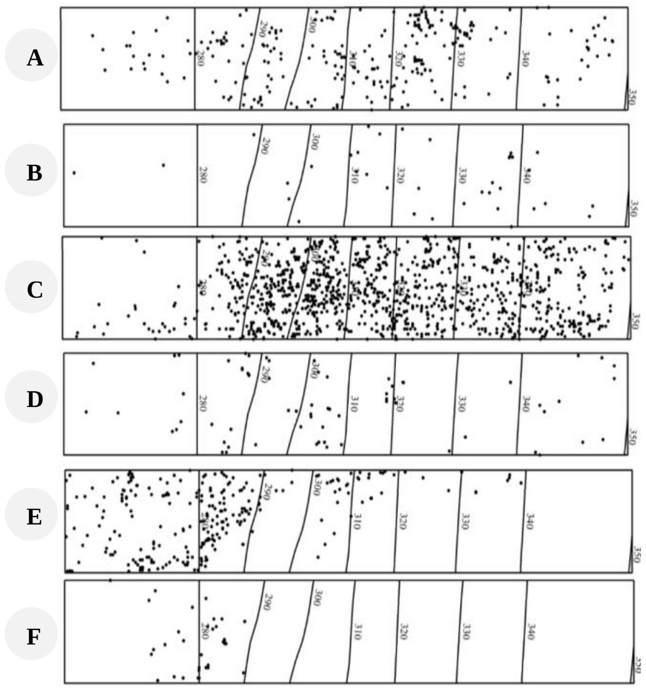

Figure 7. Trees spatial distribution of generalist species with contour lines in 1-ha permanent plot: A. *D. cochinchinense*; B. *H. ferrea*; C. *W. pinnata*; D. *V. scabra*; E. *S. ilicifolius*; and F. *L. leucocephala*

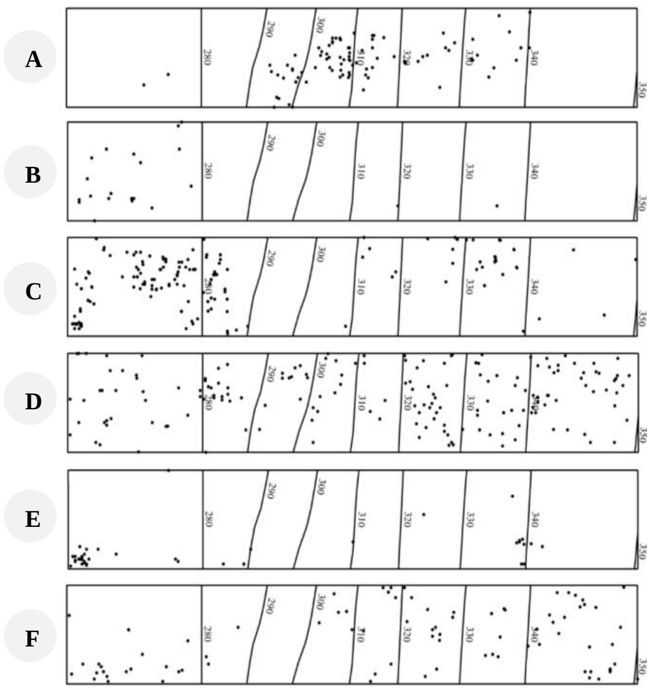

Figure 8. Trees spatial distribution of specialist species with contour lines in 1-ha permanent plot. A. *S. taxoides*; B. *M. philippensise*; C. *C. helferi*; D. *H. ilicifolia*; E. *C. papyraceus*; and F. *M. ovatum*

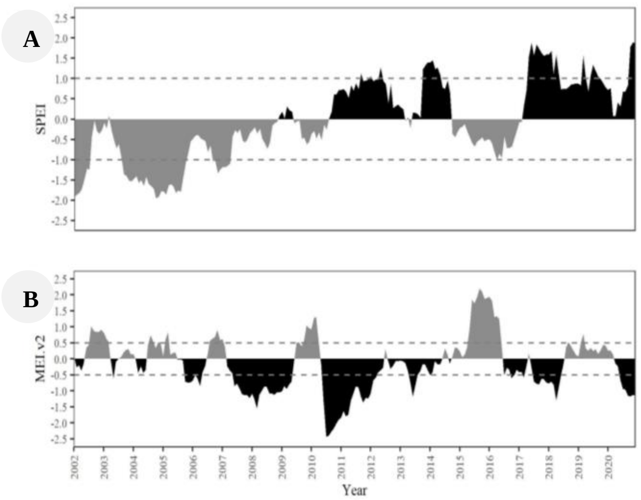

Figure 9. A. The wet and drought conditions based on SPEI at SERS; and B. The global scale of ENSO oscillation events during 2002-2020. Black color was wet years/La Niña and grey color was drought years/El Niño

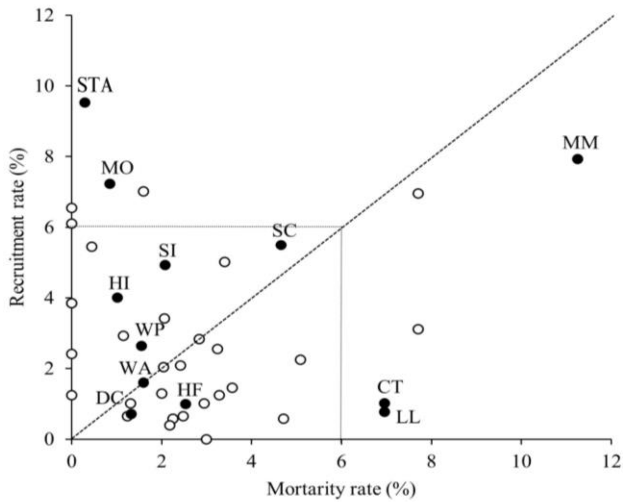

Figure 10. Relationships between RR and MR during the 18-year, the dash line was balance line. STA: *S. taxoides*; CT: *C. timorensis*; SI: *S. ilicifolius*; MO: *M. ovatum*; HI: *H. ilicifolia*; LL: *L. leucocephala*; MM: *M. minutum*; WP: *W. pinnata*; SC: *S. leferei*; WA: *W. arborea*; HF: *H. ferrea;* DC: *D. cochinchinense*

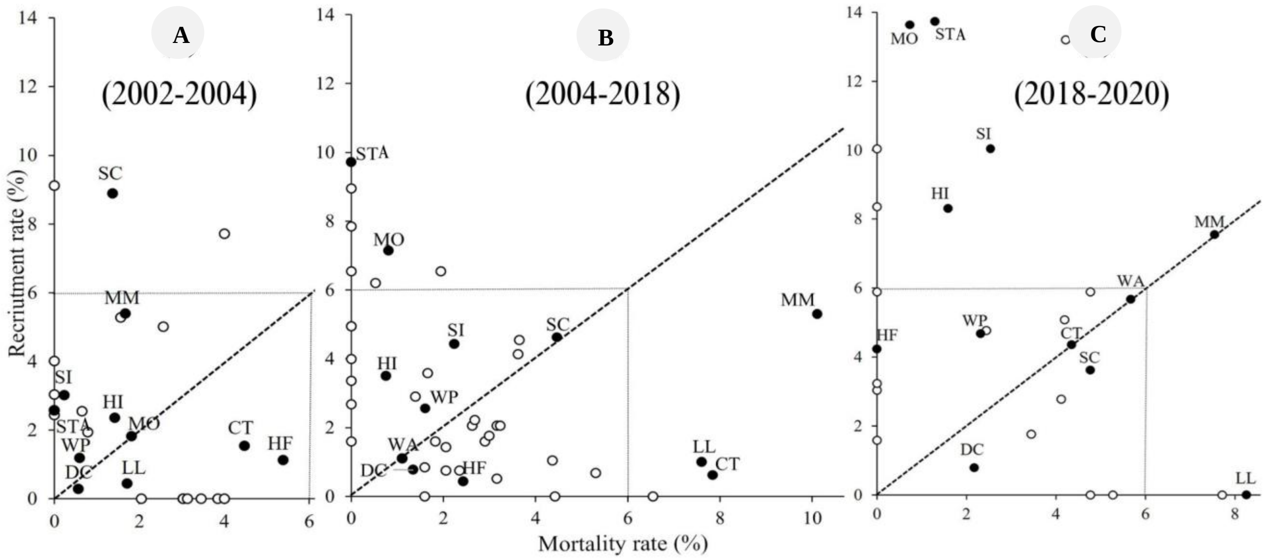

Figure 11. Relationship between RR and MR during the 18 years period, the dash line was balance line, while A.; B; and C. represent first 2002-2004, second 2004-2018 and third period 2018-2020, respectively, STA: *S. taxoides*; CT: *C. timorensis*; SI: *S. ilicifolius*; MO: *M. ovatum*; HI: *H. ilicifolia*; LL: *L. leucocephala*; MM: *M. minutum*; WP: *W. pinnata*; SC: *S. leferei*; WA: *W. arborea*, HF: *H. ferrea*, DC: *D. Cochinchinense*

Table 4. Summary table of forest dynamics (DBH≥2 cm) in 1-ha permanent plot in the dry evergreen forest at Wang Nam Khiao Forestry Research and Training Station in Wang Nam Khiao District, Nakhon Ratchasima Province, Northeastern Thailand

Variable	2002		2004		2018		2020	Mean±SD.
Density (individual.ha^{-1})	3,250		3,287		3,466		3,668	3,370 ±191.64
MR (%/yr)		1.19		2.40		2.94		2.14 ±0.73
RR (%/yr)		1.76		2.78		5.77		2.75 ±1.70
BA (m^2/ha)	16.76		16.48		19.74		20.60	18.35 ±1.80
Loss (m^2/ha)		2.28		4.48		0.75		1.88 ±1.53
Gain (m^2/ha)		2.00		7.74		1.61		2.84 ±2.80
No. of species	93		94		92		91	93 ±1.11

Notes: MR: Mortality Rate; RR: Recruitment Rate

Invasive light-demanding species populations were reduced when the recovering forest approached the state of the primary forest; a similar pattern was observed in 2 periods for *M. minutum* that has a good recruitment rate in the first period and reduced when a long time passed (14 years). Based on *M. minutum* not an invasive species, it can be maintained that the recruitment rate and mortality rate are in a balanced line in the third period under low-light intensity (Figure 11), whereas a dissimilar trend was observed for mid-canopy trees such as *M. ovatum*, *H. ilicifolius*, and *W. pinnata* (Figure 11). These species increased their populations under intermediate light conditions; notably, *W. pinnata* reached a similar population density (1,436 individuals ha^{-1}) to that reported in a previous study (Phumphuang et al. 2018). The regeneration of upper canopy climax species, such as *H. ferrea* and *D. cochinchinense*, was less successful in terms of sapling establishment; these species may require specific environmental conditions for regeneration.

In conclusion, the diversity of the species in the studied site was high (91 species from 81 genera and 36 families), consisting a mix of pioneer species and the remnant/climax species. Stratification of trees divided into 3 canopy layers with a closed canopy (72% coverage). Many species showed regular regeneration based on DBH class distributions. Net recruitment was higher than the mortality rate throughout the period studied, showing that adaptation to dry and wet conditions strongly influenced forest dynamics in the study plot. Pioneer or light-demanding species disappeared based on environmental change and were replaced by shade-tolerant shrubby dry evergreen species. The results of this research indicated that the ecological niche of each species is related to environmental factors, topographic factors, soil properties, and adaptation to climate factors. This knowledge can be useful for further application to the conservation and restoration of dry evergreen forests in the country, which increases the chance of successful forest restoration after disturbance.

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