The dynamics of deciduous dipterocarp forest in relation to climate variability in the Sakaerat Biosphere Reserve, Northeastern Thailand

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Abstract. *Yatar C, Thinkampheang S, Sungkaew S, Wachrinrat C, Asanok L, Kamyo T, Hermhuk S, Kachina P, Thongsawi J, Phumphuang W, Yarnvudhi A, Waengsothorn S, Cheysawat S, Marod D. 2024. The dynamics of deciduous dipterocarp forest in relation to climate variability in the Sakaerat Biosphere Reserve, Northeastern Thailand. Biodiversitas 25: 3088-3098.* Climate change is a major environmental problem influencing forest dynamics. To clarify tropical seasonal forest dynamics under climate change, we conducted long-term monitoring of all trees with Diameter at Breast Height (DBH) ≥4.5 cm within a 1-ha permanent plot established in 2004 in a deciduous dipterocarp forest in the Sakaerat Biosphere Reserve (SBR), Northeastern Thailand. Surveys of all trees within the plot with DBH ≥2 cm were conducted in 2008, 2015, and 2019. Climate data were obtained from the SBR climate station during 2004-2019 and used to extract dates with drought and wet conditions. Forest dynamics varied among species and periods, with stem density exhibiting a decreasing trend. Despite prolonged drought conditions from 2004 to 2009, which usually leads to increased mortality rates, the recruitment rate was 7-fold higher than the mortality rate at a site protected from fire during 2004-2008, and most of the recruited species were pioneer species, shrubs, and small trees. A contrasting trend was observed during 2015-2019, with a mortality rate almost 10-fold higher than the recruitment rate, indicating a significant ecological disturbance, likely to have been driven by a severe El Niño event during 2015-2016. Thus, climate induced disturbances (i.e., drought and fire) appear to have inhibited tree regeneration in the deciduous dipterocarp forest, particularly when they occurred in combination and for specific timing and intensity levels. Addressing the challenges posed by drought and fire to tree regeneration requires holistic management approaches that consider both ecological and climatic factors. Monitoring and adaptive management are also essential to mitigate the impact of future disturbances and support the long-term viability of forest ecosystems.

Keyword: Climate change, forest dynamics, forest fire, SPEI

INTRODUCTION

Tropical forests cover 10% of the Earth's surface (Corlett 2016), yet they harbor the highest plant species diversity globally)Brown 2014). They also serve as critical carbon sinks)Poorter et al. 2015). Currently, tropical forests face risks of deforestation due to both anthropogenic and natural disturbances, releasing carbon emissions into the atmosphere (Wohlfart et al. 2014; Baccini et al. 2017). Among several types of disturbances, drought may be one the main disturbances which influence forest dynamics (Martínez-Vilalta and Lloret 2016).

Tropical dry forests, which once represented up to 42% of all tropical forests, are characterized by deciduousness, prolonged dry periods, and low annual precipitation (Silva et al. 2015; Siyum 2020). In Thailand, the primary types of tropical dry forest are dry evergreen, mixed deciduous, and deciduous dipterocarp forests (Rundel and Boonpragob 1995). In the mixed deciduous and deciduous dipterocarp forests, large fires usually occur in extensive drought periods during the dry season, mainly as lower-intensity surface fires (Kaewsong et al. 2022). These fires may function as a key factor to control the structure of deciduous dipterocarp forest (Marod et al. 1999). Excessive burning can lead to the destruction of vegetation and habitat, potentially causing a loss of biodiversity and altering the forest's composition. On the other hand, too infrequent burning can allow for the accumulation of dead plant material, which can lead to more intense fires when they do occur, causing widespread damage and potentially

even preventing certain species from regenerating. For instance, frequent burning can hinder tree regeneration and reduce tree density (Verma and Jayakumar 2015), while prolonged fire suppression can lead to changes in species composition (Kurten et al. 2018; Shumi et al. 2019; Phumsathan et al. 2022), contrasting with the dry evergreen forests where fires rarely occur (Trouvé et al. 2020). In fire-prone communities, plants have adapted to resist fire disturbance, e.g. sprouting, thick bark, fire-activated seed, and self-pruning branches (Pausas and Keeley 2014; Prior and Bowman 2020; Stevens et al. 2020; Hartung et al. 2021); however, seedlings and saplings remain susceptible to destruction by fire (Harvey et al. 2016; Chaturvedi et al. 2017).

In the context of climate change, El Niño events often reduce rainfall and induce severe drought in the tropics (Lopes et al. 2016; Wigneron et al. 2020), critically influencing species diversity and tree dynamics (Morin et al. 2018; Miyamoto et al. 2021; Liu et al. 2024) and dramatically increasing mortality rates among young plants, seedlings, and saplings (Lalor et al. 2023; Nutiprapun et al. 2023). For example, El Niño events during 2015-2016 induced high tree mortality in Bornean tropical forests, primarily due to drought conditions (Miyamoto et al. 2021). In addition, prolonged drought can interact with large forest fuel loads, particularly in tropical dry forests, leading to high fire intensity, which inhibits tree regeneration (Marod et al. 2004). However, the impacts of drought on tropical dry forests require further elucidation, particularly through long-term ecological research based on forest dynamics plots, to achieve more accurate predictions of the effects of global climate change

or disturbance dynamics in tropical dry forests (Aubry-Kientz et al. 2015; Phumphuang et al. 2018; Siyum 2020).

In Thailand, permanent plots for monitoring forest dynamics have been established in various ecosystems, with large plots (>10 ha) located mainly in evergreen forests such as lower montane (Rueangket et al. 2021), moist evergreen (Kurten et al. 2018), and dry evergreen forests (Davies et al. 2021; Kaewsong et al. 2022; Phumphuang et al. 2024). In contrast, small forest dynamics plots (1-4 ha) are located mainly in deciduous forests such as mixed deciduous (Marod et al. 1999) and deciduous dipterocarp forests (Sahunalu 2009; Kaewfoo et al. 2024). Because of such discrepancy, the effects of climate change on drought- and fire-prone deciduous dipterocarp forest community dynamics remain poorly understood. In this study, we investigated the influence of climate change, particularly intensified drought conditions, on deciduous dipterocarp forest dynamics in a permanent plot established in the Sakaerat Biosphere Reserve (SBR), Northeastern Thailand. Insights gained from this research will enhance our understanding of the forest dynamics response to climatic variations and provide essential guidelines for future biodiversity conservation plan to mitigate the climate change.

MATERIALS AND METHODS

Study site

The SBR is associated with the Sakaerat Environmental Research Station (SERS), Sakaerat Biosphere Reserve (SBR), Nakhon Ratchasima Province, Northeastern Thailand (14°30'N, 101°51'E; Figure 1).
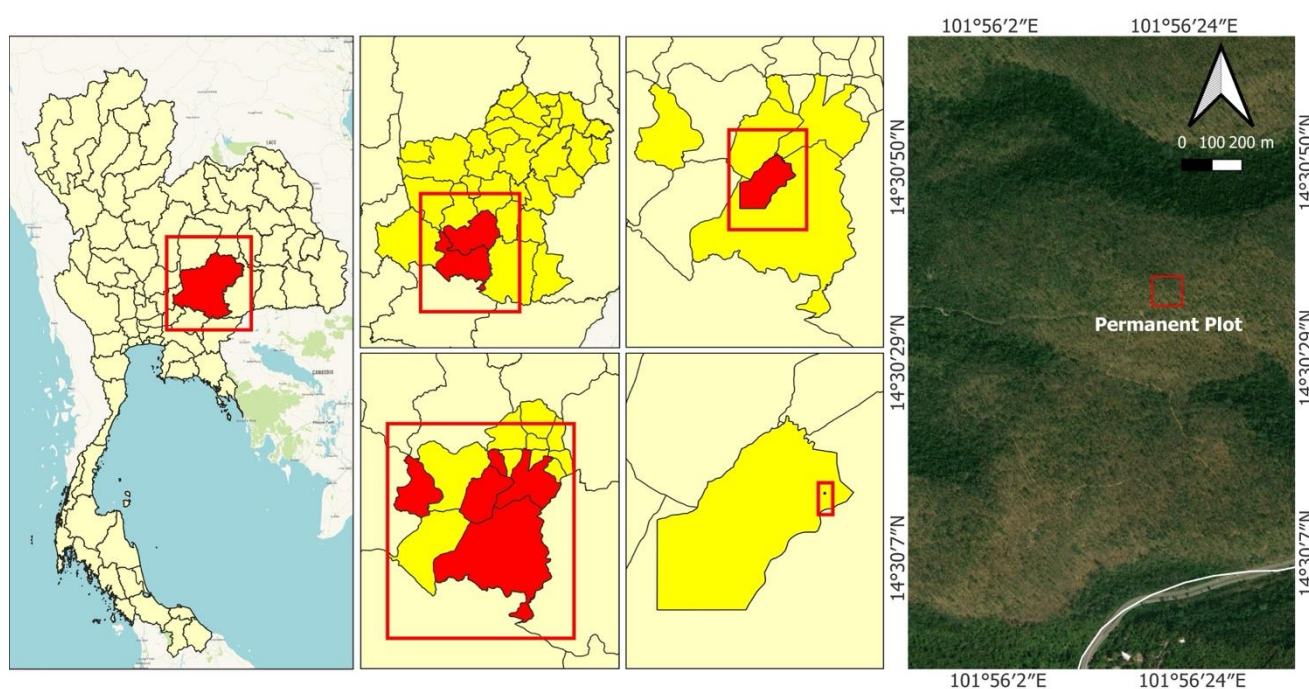

Figure 1. Map of study area showing Forest Dynamic Plots (FDP) in Sakaerat Biosphere Reserve (SBR), Nakhon Ratchasima Province, Thailand
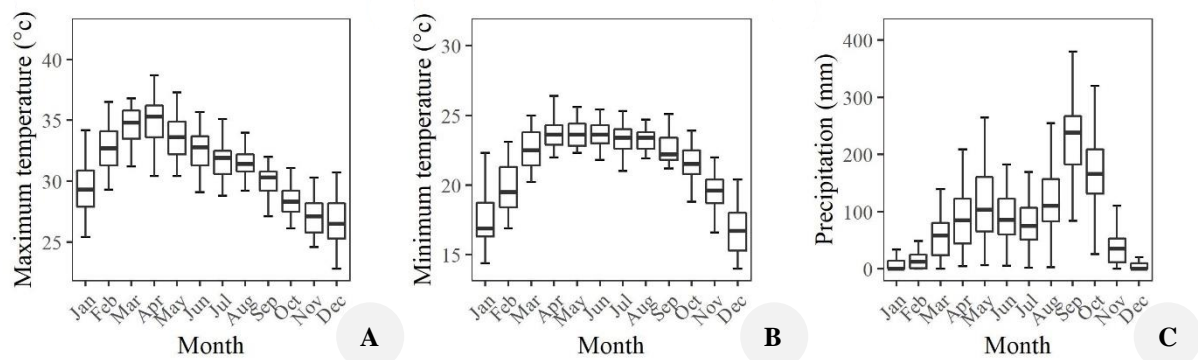
Figure 2. Mean monthly of climatic data during January 1983 to December 2019 at Sakaerat Biosphere Reserve, Nakhon Ratchasima Province, Thailand: A. Mean maximum temperature; B. Mean minimum temperature; and C. Mean precipitation. The upper and lower whiskers of each boxplot indicated the maximum and minimum value of each parameter in each month

Since its establishment in 1967, the SBR has been managed for biodiversity conservation and sustainable forestry according to the Man and Biosphere Reserve Programme, and used as a long-term ecological research site. The SERS encompasses approximately 78.08 km^2 on the Korat Plateau, surrounded mainly by mountains at elevation of 280-762 m a.s.l. with slopes of 10-30%. The sedimentary rock is sandstone of the Phra Wihan formation in the Korat group (Methikul and Silpalit 1968). The soil is predominantly laterite and is generally poor, with rocky outcrops. The upper soil texture is mainly sandy, particularly in deciduous dipterocarp forests, with sandy loam and sandy clay loam (Sakurai et al. 1998). The site has a tropical monsoon climate, with a mean annual rainfall and temperature of 1,032 mm and 26.36°C, respectively, according to climate data collected by SERS from 1983 to 2019. The monthly rainfall is <50 mm in the dry season (November-April) and >100 mm in the rainy season (May-October), reaching a maximum in September (Figure 2.C). The maximum monthly temperature is reached in March and April (37-38°C), and the minimum is reached in December and January (15-18°C) (Figures 2.A and 2.B). Natural forests in the SBR are comprised, mainly, of dry evergreen forest followed by deciduous dipterocarp and mixed deciduous forest, some of which are secondary forests (Figure 1). The top canopy layer of the deciduous dipterocarp forests is mainly comprised of deciduous species of Dipterocarpaceae, such as *Shorea siamensis* (Kurz) Miq., *Shorea obtusa* Wall., *Dipterocarpus intricatus* Dyer, and *Dipterocarpus tuberculatus* Roxb. (Rundel et al. 2017). Surface fires occur frequently during the dry season in the deciduous dipterocarp forests. The study area was protected from fire during 2004-2008, after which fires occurred in 2009, 2010, 2012, 2013, 2015, and 2018.

Plot establishment and tree species

In 2004, a 1-ha (100 m × 100 m) permanent plot was established in deciduous dipterocarp forest, and divided into subplots of 10 m × 10 m for a total of 100 subplots. All trees with diameter at breast height (DBH, i.e., 1.30 m) ≥4.5 cm were marked with aluminum tags and their ID number, position (x, y), height, and DBH were recorded. A

mark was painted on the trunk at the DBH measurement point, and the tree was identified to species according to the specimen collection at the Bangkok Forest Herbarium of the Department of National Parks, Wildlife and Plant Conservation, with nomenclature following The Forest Herbarium (2014). The trees were monitored in three subsequent surveys, in 2008 (1st), 2015 (2nd), and 2019 (3rd), for a total study period of 15 years. Starting in the 2nd survey, all trees with DBH ≥2 cm were monitored.

Climatic data

Climatic data from 1983 to 2019 were retrieved from SBR weather station and monthly maximum temperature (°C), minimum temperature (°C), and total monthly precipitation (mm) were analyzed (Figure 2). However, the climate change analysis, we selected only data from the years 2004 to 2019 relating to tree monitoring period.

Data analysis

Forest structure and tree regeneration

Tree species composition was analyzed based on data collected for trees with DBH ≥4.5 cm in the latest survey (2019). Forest structure was described in terms of the number of tree stems, and basal area of the dominant species (Berhanu et al. 2017), which was identified according to the importance value index (IVI). The IVI was calculated by summing relative density, relative frequency, and relative dominance scores (Curtis and Mcintosh 1950).

Regeneration was evaluated according to the DBH size class distributions of all tree species, with at least 20 individuals having DBH ≥2 cm, following the method described by Shumi et al. (2019).

Climate change

Drought and wet conditions were extracted from air temperature and precipitation data for 2004-2019 according to the Standardized Precipitation-Evapotranspiration Index (SPEI), which is a multi-scalar drought index based on climate data (Vicente-Serrano et al. 2010). The SPEI was calculated for 12-month periods for drought area analysis as previously described (Yu et al. 2014) using the SPEI package (Beguería et al. 2014) in R v3.6.2 (R Core Team,

Vienna, Austria). Potential Evapotranspiration (PET) was estimated as previously described (Hargreaves and Samani 1985).

To compare climatic conditions between local and global scales, we used the Multivariate El Niño Southern Oscillation (ENSO) Index v2 (MEI.v2) data product compiled by the National Oceanic and Atmospheric Administration Physical Sciences Laboratory (https://psl.noaa.gov/enso/mei/). MEI.v2 index values ≥0.5 and ≤-0.5 are classified as warm and cold phases, respectively (Zhang et al. 2019).

Forest dynamics

Forest dynamics were considered only for woody plants with DBH ≥4.5 cm and characterized using the mortality rate (m) and recruitment rate (r) based on Condit et al. (1999) as follows:

$$m = \frac{\ln n_0 - \ln S_t}{t}, r = \frac{\ln n_t - \ln S_t}{t}$$

Where:

n_0 and n_t: The population size at time 0 and time *t*, respectively

S_t : The number of survivors at time *t*

t : The census interval

Dominant tree species with more than 10 individuals at each census were used to evaluate the relationship between recruitment and mortality rates. Tree density and basal area differences among census years were evaluated using Analysis of Variance (ANOVA).

RESULTS AND DISCUSSION

The structure of deciduous dipterocarp forest

At 3rd monitoring in 2019, our surveys recorded 533 trees with DBH ≥4.5 cm, comprising 54 species belonging to 43 genera and 23 families. The tree density and basal area were 581 stems ha-1 and 16.47 m2 ha-1, respectively. The dominant families based on species number were Fabaceae (9 species), Rubiaceae (7), Dipterocarpaceae (4),

Ebenaceae (4), Malvaceae (4), Phyllanthaceae (4), and Anacardiaceae (3); the remaining families were represented by only 1 or 2 species (Figure 3.A). High tree density was observed among the families Fabaceae, Rubiaceae, and Dipterocarpaceae (Figure 3.B). The 10 tree species with the highest IVI values were *Pterocarpus macrocarpus* Kurz (IVI = 59.54%), *Xylia xylocarpa* (Roxb.) W.Theob. (33.29%), *Bauhinia saccocalyx* Pierre (26.40%), *D. Intricatus* (24.38%), *Mitragyna rotundifolia* (Roxb.) Kuntze (16.04%), *S. obtusa* (15.03%), *Lannea coromandelica* (Houtt.) Merr. (15.02%), *Sindora siamensis* Teijsm. ex Miq. (13.06%), *Morinda coreia* Buch.-Ham. (11.38%), and *Albizia odoratissima* (L.f.) Benth. (10.76%) (Table 1).

Tree regeneration

A total of 11 species with population greater than 20 individuals were selected for DBH class distribution analysis, which divided the DBH classes into three distributions. Three species (*X. xylocarpa*, *Rothmannia wittii* (Craib) Bremek., and *B. saccocalyx*) had a negative exponential (inverted J shape) distribution, characterized by large populations of small trees and small populations of large trees (Figure 4). Five species (*L. coromandelica*, *M. coreia*, *A. odoratissima*, *S. obtusa*, and *D. intricatus*) had an irregular distribution, characterized by discontinuous populations (Figure 5). Finally, three species (*P. macrocarpus*, *M. rotundifolia*, and *Morinda tomentosa* B.Heyne ex Roth) had a bell-shaped distribution, with large populations of intermediate-sized trees and small populations of small and large trees, respectively (Figure 6). These results indicate that regeneration rates varied among species, such that deciduous dipterocarp forest climax species such as *S. obtusa* and *D. intricatus* were less successfully established within the lower size classes. In contrast, the mixed deciduous forest climax species *X. xylocarpa* and pioneer species *B. saccocalyx* showed a negative exponential distribution, indicating highly successful regeneration that allowed them to maintain lower size classes that will eventually become large trees.
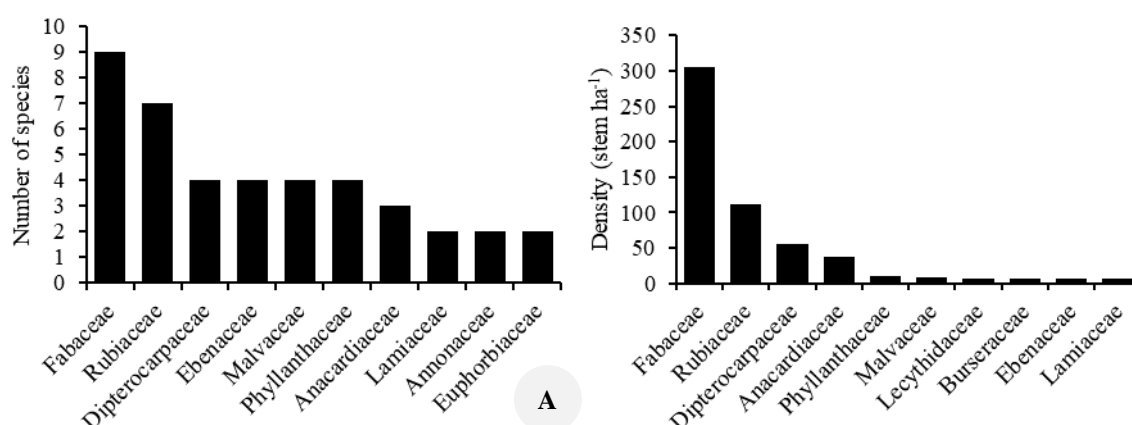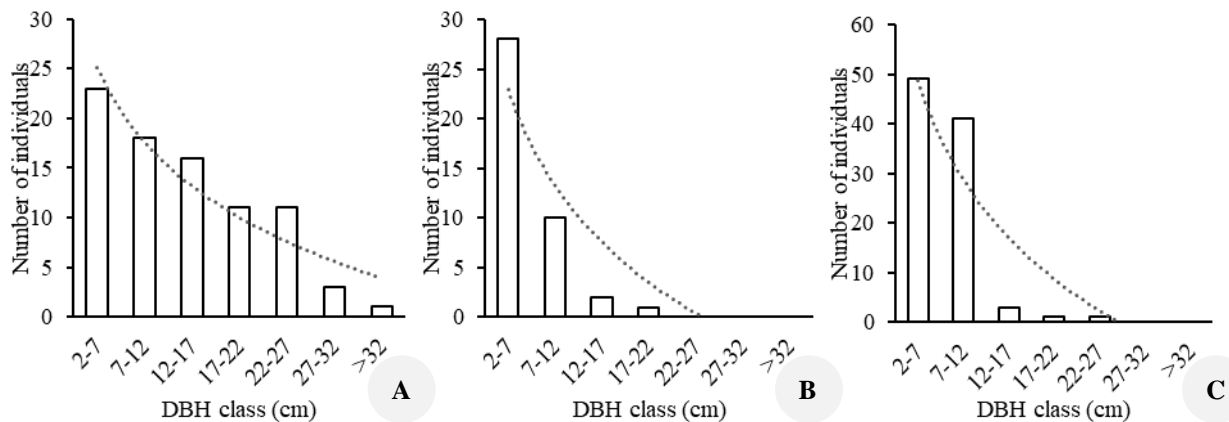

Figure 3. A. The dominant families based on number of species; and B. tree density of found species at forest dynamics plots of deciduous dipterocarp forest in 2019 at Sakaerat Biosphere Reserve, Nakhon Ratchasima Province, Thailand

Table 1. Dominant tree species with DBH ≥4.5 cm in the deciduous dipterocarp forest in 2019 at Sakaerat Biosphere Reserve, Nakhon Ratchasima Province, Thailand

Species	Family	Density (stem ha⁻¹)	BA (m ha⁻¹)	IVI (%)	Growth forms
Pterocarpus macrocarpus Kurz	Fabaceae	99	4.40	59.54	T
Xylia xylocarpa (Roxb.) W.Theob.	Fabaceae	72	1.52	33.29	T
Bauhinia saccocalyx Pierre	Fabaceae	84	0.48	26.40	ST
Dipterocarpus intricatus Dyer	Dipterocarpaceae	23	2.53	24.38	T
Mitragyna rotundifolia (Roxb.) Kuntze	Rubiaceae	32	0.65	16.04	T
Shorea obtusa Wall.	Dipterocarpaceae	22	1.13	15.03	T
Lannea coromandelica (Houtt.) Merr.	Anacardiaceae	34	0.83	15.02	T
Sindora siamensis Teijsm. ex Miq.	Fabaceae	15	1.21	13.06	T
Morinda coreia Buch.-Ham.	Rubiaceae	22	0.53	11.38	ST
Albizia odoratissima (L.f.) Benth.	Fabaceae	23	0.48	10.76	T
Morinda tomentosa B.Heyne ex Roth	Rubiaceae	20	0.28	9.05	ST
Rothmannia wittii (Craib) Bremek.	Rubiaceae	20	0.13	7.17	S
Shorea roxburghii G.Don	Dipterocarpaceae	8	0.28	5.03	T
Gardenia sootepensis Hutch.	Rubiaceae	10	0.16	4.65	ST
Canarium subulatum Guillaumin	Burseraceae	6	0.29	4.58	T
Careya arborea Roxb.	Lecythidaceae	7	0.10	3.51	T
Dalbergia dongnaiensis Pierre	Fabaceae	6	0.20	3.45	T
Litsea glutinosa (Lour.) C.B.Rob.	Lauraceae	5	0.14	2.66	T
Grewia eriocarpa Juss.	Malvaceae	4	0.11	2.31	T
Antidesma ghaesembilla Gaertn.	Phyllanthaceae	5	0.02	2.20	S/T
Other species (34)		64	1.00	30.48	
Total		581	16.47	300	

Note: T: Tree; ST: Shrubby Tree; S: Shrub; S/T: Shrub or Tree

Figure 4. DBH class distributions of species with an inverted J-shape: A. *X. xylocarpa*; B. *R. wittii*; C. *B. saccocalyx*

Climate change

The 12-month SPEI values showed significant variation between -2.0 and 2.0 in drought/wet conditions among years (F = 58.92, P <0.0001) due to ENSO events. Based on the 15-year period from 2004 to 2019 of SPEI results (Figure 7.A), climate conditions were normal in SBR for 68.23% of the study period, moderate for 17.19%, and severe for 14.58%, according to the classification scheme of Li et al. (2015). The severe drought in SBR persisted from 2004 to 2007, followed by moderate drought conditions during 2015-2016. In addition, global ENSO data obtained from the MEI.v2 product also showed that the neutral phase was most common (43.23%), followed by

the cool phase (i.e., La Niña; 38.54%) and warm phase (i.e., El Niño; 18.23%) (Figure 7.B). However, an extreme El Niño event occurred during 2015-2016, followed by increasingly moderate conditions in 2009-2010, 2007, 2004-2005, and 2018-2019, respectively. Drought conditions based on SPEI values in SBR were generally correlated with El Niño events, with different trends in certain years, such as 2019, in which conditions were wetter despite an El Niño event. Both indices are important for understanding climate variability and its impact on forest dynamics, but they operate at different spatial scales (local and global).
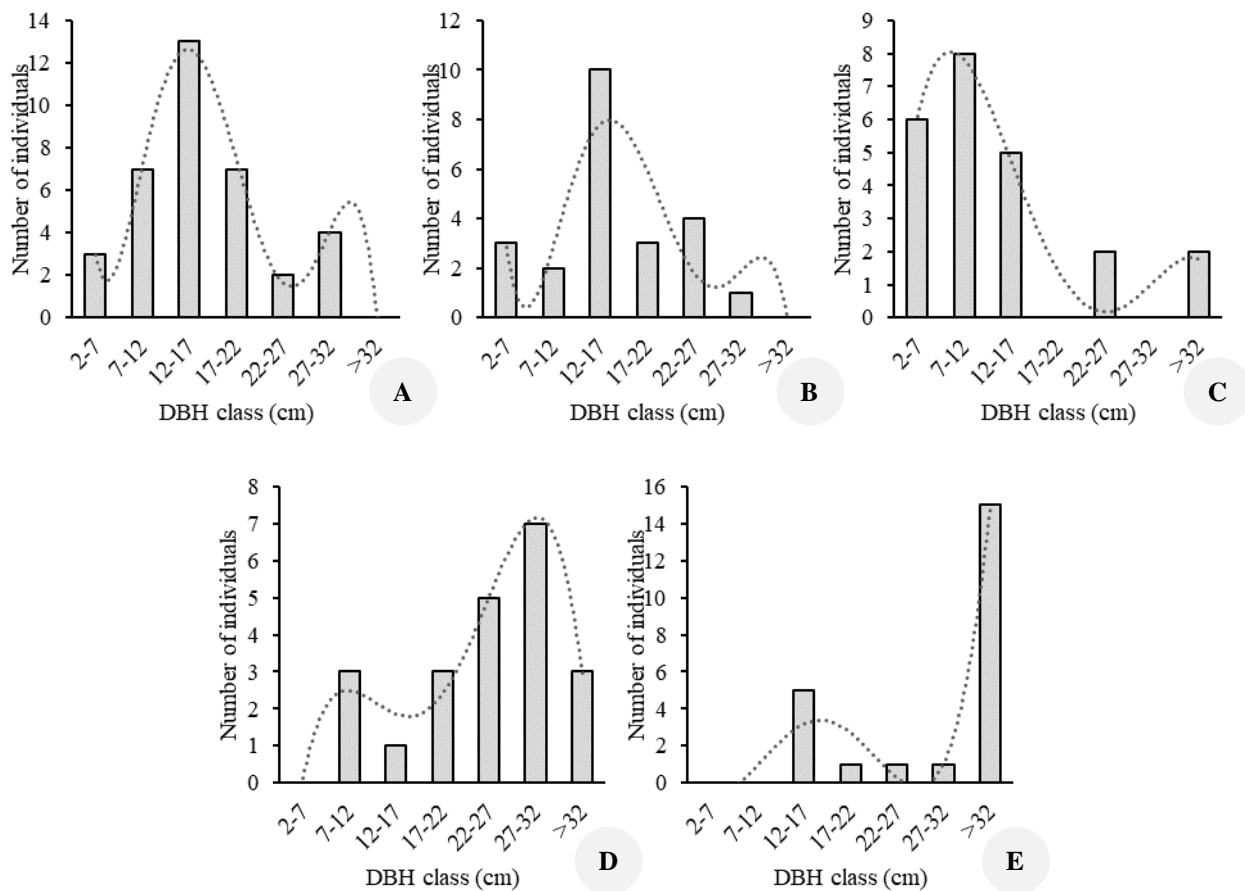
Figure 5. DBH class distributions of species with an irregular distribution pattern: A. *L. Coromandelica*; B. *M. coreia*; C. *A. odoratissima*; D. *S. obtusa*; and E. *D. intricatus*
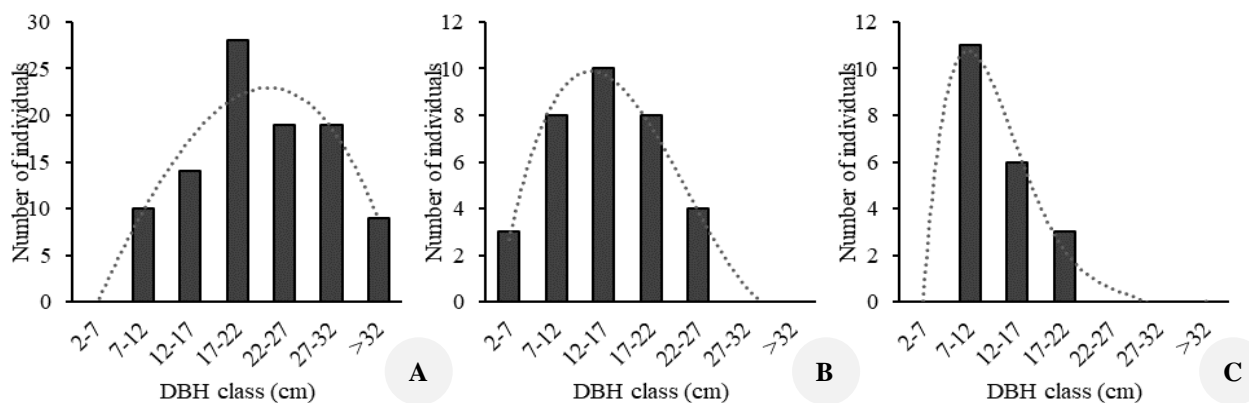

Figure 6. DBH class distributions of species with a bell-shape: A. *P. macrocarpus*; B. *M. rotundifolia*; C. *M. tomentosa*

Forest dynamics

The number of species fluctuated slightly between surveys during the 15-year study period (Table 2), increasing during 2008 and 2015, and then decreasing in 2019 to approximately the initial numbers. Additional species found in the 2nd and 3rd surveys were mainly pioneer shrub and small tree species such as *Microcos tomentosa* Sm., *Wrightia arborea* (Dennst.) Mabb., *Mallotus philippensis* (Lam.) Müll.Arg., *Pavetta tomentosa* Roxb. ex Sm., *Symplocos racemosa* Roxb., and *Vitex scabra* Wall. ex Schauer.

Tree density varied significantly among the three surveys (F = 11.46, P<0.0001). The highest and lowest density values were recorded in 2008 and 2019, at 968 and

581 stems ha^{-1}, respectively. These trends were strongly correlated with recruitment and mortality rates in each period (Table 2). The overall mean mortality rate (4.31±5.47% year^{-1}) was higher than the overall mean recruitment rate (2.76±3.76% year^{-1}), but with variation among periods. During 2004-2008, the recruitment rate (7.09% year^{-1}) was approximately 7-fold higher than the mortality rate (0.94% year^{-1}), whereas a contrasting trend was observed during 2015-2019, when the mortality rate (10.62% year^{-1}) was nearly 10-fold higher than the recruitment rate (0.88% year^{-1}). Fire protection during 2004-2008 may have allowed some plant species to experience population increases; however, after this protection was lifted, frequent fire occurrence killed many trees. Tree mortality differed significantly among size classes (χ^2 = 316.33, df = 5, P<0.0001), with size-dependent mortality particularly evident in the lowest size class (DBH = 4.5-10 cm), followed by the intermediate (20-40 cm) and highest size classes (>40 cm) (Figure 8). The mortality and recruitment rates were strongly influenced by basal area changes; basal area varied significantly among surveys (F = 21.38, P<0.0001), showing an increasing trend from 2008 to 2015, and decreasing in 2019 (Table 2). The lowest basal area (16.47

m^2 ha^{-1}) was recorded in 2019 due to the death of several large trees, with a total basal area loss of 8.26 m^2 ha^{-1} (Figure 8). This result may be associated with the prolonged drought that occurred during 2015-2016, which appears to have led to a fire in 2015; a severe fire in 2018 also killed many intermediate-sized trees (Figure 9).
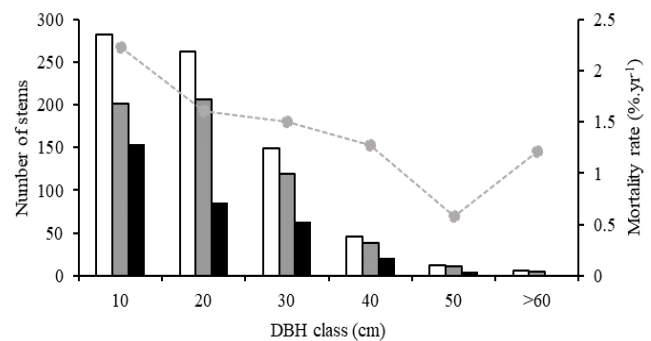
Figure 8. DBH-distribution (bars) and size-specific mortality rate (dot and broken line) from 2004-2019. Open bars are trees alive in 2004, grey bars are trees alive in 2019 and black bars are trees that died between 2004 and 2019
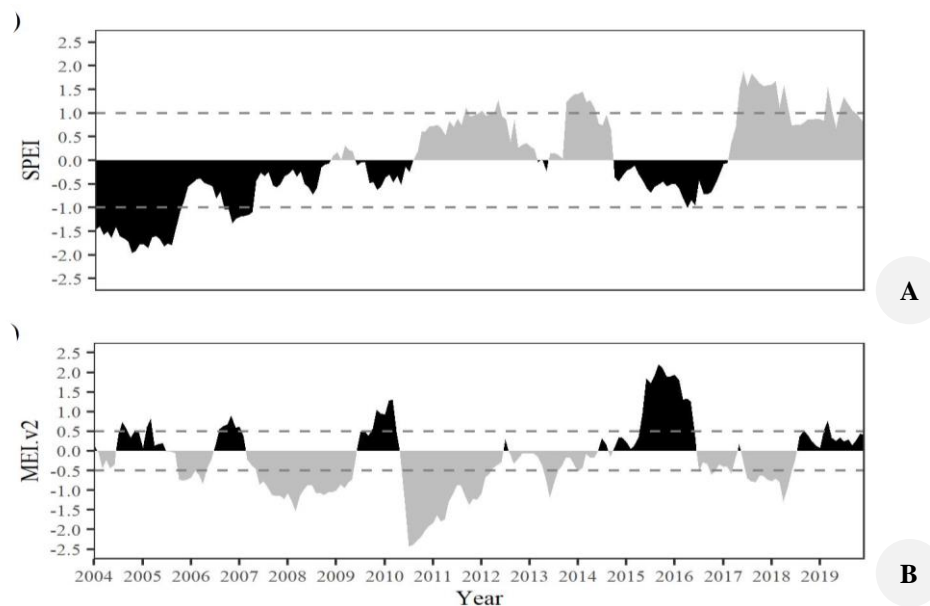
Figure 7. A. The wet and drought conditions based on SPEI in SBR; and B. The global ENSO oscillation events during 2004-2019. Black and grey color represented drought/El Niño, and wet/La Niña, respectively

Table 2. Variables of DDF dynamics during 15-yr period in Sakaerat Biosphere Reserve, Nakhon Ratchasima Province, Thailand

Variable	Year				Mean±SD
	2004	**2008**	**2015**	**2019**	
Species (number)	55	61	62	54	58±4
BA (m^2 ha^{-1})	20.16	22.72	23.98	16.47	20.83±3.32
Loss (m^2 ha^{-1})		0.55	1.84	8.26	3.55±4.13
Gain (m^2 ha^{-1})		3.11	3.10	0.75	2.32±1.36
Density (stem ha^{-1})	757	968	899	581	801±171
M (% yr^{-1})		0.94	1.38	10.62	4.31±5.47
R (% yr^{-1})		7.09	0.32	0.88	2.76±3.76

Relationship between recruitment and mortality rates

Based on the relationship between net recruitment and mortality rates during 2004-2019 (Figure 10.A), we classified the tree species into three groups. Trees in group 1 (e.g., *Gardenia sootepensis* Hutch. and *X. xylocarpa*) exhibited a balance between mortality and recruitment; trees in group 2 (e.g., *B. saccocalyx* and *A. odoratissima*) had higher recruitment rates than mortality rates; and trees in group 3 (e.g., *S. obtusa*) had higher mortality rates than recruitment rates. An analysis of the relationships during each period indicated that groups 1 and 2 consisted predominantly of pioneer or mixed deciduous forest climax species, exhibiting high recruitment in the 1st survey, followed by a decrease in the 3rd survey (Figures 10.B-10.D). In contrast, group 3 consisted of deciduous dipterocarp forest climax species, for which recruitment and mortality were relatively balanced in the 1st and 2nd surveys, followed by a substantial increase in mortality in the 3rd survey. Nevertheless, it is evident that each species experienced decreasing recruitment and increasing mortality as it transitioned through the time intervals between surveys.

Discussion

Forest structure and tree regeneration

Relatively low tree density and basal area are common structural features among seasonally dry forests (Marod et al. 1999; Sahu et al. 2016); however, the structural parameters of our study site were generally lower than those reported in previous studies (Sahunalu 2009). This result may be attributable to significant mortality (8.26 m^2 ha^{-1}) and basal area loss (10.62% $year^{-1}$) during the years 2015-2019. Based on IVI values, the three most dominant species belonged to the family Fabaceae (*P. macrocarpus*, *X. xylocarpa*, and *B. saccocalyx*); indeed, *P. macrocarpus* and *X. xylocarpa* coexist in both mixed deciduous and deciduous dipterocarp forests, particularly in loamy soil (Saikhammoon et al. 2023). However, some generally dominant deciduous dipterocarp species exhibited low population density, such as *S. obtusa* and *D. intricatus*, which are mainly found in sandy soil (Sakurai et al. 1998; Marod et al. 2019). This finding indicates that ecological niches based on soil properties differ between mixed deciduous and deciduous dipterocarp forests. The species composition of these forests is typically influenced by severe seasonal water stress and surface fire (Marod et al. 1999, 2004). We also observed variation in tree regeneration rates based on DBH class distributions. The dominant species in deciduous dipterocarp forests, such as *S. obtusa* and *D. intricatus*, had discontinuous population distributions (Figures 5.D and 5.E), unlike the mixed deciduous forest climax species *X. xylocarpa* (Figure 4.A) and the pioneer species *B. saccocalyx*, which had a negative exponential distribution (Figure 4.C). Pioneer species are typically light-demanding, found beneath canopy gaps with the strong light conditions necessary for their establishment, particularly in areas disturbed by large fallen trees (Marra et al. 2014; Barlow et al. 2016; Marod et al. 2022).

Climate changes and forest dynamics

ENSO events and drought conditions strongly influenced forest conditions at the SBR, although different trends were found. For example, wet conditions were observed in 2019 despite the occurrence of an El Niño event (Figures 7.A and 7.B). Although projections of El Niño variability and its impact on rainfall patterns in the 21st century are associated with complexity and uncertainty, a recent study suggested that rainfall variability associated with El Niño could intensify significantly in the latter half of the 21st century (Arias et al. 2021). Several studies have raised growing concerns regarding stronger and more frequent droughts in tropical regions as a consequence of climate change (Thirumalai et al. 2017; Esquivel-Muelbert et al. 2019). Understanding the impacts of drought events on tropical forests is crucial for accurately predicting the effects of global climate change and elucidating their underlying mechanisms.

Figure 9. Condition after severe fire occurred in February 2018 in Sakaerat Biosphere Reserve, Nakhon Ratchasima Province, Thailand
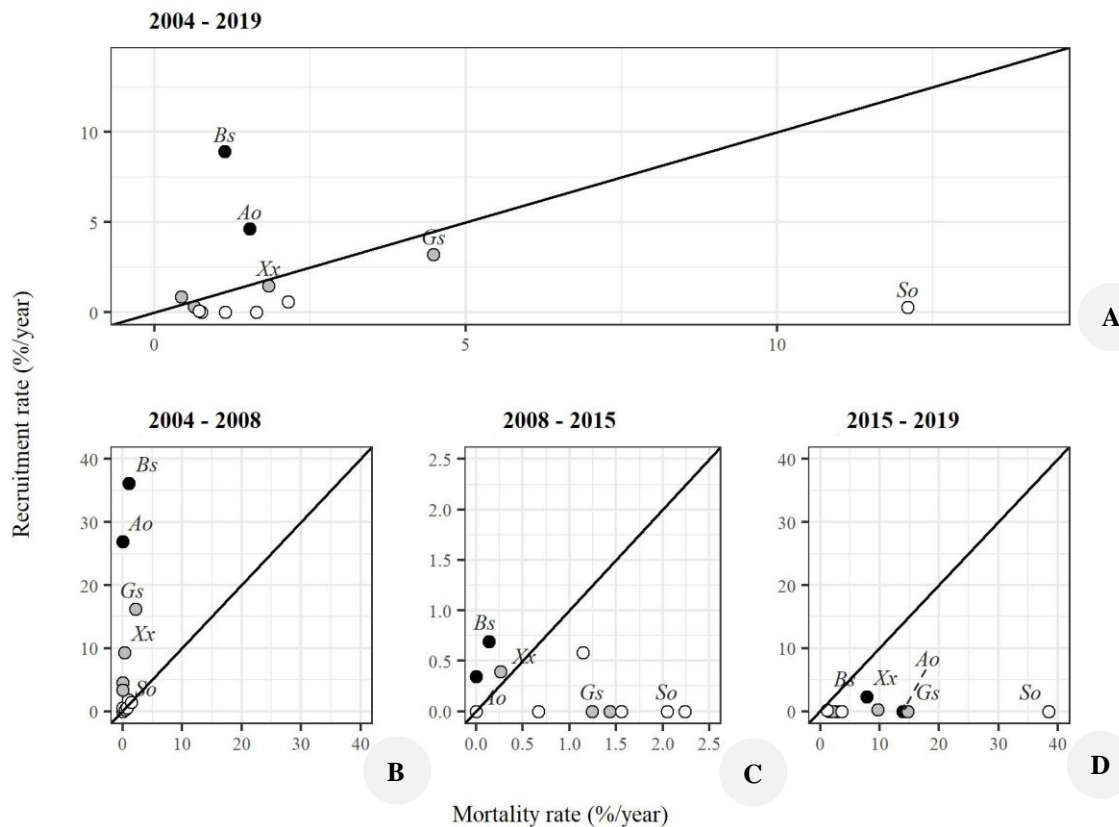
Figure 10. Relationships between recruitment and mortality rates during the 15-year period (2004-2019). Black line is aspect ratio 1:1, Black dots are a group of species with high recruitment than mortality, grey dots are a group of species with balance between mortality and recruitment, and white dots are a group of species with high mortality than recruitment. Species abbreviations are: *Ao*: *A. odoratissima*; *Bs*: *B. saccocalyx*; *Gs*: *G. sootepensis*; *So*: *S. obtusa*; *Xx*: *X. xylocarpa*

We also found that mortality rates were higher among small trees than among large trees, which is consistent with the findings of previous studies (Marod et al. 1999; Crouchet et al. 2019; Valkonen et al. 2020). Despite prolonged drought conditions during 2004-2009 (Figure 4.A), which typically impose significant stress on vegetation and can lead to increased mortality rates, forest fire protection in our site from 2004 to 2008 led to a 7-fold higher recruitment rate than the mortality rate (Table 2). During this time, high recruitment was observed among pioneer shrub and small tree species (e.g., *B. saccocalyx* and *G. sootepensis*), as seedlings and saplings of these pioneers can grow rapidly in open canopies with full sunlight (Manohan et al. 2023). When juvenile trees were not destroyed by fire, their establishment was successful. However, the contrasting trend detected from 2015 to 2019, characterized by a nearly 10-fold higher mortality rate than recruitment rate, indicated significant ecological disturbance, likely to have been driven by a severe El Niño in 2015-2016 and an extreme forest fire. The severe forest fire occurred in 2018 due to the accumulation of large amounts of fuel (forest litter) based on prior fire prevention efforts. This situation promoted high tree mortality similar to that observed in Bornean tropical forests (Miyamoto et al. 2021) and seedling mortality in seasonally dry tropical forests in Northern Thailand (Nutiprapun et al. 2023). During this time, many small native trees, such as *S. obtusa*

and *G. sootepensis*, died due to the fire, resulting in a recruitment bottleneck at the sapling stage and consequently leading to regeneration failure (Nguyen and Baker 2016; Nguyen et al. 2019). Furthermore, Kenzo et al. (2017) reported a positive relationship between tree size class and wood density in *S. obtusa*. This indicated that the lower size class of this species had less wood density than greater ones. Trees with low wood density and high specific leaf areas are at greater risk of increased mortality under drought conditions due to their high susceptibility to water stress (Greenwood et al. 2017). The effects of drought and fire both lead to increased tree mortality due to xylem hydraulic failure (Bär et al. 2018; Choat et al. 2018). This may explain the high mortality of *S. obtusa* occurring in the last period. Thus, these results suggested that the cumulative effects of drought and fire disturbances underscore the complex interplay of physiological and ecological stressors impacting forest dynamics and resilience.

The deciduous dipterocarp forest in the SBR generally had low density and basal area (533 individuals of 54 species, comprising 43 genera and 23 families). Some climax species showed irregular regeneration based on DBH class distributions. Both drought stress and forest fire can inhibit tree regeneration, particularly when they occur in combination and with specific conditions that increase fire intensity, such as the high litter accumulation during

2015-2018. Addressing the challenges posed by drought and fire to tree regeneration requires holistic management approaches that consider both ecological and climatic factors. Strategies may include fuel management to reduce fire risk, promoting drought-resistant tree species, and implementing restoration practices to enhance ecosystem resilience. Additionally, monitoring and adaptive management are essential for mitigating the impacts of future disturbances and supporting the long-term viability of forest ecosystems.

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