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Forest Restoration in an Abandoned Seasonally Dry Tropical Forest in the Mae Klong Watershed, Western Thailand

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ABSTRACT

Deforestation for the development of agricultural land is a critical driver of biodiversity loss. We examined the relationships between tree species and environments after the abandonment of a plot of land at the Mae Klong Watershed Research Station, Western Thailand. Vegetation monitoring was conducted every two years on a 16-ha permanent plot established in 2011 until 2019. All trees with diameter at breast height (DBH)≤1 cm were measured. Canonical correspondence analysis (CCA) was performed to investigate the relationships between tree species and environments. We found a total of 199 tree species in the plot, which comprised both pioneer and climax species. The high tree density and low basal area were 1,280 stem/ha and 7.30 m^2/ha, respectively. During 2011-2019, the species richness and total tree density were decreased by nine species (from 206 to 197 species) and 83 stem/ha (from 1,120 to 1,037 stem/ha). In contrast, the total basal area increased from 6.41 to 7.26 stem/ha. According to the measured environmental variables, mixed deciduous species such as *Pterocarpus macrocarpus* and *Xylia xylocarpa* var. *kerrii* preferred higher elevations and drier sites compared to dry evergreen species such as *Dipterocarpus alatus*. Early colonizing species such as *Trema orientalis* and *Ficus* species exhibited rapid population decreases, whereas climax species such as *Lagerstroemia tomentosa* exhibited highly successful regeneration under natural conditions. Artificial reforestation efforts may be required in areas with large disturbance, including the planting of mixed tree species to promote natural regeneration and reduce the recovery period.

1. INTRODUCTION

Compared to other forest types worldwide, tropical forests have high biodiversity and carbon density (Sullivan et al., 2017), which play important roles in ecosystem services such as climate regulation, carbon and water cycles, and food resource production (Good et al., 2015; Lewis et al., 2015; Hansen and DeFries, 2004). However, the rates of deforestation and land use change are increasing rapidly, with losses of over 80 million ha of primary tropical forest since 1990 (FAO and UNEP, 2020). Across the tropics, primary forest is mainly lost through agricultural development, including the promotion of large-scale crop production and commercial tree plantation (Curtis et al., 2018; Klemick, 2011), which are accompanied by biodiversity loss and forest degradation (Chazdon, 2014; Laurance, 2007; Geist and Lambin, 2002). Many such crop areas have been abandoned due to unsustainable practices, leading to the creation of post-disturbance vegetation communities (Van Hall et al., 2017) that vary according to habitat conditions. The impacts of abandonment on biodiversity and ecosystem services also vary greatly, depending on disturbance intensity and frequency (Chazdon, 2003; Collins et al., 2001). Despite the importance of tropical forests, there is relatively little information on succession or recovery in these forests (Poorter et al., 2021).

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Degraded or abandoned cropland is typically characterized by canopy openness, with high sunlight intensity reaching the soil surface and affecting air and soil temperature and humidity near the ground. In tropical forests, plants are categorized into two functional groups based on light requirements: light-demanding (i.e., pioneer) and shade-tolerant (i.e., late successional) species (Matsuo et al., 2021). Generally, pioneer plant species are more abundant along forest edges or in open areas than shade-tolerant species (Marod et al., 2004), due to germination stimulated by light exposure (Aide et al., 2000), whereas late successional species establish later and co-exist with recruited pioneer or early successional species according to environmental gradients (Gustafsson et al., 2016; Swinfield et al., 2016). In seasonally dry tropical forests, degraded sites undergoing natural recovery are susceptible to recurrent disturbances such as fire (Marod et al., 2004), and may experience slower colonization due to large distances from the intact forest edge (Marod et al., 2012). Compared with humid tropical regions, vegetation recovery occurs slowly in the dry tropics, where combustion is easily initiated (Scheper et al., 2021), particularly under the influence of anthropogenic factors (Quesada and Stoner, 2004; Miles et al., 2006; Mabry and Fraterrigo, 2009). Colonization by grasses, bamboos, lianas, and shrubs can also inhibit the survival and regeneration of climax tree species and delay forest restoration (Rother et al., 2015). Various environmental factors can also affect the ability of plants to acquire resources, leading to differences in regeneration rates, forest structure, and species composition among different successional sites (Wang et al., 2019; Mondoni et al., 2020). Early successional species modify light availability within the canopy by providing shade, which also influences the thermal and moisture microclimates to shape the species diversity, composition, and productivity of shade-tolerant species (Gravel et al., 2010). Therefore, an understanding of natural succession processes is important for developing forest conservation strategies for recovering degraded or abandoned areas (Wright, 2005; Sanchez-Azofeifa et al., 2005). Forest restoration programs based on planting suitable species for a given ecological niche should be developed at both regional and national levels to reduce the time required to reach successional climax, which would support ecosystem restoration and mitigate damage related to climate change.

In Thailand, seasonally dry tropical forests are classified into three categories: mixed deciduous forest (MDF) on zonal soils; deciduous dipterocarp forest on poor, leached soils and laterites; and savanna forest on fertile soils (Takahashi et al.; 2012; Marod et al., 2002). The dominant species of MDF include many commercial tree species in the upper canopy such as teak (*Tectona grandis*), *Pterocarpus macrocarpus*, *Xylia xylocarpa* var. *kerrii*, and *Afzelia xylocarpa* and bamboos mainly occupy the middle layer (Marod et al., 2004). Teak generally has the highest commercial value for logging, although it may be absent from MDFs (Thein et al., 2007).

The Mae Klong watershed of western Thailand is predominated by MDF, followed by deciduous dipterocarp forest on mountain ridges and dry evergreen forest along creeks (Marod et al., 1999). Forest degradation in the watershed has mainly been caused by logging and conversion into agricultural areas for upland rice production. Natural disturbance is frequent during the dry season due to forest fires and drought (Marod et al., 2002). These disturbed areas were abandoned after a logging ban in 1989, and natural reforestation was allowed. High recovery rates from non-forest to forested areas were detected in satellite images, especially during the initial phase (1992-1996) (Kamyo, 2016). The early successional stage (1989-1994) was initiated by colonization by short-lived pioneer species including herbaceous species and shrubs such as *Eupatorium odoratum*, *Musa acuminata*, *Saccharum spontaneum*, *Trema orientalis*, *Bauhinia viridescens*, and *Sterculia macrophylla* (Marod, 1995; Takahashi et al., 1995). However, few studies have examined successional processes in seasonally dry tropical forests using large permanent plots. Therefore, the objectives of this study were to examine secondary forest structure and species composition and their influential environmental factors in an abandoned agricultural area undergoing forest recovery, in the Mae Klong Watershed, Kanchanaburi Province, Thailand.

2. METHODOLOGY

2.1 Study area

The study was conducted in a mixed deciduous forest (MDF) on abandoned (post-agricultural) land at the Mae Klong Watershed Research Station (14°35′N, 98°52′E), Thong Pha Phum District, Kanchanaburi Province, western Thailand (Figure 1), covering an area of approximately 109 km^2 and elevation range of 100-950 m.a.s.l. The climate is subtropical, with a long wet season followed by a short, cool and dry season. Annual rainfall normally exceeds 1,650 mm, and is concentrated from late April to October. The mean monthly temperature is ca. 27.5°C, with a maximum of 39.1°C in April and minimum of 14.6°C in December (Marod et al., 1999). The soil was weathered from alluvial parent material containing sandstone, limestone and quartzite (Suksawang, 1993).

The study area can be classified into four main forest types: MDF with bamboos, deciduous dipterocarp forest (on mountain ridges), dry evergreen forest, and disturbed forest (Kutintara et al., 1995). MDF is mostly scattered the whole areas with deciduous dipterocarp forest on some mountain ridges. The dominant tree species are *Xylia xylocarpa* var. *kerrii*, *Vitex peduncularis*, *Schleichera oleosa*, and *Pterocarpus macrocarpus*. Bamboos are dominant in the understory, including *Bambusa tulda*, *Cephalostachyum pergracile*, *Gigantochloa albociliata*, and *Gigantochloa hasskarliana* (Marod et al., 1999). Signs of forest disturbance from burning and cultivation are observed on the gentler slopes, where the dominant vegetation consists of wild banana (*Musa acuminata*), bamboos, lianas and pioneer tree species such as *Trema orientalis*, *Bauhinia viridescens*, and *Sterculia macrophylla* (Marod, 1995).

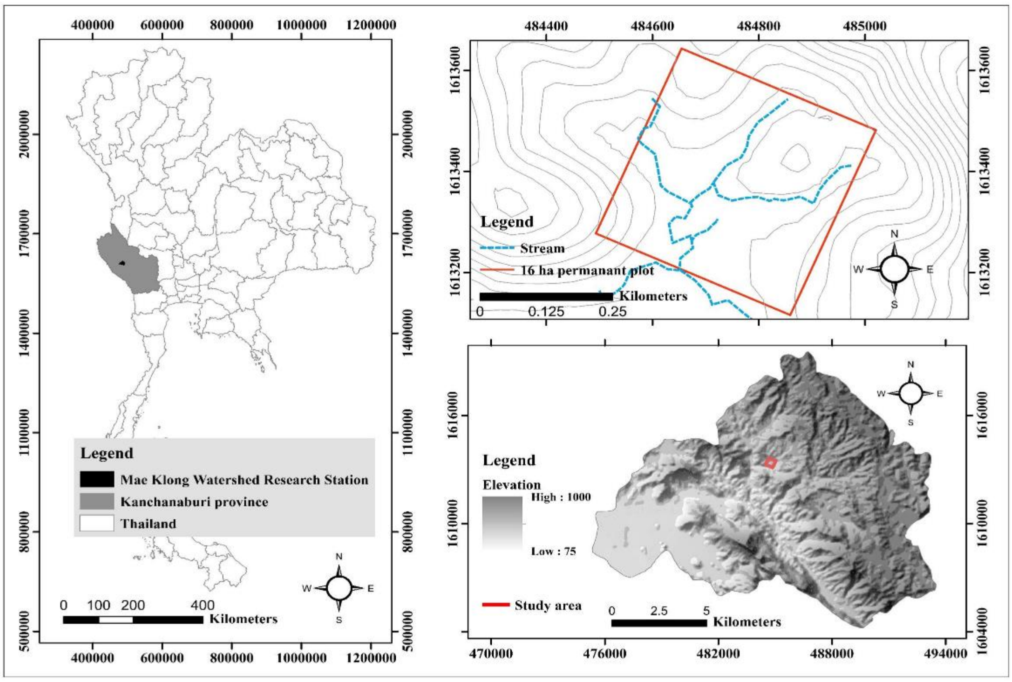

Figure 1. The location of the study area and 16 ha permanent plot in abandoned area of MDF at MKWRS, Kanchanaburi Province

2.2 Plot establishment and tree species investigation

In 2011, a 16-ha permanent plot (400 m × 400 m) was established in an abandoned area where MDF was devastated by cultivation and recovered based on natural succession (Kamyo et al., 2013). The plot was divided into 1,600 subplots (10 m × 10 m) and all trees with diameter at breast height (DBH) ≥2 cm were tagged, identified, and their DBH and positions were recorded every 2 years until 2019. As of 2019, all trees with DBH ≥1 cm were included in the survey. Samples of unidentified species were collected and identified by comparison with specimens at the Forest Herbarium, Department of National Parks, Wildlife and Plant Conservation. Species nomenclature follows Smitinand (2014).

2.3 Environmental data collection

2.3.1 Topographic factors

For each 50 m × 50 m subplot, topographic variables included the mean elevation of the four plot corners, the average slope, and the distance from the nearest stream. These variables were analyzed using the *fgeo* package (Lepore et al., 2019) in the R v3.6.1 software (R Core Team, 2017).

2.3.2 Soil properties

To collect soil samples, the 16-ha plot was divided into 64 subplots, each with 50 m × 50 m, followed the method of Delgado-Baquerizo et al. (2020). In each subplot, five soil samples (center and four corners) were collected from the topsoil (depth, 0-15 cm) and combined into a composite soil sample.

Soil physical and chemical properties were analyzed. The percentages of sand, silt and clay were determined using a hydrometer, according to a modified protocol (Soil Science Division Staff, 2017). Soil pH was determined using a pH meter in a 1:1 soil:water mixture (Beck, 1999). Organic matter was measured using the wet oxidation method (Allison, 1965). Available P was calculated using the Bray II method (Bray and Kurtz, 1945) and exchangeable cations (K^+, Ca^{2+}, and Mg^{2+}) were analyzed using an atomic absorption spectrophotometer with 1 N ammonium acetate (NH_4Oac) (Chapman, 1965). All soil samples were analyzed at the Laboratory of Soil Science, Faculty of Agriculture, Kasetsart University.

2.4 Data analysis

2.4.1 Plant ecological indices

To evaluate the forest structure and species composition, plant ecological indices were constructed based on structural parameters (tree density and basal area) and taxon richness (at species, genus and family levels) (Mohandass et al., 2016). The dominant species and importance value index (IVI) were calculated based on the summation of relative density, dominance and frequency (Krebs, 1994). The Shannon-Wiener index ($H^/$) was analyzed following Shannon and Weaver (1949).

2.4.2 Tree species regeneration

A DBH class-distribution based on trees in the 16-ha plot with at least 30 stems was utilized for estimating tree regeneration. We divided the diameter of the stems into classes with 5 cm intervals for each species of tree. We estimated the total stem counts for each diameter class for each tree species to determine the DBH distribution form. Following Shumi et al. (2019), we then visually categorized the DBH distribution form by grouping forms with similar shapes.

2.4.3 Relationships between plant community occurrence and environmental variables

To investigate the influence of environmental factors on plant community establishment, we performed canonical correspondence analysis (CCA). CCA ordination was conducted at the subplot scale (50 m × 50 m) using the cca function in the *vegan* package in R v3.6.1. Tree species classification was performed separately for trees (DBH ≥ 4.5 cm) and saplings ($1 \leq$ DBH < 4.5 cm) for inclusion in the first matrix, constructed based on IVI values for each subplot. The environmental variables including soil properties (i.e., sand, silt, clay and organic matter content and pH) and topographic factors (i.e., elevation, slope) were used to construct the second matrix.

2.4.4 Statistical analyses

Correlations between species and environmental variables were evaluated using Monte Carlo simulations, with 999 permutations. Correlations between environmental variables were evaluated using Pearson correlation coefficient (R). The significance threshold was $p<0.05$.

3. RESULTS AND DISCUSSION

3.1 Forest structure and species composition

In the 16-ha plot, a total of 20,478 individuals were identified with DBH ≥ 1 cm. These comprised of 199 species, 129 genera and 49 families, the tree density and basal area (BA) were 1,280 stems/ha and 7.30 m^2/ha, respectively. Tree species diversity based on the Shannon-Wiener index was high ($H^/=4.28$). In addition, the forest structure (species composition, tree density and BA) based on trees with DBH ≥ 2 cm varied between the first census (2011) and the last monitor (2019). Across the forest recovery, the decreased trend in density and species number was detected, with 83 stems and 9 species disappearing. Most of these were pioneer species such as *Mallotus paniculatus*, *Bauhinia malabarica*, and *Gmelina asiatica*. While the overall BA had increased from 6.41 to 7.26 m^2/ha.

Among tree species with DBH ≥ 4.5 cm, the tree density was 605 stems/ha and the basal area was 6.91 m^2/ha; these included 176 species, 121 genera and 47 families (Table S1). The species with the highest tree density was *Lagerstroemia tomentosa* (42 stems/ha) followed by *Callerya atropurpurea* (32 stems/ha), *Markhamia stipulata* (29 stems/ha), *Garuga pinnata* (21 stems/ha), *Toona ciliata* (20 stems/ha), *Stereospermum neuranthum* (20 stems/ha), *Croton persimilis* (18 stems/ha), *Albizia lucidior* (18 stems/ha), *Mitragyna rotundifolia* (17 stems/ha), and *Artocarpus lacucha* (13 stems/ha). The 10 most dominant tree species based on relative basal area (%) accounted for 40% of the total basal area; these were *Duabanga grandiflora* (7.92%), followed by *Litsea grandis* (4.61%), *Dipterocarpus alatus* (4.33%), *Lagerstroemia tomentosa* (4.05%), *Albizia lucidior* (3.85%), *Garuga pinnata* (3.44%), *Gmelina arborea* (3.22%), *Toona ciliata* (3.15%), *Callerya atropurpurea* (2.83%), and *Ficus racemosa* (2.53%).The dominant species based on IVI (%) was *Lagerstroemia tomentosa* (16.77%) followed by *Markhamia stipulata* var. *stipulata* (11.91%), *Callerya atropurpurea* (11.77%), *Garuga pinnata* (10.35%), *Duabanga grandiflora* (9.62%), *Albizia lucidior* (9.59%), *Toona ciliata* (9.31%), *Stereospermum neuranthum* (8.31%), *Litsea grandis* (8.18%), and *Mitragyna rotundifolia* (6.70%).

In family level, Fabaceae, Moraceae, Malvaceae, Phyllantaceae, Lythraceae, and Lamiaceae families had the most species in the permanent plot (21, 15, 13, 11, 8, and 7, respectively). Species of the Fabaceae had the highest tree density, with 88 stems/ha followed by Moraceae (74 stems/ha), Lythraceae (58 stems/ha), Bignoniaceae (57 stems/ha), and Phyllantaceae (35 stems/ha). Species of the Fabaceae also had the highest basal area, with 1.03 m^2/ha, followed by the Lythraceae (0.90 m^2/ha), Moraceae (0.88 m^2/ha), Lauraceae (0.49 m^2/ha), and Bignonaceae (0.45 m^2/ha) (Figure 2).

After 30 years of abandonment (1989-2019), herbaceous species such as *Eupatorium odoratum*, *Musa acuminata*, and *Saccharum spontaneum* were drastically depleted and replaced by woody species at high tree density (605 stems/ha) and low basal area (6.91 m^2/ha), which were lower than many reported values from natural MDF, with tree density and basal area values ranging from 170 to 450 stems/ha and from 17 to 37 m^2/ha, respectively (Marod et al., 1999; Chaiyo et al., 2012). High species diversity (87.94±10.38 species/ha) was observed and a similar trend as previously reported. Kamyo et al. (2013) studied at the same study site with different areas (4-ha permanent plot) and reported tree species diversity increased during 18 years (1992 to 2010) after abandonment from 32 species into 147 species, respectively. In addition, it is also higher than in some selective cutting in MDF permanent plots in this watershed which only 49 species/ha were reported (Yarwudhi et al., 2000). It was high due to the coexisted species between pioneer and late succession species, which is a common phenomenon during forest recovery (Phumphuang et al., 2018; Chen et al., 2020). Likewise, the regeneration of this area was primarily explained by the decline of some pioneer species and the development of some late successional species from 2011-2019. This was consistent with the forest on Barro Colorado Island in Panama, where the abundance of species with heavy wood increased throughout succession (Chave et al., 2008). Thus, the recovery process is still ongoing, as shown by the variation of composition and structure of the forest, especially in a large number of small trees (Sann et al., 2016).

Furthermore, the influences of disturbed factors such as drought, forest fire and undergrowth may be prohibited forest recovery during the successional stages (Lacerda and Kellermann, 2019; Marod et al., 2002). The deep shade of bamboo had a high impact on forest floor light intensity, while a large amount of bamboo litter may have an impact on seedling recruitment by interfering with seedling emergence and preventing newly distributed seeds from reaching an appropriate soil substrate (Larpkern et al., 2011). The intensity of forest fires that can be killed small trees that can also be influenced by the quantity of bamboo litter on the ground (Keeley and Bond, 1999). Forest fires frequently occurred in the study area during the first ten-year period (1990-2000). It not only burnt the herbaceous species but also some pioneer species such as *Trema orientalis* (Kamyo et al., 2013). However, some tree species received a significant vacant area from the forest fire (Marod et al., 1999). Thus, such an environment and natural disturbances significantly contributed to this forest's fluctuation, especially in terms of species composition. The most abundant pioneer species were *Ficus* trees of family Moraceae, including *Ficus hispida*, *Ficus racemosa*, *Ficus auriculata*, *Ficus chartacea*, *Ficus variegata*, *Ficus callosa*, and *Ficus semicordata*. Other pioneer species included *Croton persimilis* (Euphorbiaceae), *Trema orientalis* (Cannabaceae), *Rhus Javanica* (Anacardiaceae), *Litsea grandis* (Lauraceae), *Litsea glutinosa* (Lauraceae), *Microcos paniculata* (Malvaceae), *Colona flagrocarpa* (Malvaceae), *Berrya mollis* (Malvaceae), *Sterculia pexa* (Malvaceae), *Sterculia foetida* (Malvaceae), *Albizia odoratissima* (Fabaceae), *Wrightia arborea* (Apocynaceae), *Morus macroura* (Moraceae), *Erythrina subumbrans* (Fabaceae), *Senna timoriensis* (Fabaceae), *Oroxylum indicum* (Bignoniaceae), and *Bridelia ovata* (Phyllanthaceae). Many of these species facilitate the establishment of late successional species and supply food resources for wildlife (Rueangket et al., 2019). The climax species in this MDF (Marod et al., 1999; Khamyong et al., 2018) have already colonized the area and some species became dominance, such as *Lagerstroemia tomentosa*, *Garuga pinnata*, *Xylia xylocarpa* var. *kerrii*, *Pterocarpus macrocarpus*, *Anogeissus acuminata*, *Schleichera oleosa*, and *Vitex peduncularis*. Some remnant species from the dry evergreen forest, such as *Dipterocarpus alatus*, *Aphanamixis polystachya*, and *Toona ciliata*, which mainly occupy riverbanks with high moisture, have performed well in co-establishing with other species. Presently, the forest is recovering, with degraded and non-forest areas have been becoming forested as previously described by Kamyo et al. (2016).

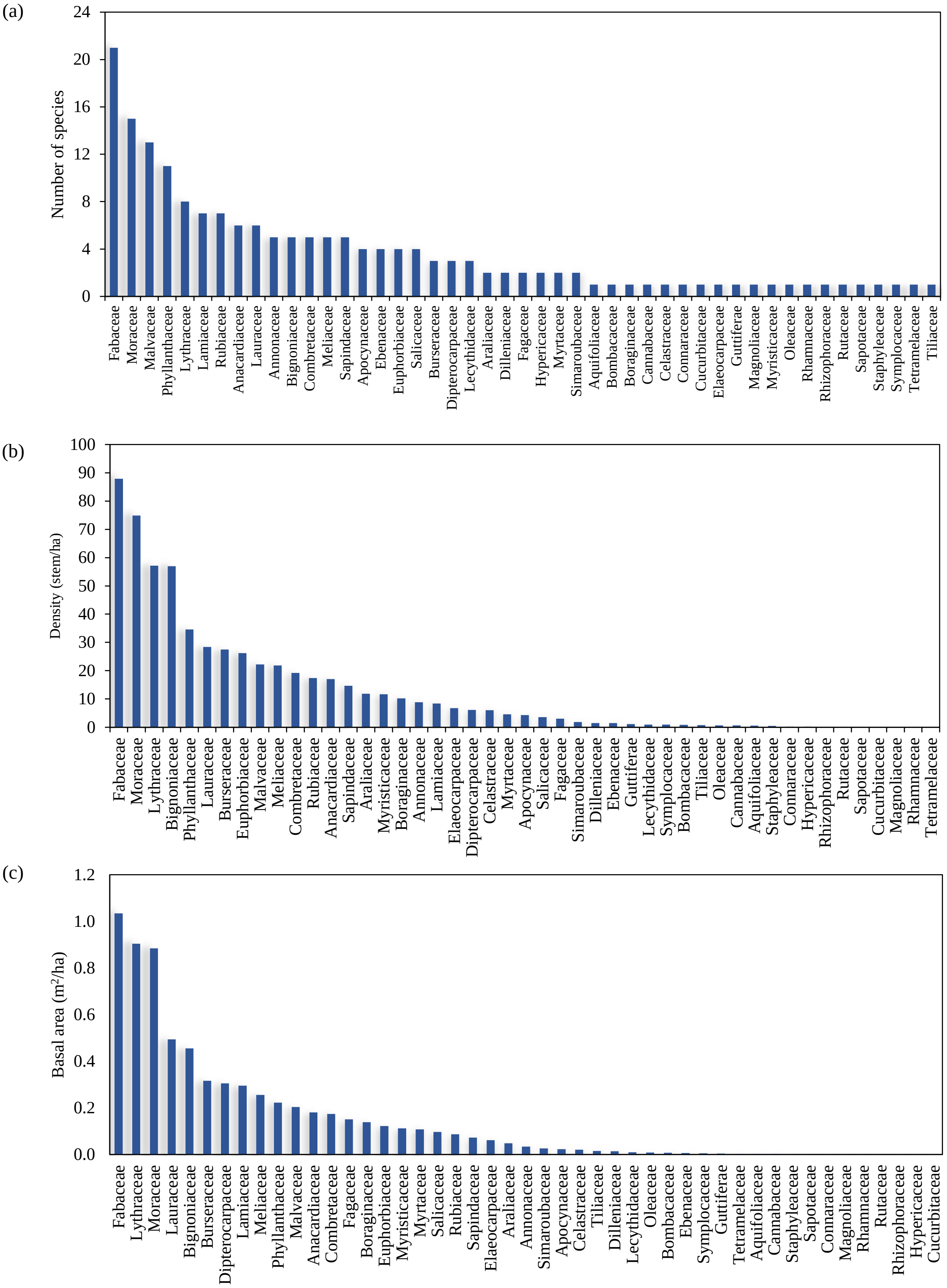

Figure 2. (a) Number of species, (b) tree density, and (c) basal area of families in the permanent plot. Only trees with diameter at breast height (DBH) ≥4.5 cm are included.

3.2 Tree species regeneration

Our analysis of the regenerating tree populations according to DBH class distributions included a total of 94 tree species with populations of ≥ 30 stems. The results showed two types of DBH class distribution: inverted J-shaped (30 species) and irregular (64 species). In both distributions, most stems occur in the lowest DBH classes, with progressively fewer stems in larger DBH classes (Table S1). Considering the dominance of MDF species, only some species in the upper canopy followed an inverted J-shaped distribution, such as *Terminalia triptera*, *Terminalia calamansanai*, and *Artocarpus rigidus* (Figure 3(a-c)). Most shrubby trees in the middle layer also followed an inverted J-shaped distribution, such as *Lepisanthes rubiginosa*, *Millettia leucantha*, and *Millettia brandisiana* (Figure 3(d-f)). These results indicate that these recovering species have a high capacity to maintain a stable population structure because small trees will grow into larger size classes and replace larger trees as they die. Notably, these species will be sustained if mortality is higher among small (suppressed) trees and large trees than among medium-sized co-dominants (Marod et al., 2022).

Species exhibiting irregular DBH class distributions included both climax and pioneer species (Table S1). Climax MDF species with discontinuous DBH class distributions included *Lagerstroemia tomentosa* and *Pterocarpus macrocarpus* (Figure 4(a-b)). The irregular distributions were also observed in pioneer species such as *Morus macroura*, *Litsea glutinosa*, and *Erythrina subumbrans* (Figure 4(c-e)); these were found mainly in canopy gaps, which suggests that the high light conditions characteristic of disturbed areas are required for their successful establishment (Sangsupan et al., 2021; Swinfield et al., 2016; Goodale et al., 2012). Some remnant tree species of dry evergreen forests such as *Dipterocarpus alatus* showed good regeneration performance, with increasing population sizes, despite irregular DBH class distributions (Figure 4(f)). This finding indicates that remnant trees during the early stage after abandonment are important for forest restoration, likely through enhancing seed dispersal and creating suitable environments for plant establishment.

3.3 Environmental factors

The mean±standard deviation (SD) elevation and slope of the study area were 303.05±7.60 m.a.s.l. and 11.97±8.27%, respectively. The soil was slightly acidic (pH 6.32±0.72), with high organic matter content (6.22±0.15%). The soil texture was classified as loam due to the relative content of sand (38.75±0.001%), silt (34.88±4.55%) and clay (26.27±6.11%). Among eight environmental variables including topographic variables (elevation, slope and distance to the nearest stream) and soil properties (soil texture, soil pH and organic matter content), Pearson's correlation analysis showed a strongly positive correlation (R>0.8) only between sand content and pH (R=0.96; Table 1). Among the remaining environmental variables, positive correlations were detected between silt content and pH (R=0.49), sand and silt content (R=0.43), elevation and slope (R=0.63), elevation and distance to the nearest stream (R=0.65), and slope and distance to the nearest stream (R=0.37). By contrast, clay content was negatively correlated with sand content (R=-0.78), silt content (R=-0.78) and soil pH (R=-0.73). Organic matter content was not significantly correlated with any other variable.

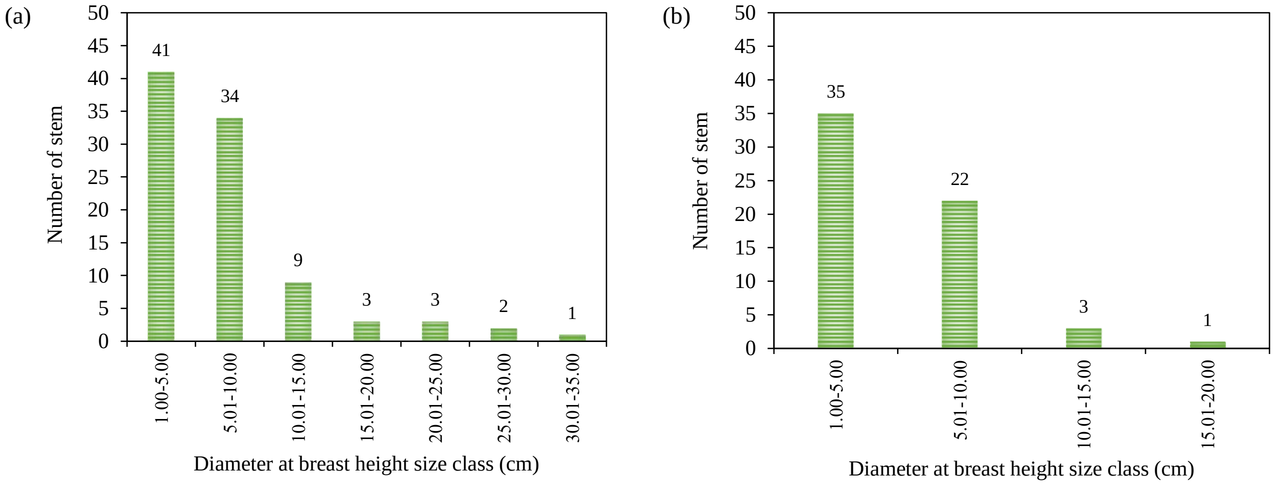

Figure 3. DBH class distributions plotted, showing an inverted J-shaped distributions. (a) *Terminalia triptera*, (b) *Terminalia calamansanai*, (c) *Artocarpus rigidus*, (d) *Lepisanthes rubiginosa*, (e) *Millettia leucantha*, and (f) *Millettia brandisiana*

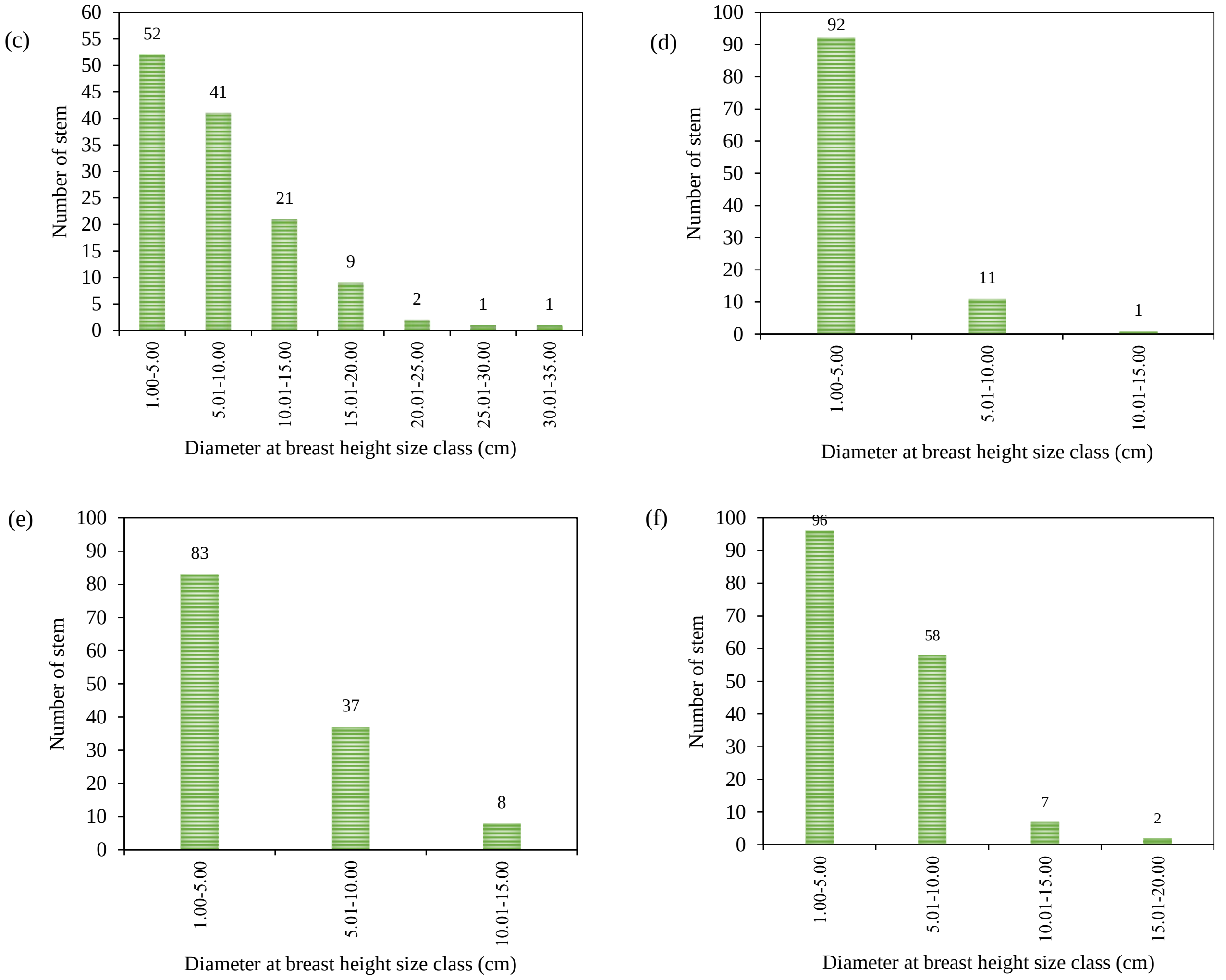

Figure 3. DBH class distributions plotted, showing an inverted J-shaped distributions. (a) *Terminalia triptera*, (b) *Terminalia calamansanai*, (c) *Artocarpus rigidus*, (d) *Lepisanthes rubiginosa*, (e) *Millettia leucantha*, and (f) *Millettia brandisiana* (cont.)

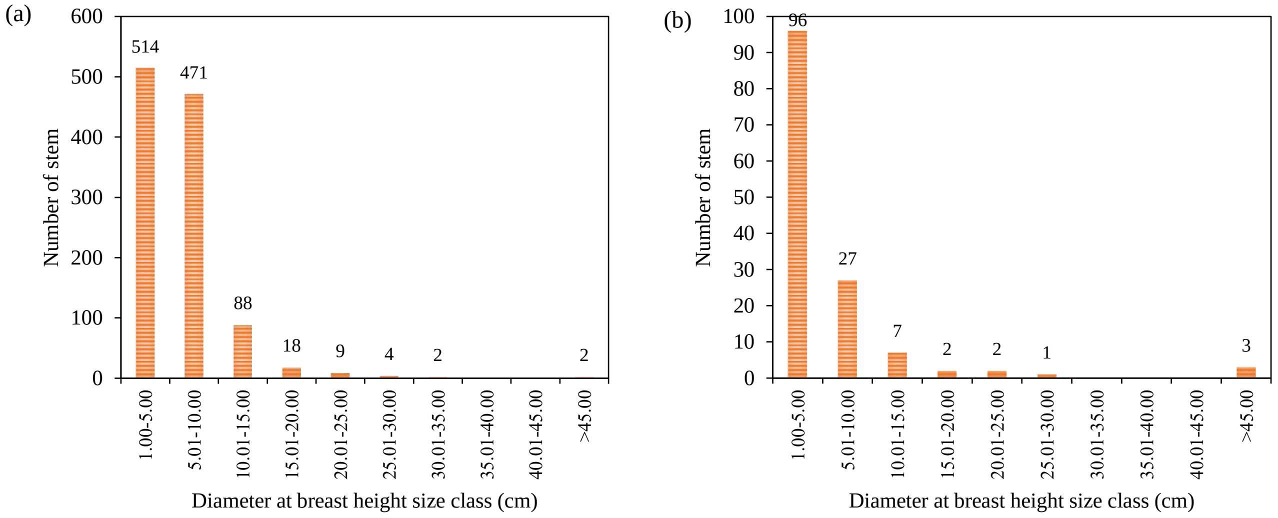

Figure 4. DBH class distributions plotted, showing an irregular distributions: (a) *Lagerstroemia tomentosa*, (b) *Pterocarpus macrocarpus*, (c) *Morus macroura*, (d) *Litsea glutinosa*, (e) *Erythrina subumbrans*, and (f) *Dipterocarpus alatus*

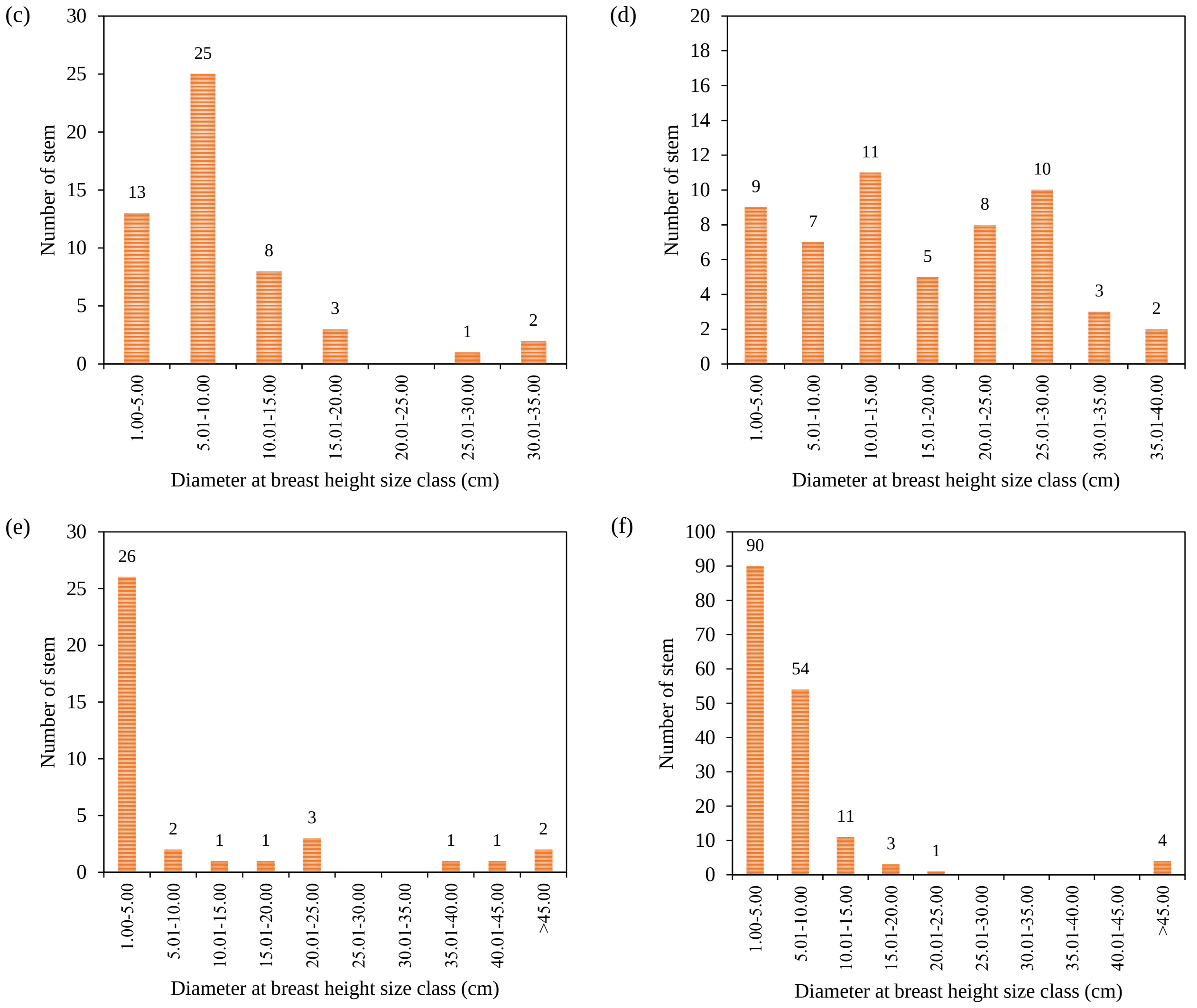

Figure 4. DBH class distributions plotted, showing an irregular distributions: (a) *Lagerstroemia tomentosa*, (b) *Pterocarpus macrocarpus*, (c) *Morus macroura*, (d) *Litsea glutinosa*, (e) *Erythrina subumbrans*, and (f) *Dipterocarpus alatus* (cont.)

Table 1. Pearson's correlation coefficient matrix for environmental factors examined in this study

Factor	Elevation	Slope	Distance to stream	Sand content	Silt content	Clay content	Soil pH	Organic matter content
Elevation	1.00							
Slope	0.631^{***}	1.00						
Distance to stream	0.647^{***}	0.372^{**}	1.00					
Sand content	-0.051	0.012	-0.087	1.00				
Silt content	0.133	-0.023	-0.232	0.427^{**}	1.00			
Clay content	0.037	0.067	0.236	-0.781^{**}	-0.779^{***}	1.00		
pH	-0.016	-0.003	-0.052	0.956^{***}	0.49^{***}	-0.728^{***}	1.00	
Organic matter content	0.172	0.212	0.024	0.02	0.104	0.156	0.043	1.00

Asterisks indicate significant differences (*=p<0.05; **=p<0.01; ***=p<0.001)

During forest succession after abandonment, several environmental factors change rapidly, particularly soil properties. In the early stages of succession, soil is typically poor in nutrients and organic matter. However, as the forest matures, organic matter accumulates and new vegetation growth leads to improved soil quality and nutrient availability (Hooker and Compton, 2003). In the study area, soil in the recovering forest had high organic matter content and was slightly acidic, which is within the suitable range for plant growth (Marod and Kutintara, 2009). The soil texture was similar to those reported in previous studies for MDF dominated by sandy loam and loam soils (Staelens et al., 2011). Furthermore, environmental factors are complex and interrelated. Topographic factors such as elevation and slope are positively interrelated (Du et al., 2017; Zhang et al., 2013). The elevation range of the permanent plot was 290-360 m.a.s.l., and higher elevation and slope have been associated with increased distance to the nearest stream, which produces a soil moisture gradient (Rong et al., 2017).

3.4 Relationships between tree species occurrence and environmental factors

We performed CCA analyses to evaluate the effects of various environmental factors on species occurrence separately for saplings (DBH<4.5 cm) and trees (DBH ≥4.5 cm). Among trees, the results showed strong correlations between species and all environmental variables, with eigenvalues of 0.31 and 0.20 for the first (CCA1) and second (CCA2) axes, respectively. These high values indicate good predictive performance for species distribution and abundance**.** Pearson correlation analysis showed that the environmental factors were strongly correlated to species occurrence for axis 1 (R=0.860) and axis 2 (R=0.810). The Monte Carlo permutation test confirmed that axis 1 significantly explained the relationship between species occurrence and environmental factors ($p<0.01$). Elevation, slope and distance to the nearest stream strongly influenced the distributions of *Pterocarpus macrocarpus*, *Anogeissus acuminata*, *Terminalia bellirica*, *Markhamia stipulata* var. *stipulata*, and *Gmelina arborea*. These species favored high elevation and longer distances from the nearest river, indicating that they prefer dry conditions for establishment (Phumphuang et al., 2018; Sasunti, 2021). By contrast, dry evergreen forest species such as *Duabanga grandiflora* and *Albizia lucidior* were mainly located in moist sites close to rivers. Some pioneer species were also found in these areas, such as *Ficus auriculata*, *Ficus racemose*, and *Bischofia javanica* (Figure 5). Silt and sand content, as well as soil pH strongly influenced the occurrence of *Horsfieldia amygdalina*, *Pterospermum acerifolium*, *Artocarpus rigidus*, *Protium serratum*, and *Persea declinata*. Clay content, which was negatively correlated with silt and sand content and pH, influenced the distribution of *Xylia xylocarpa* var. *kerrii*, *Dipterocarpus alatus*, and *Artocarpus lacucha*. Many pioneer species such as *Ficus* species and late succession species such as *Duabanga grandiflora* mainly occupied areas with high soil moisture content, as reported previously (Pothasin et al., 2014; Albrecht et al., 2017; Leishangthem and Singh, 2018).

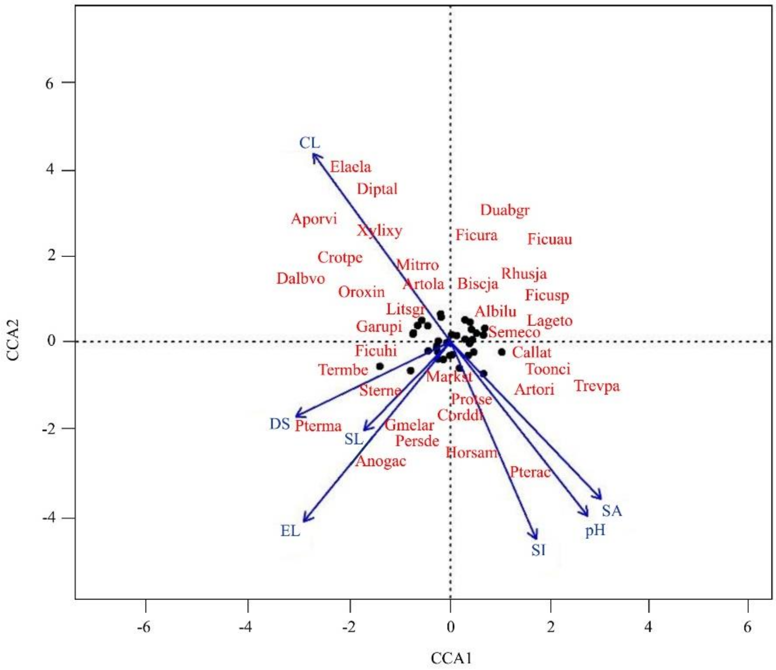

Figure 5. Canonical correspondence analysis ordination diagram for tree species occurrence and environmental factors. Tree species abbreviations are provided in Table S1.

The CCA results for saplings showed eigenvalues of 0.26 and 0.16 for the first (CCA1) and second (CCA2) axes, respectively, and high Pearson's correlation coefficients for both axis 1 (R=0.882) and axis 2 (R=0.872).The Monte Carlo permutation test confirmed that axis 1 significantly explained the tree occurrence variation ($p<0.01$). Silt content, elevation and slope strongly influenced the occurrence of *Monoon viride*, *Siphonodon celastrineus*, *Croton persimilis*, and *Pterospermum acerifolium* (Figure 6). Clay content influenced the regeneration of lowland species such as *Streblus ilicifolius*, *Flacourtia indica*, *Rhus javanica*, *Millettia brandisiana*, and *Baccaurea ramiflora*. Organic matter strongly influenced the occurrence of species including *Dalbergia volubilis*, *Ficus hispida*, and *Terminalia bellirica* but did not influence tree regeneration. These findings indicate that organic matter is more important for providing soil nutrients at the sapling stage than at the mature stage. Previous studies also reported that nutrient availability and soil texture were the major determinants of plant species distribution (Sellan et al., 2019; Marod et al., 2019).

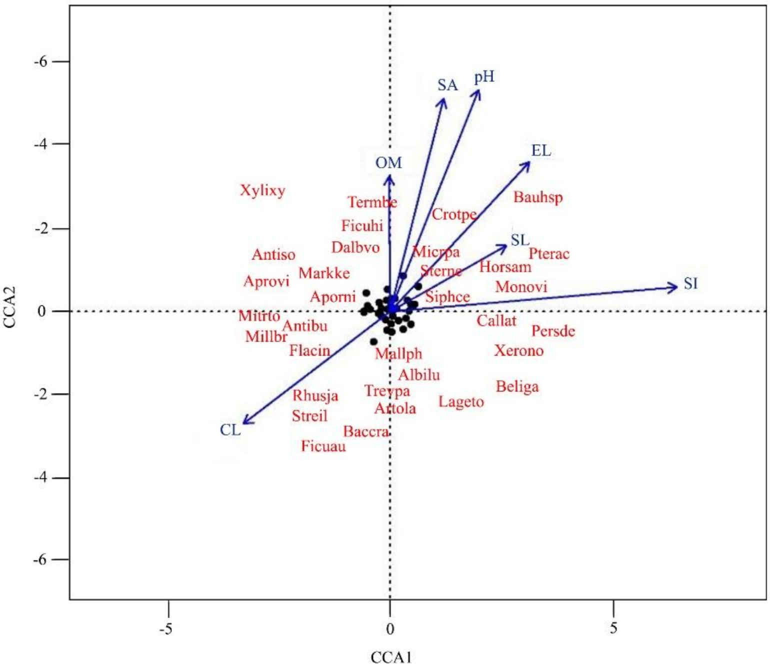

Figure 6. Canonical correspondence analysis ordination diagram for sapling species occurrence and environmental factors. Tree species abbreviations are provided in Table S1.

During the early successional stages, environmental factors significantly influence tree species regeneration, particularly under drought and poor soil conditions (Lebrija-Trejos et al., 2011). Facilitation allows plant species to resist and survive under adverse climate conditions (Bagousse-Pinguet et al., 2014). Thus, pioneer species play a major role in forest restoration in large disturbed areas, by facilitating the establishment of suitable conditions for vegetation restoration, especially soil properties such as increased soil organic matter and nutrients through the accumulation of plant litter (Wang et al., 2016; Zhao et al., 2017). Recently, the cultivation of fast-growing pioneer species (i.e., nurse crops or framework species) has been applied to accelerate natural regeneration (Elliott et al., 2003; Fagundes et al., 2018; Boeschoten et al., 2021). Thus, larger populations of climax species such as *Lagerstroemia tomentosa* in MDF and *Callerya atropurpurea* in dry evergreen forests are establishing throughout the permanent plot, particularly at moist, low-elevation sites (Figure 7(a, b)). By contrast, species such as *Pterocarpus macrocarpus* prefer dry conditions, and are mainly distributed at higher elevations (Figure 7(c)). Some pioneer species persist, such as *Croton persimilis* (Figure 7(d)), whereas species such as *Trema orientalis* was dense on high soil moisture area (180.43 stem/ha) in the early successional stage (Marod, 1995; Takahashi et al., 1995) have almost become depleted (0.625 stem/ha) at present. *Trevesia palmata* was almost exclusively found along river banks (Figure 7(e)), indicating an ecological niche for this species. These data are important for the selection of suitable pioneer and late successional or climax species for forest restoration programs, to shorten the forest recovery period in degraded areas of Thailand.

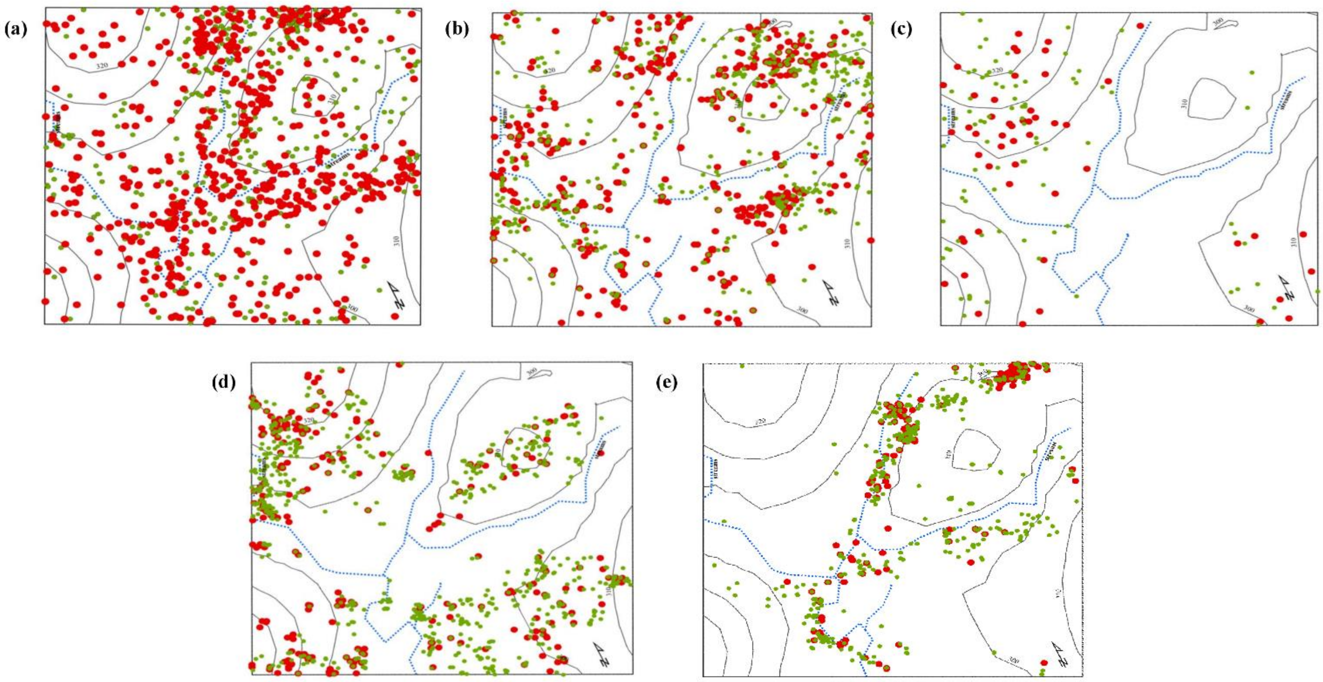

Figure 7. Tree species distribution in the 16-ha permanent plot: (a) *Lagerstroemia tomentosa*, (b) *Callerya atropurpurea*, (c) *Pterocarpus macrocarpus*, (d) *Croton persimilis*, and (e) *Trevesia palmata*. Each dots indicate position of tree (DBH ≥ 4.5, red dots) and sapling (DBH < 4.5, green dots) in the 16 ha permanent plot.

4. CONCLUSION

The natural forest restoration in the 16-ha permanent plot after abandonment about 30 years from shifting cultivation is under well-recovery. The initiated recovery was occupied by herbaceous species, then, drastically depleted and replaced by woody species at high tree density (605 stems/ha) and low basal area (6.91 m^2/ha). Forest fire disturbances were observed, in particular, during the first ten-year recovery period (1990-2000). It not only burnt the herbaceous species but also some pioneer species such as *Trema orientalis*. Then, the coexisted tree species between pioneer and climax species were observed, although, less diversity of pioneer was found. The result from CCA showed that high relationship between tree species and environments for their distribution and coexisting was found. Some species had distinct ecological niches, with dry evergreen forest species preferring moist lowland sites, compared with MDF species. The climax species as *Lagerstroemia tomentosa* showed particularly successful regeneration in the study area which represented by highest IVI, whereas other species recovered more slowly in response to environmental changes. While, pioneer species such as *Musa acuminata*, *Eupatorium odoratum*, *Trema orientalis*, and several *Ficus* species facilitated the formation of a suitable environment for climax species establishment, particularly in terms of increased soil fertility and moisture content. This study was conducted in a watershed with a small area of degraded land (ca. 1 km^2); therefore, the environmental conditions were not so severe as to preclude plant succession, and remnant climax species provided potential seed sources for natural forest regeneration, which can be a key factor in forest recovery.

Therefore, the history of land use changes and the scale and intensity of past disturbances should be considered in designing management strategies to promote natural forest restoration. However, artificial restoration programs should be conducted in regions with large degraded areas and high disturbance intensity. In such regions, we recommend planting both pioneer species such as *Trema orientalis* and *Ficus* trees, and late successional or climax species, *Pterocarpus macrocarpus*, *Terminalia bellirica*, *Lagerstroemia tomentosa*, and *Artocarpus rigidus*, to shorten the recovery period and promote natural regeneration where possible.

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REFERENCES

Aide TM, Zimmerman JK, Pascarella JB, Rivera L, Marcano-Vega H. Forest regeneration in a chronosequence of tropical abandoned pastures: Implications for restoration ecology. Restoration Ecology 2000;8(4):328-38.

Albrecht L, Stallard RF, Kalko EK. Land use history and population dynamics of free-standing figs in a maturing forest. PLoS ONE 2017;12(5):e0177060.

Allison L. Organic carbon. In: Black CA, editor. Methods of Soil Analysis: Part 2 Chemical and Microbiological Properties. Wisconsin: American Society of Agronomy; 1965. p. 1367-78.

Bagousse-Pinguet Y, Xiao S, Brooker RW, Gross N, Liancourt P, Straile D, et al. Facilitation displaces hotspots of diversity and allows communities to persist in heavily stressed and disturbed environments. Journal of Vegetation Science 2014;25(1):66-76.

Beck R. Soil Analysis Handbook of Reference Methods. New York, USA: CRC Press; 1999.

Boeschoten LE, van Breugel M, Bailon M, Balbuena J, Nuñez M, Cerezo A, et al. Framework species approach proves robust in restoring forest on fire prone invasive grass: A case study from Panama. Journal of Sustainable Forestry 2021;40(2):197-215.

Bray RH, Kurtz LT. Determination of total, organic, and available forms of phosphorus in soils. Soil Science 1945;59(1):39-46.

Chaiyo U, Garivait S, Wanthongchai K. Structure and carbon storage in aboveground biomass of mixed deciduous forest in western region, Thailand. GMSARN International Journal 2012;6:143-50.

Chapman HD. Cation exchange capacity. In: Black CA, Evans DD, White JL, Ensminger LE, Clark FE, Dinauer DC, editors. Method of Soil Analysis, Part 2: Chemical and Microbiological Properties. Madison (WI): The American Society of Agronomy; 1965. p. 891-913.

Chave J, Condit R, Muller-Landau HC, Thomas SC, Ashton PS, Bunyavejchewin S, et al. Assessing evidence for a pervasive alteration in tropical tree communities. PLoS Biology 2008;6(3):e45.

Chazdon RL. Tropical forest recovery: Legacies of human impact and natural disturbances. Perspectives in Plant Ecology, Evolution and Systematics 2003;6(1-2):51-71.

Chazdon RL. Second Growth. Chicago: University of Chicago Press; 2014.

Chen X, Wang X, Li J, Kang D. Species diversity of primary and secondary forests in Wanglang Nature Reserve. Global Ecology and Conservation 2020;22:e01022.

Collins LM, Schafer JL, Kam CM. A comparison of inclusive and restrictive strategies in modern missing data procedures. Psychological Methods 2001;6(4):Article No. 330.

Curtis PG, Slay CM, Harris NL, Tyukavina A, Hansen MC. Classifying drivers of global forest loss. Science 2018; 361(6407):1108-11.

Delgado-Baquerizo M, Reich PB, Trivedi C, Eldridge DJ, Abades S, Alfaro FD, et al. Multiple elements of soil biodiversity drive ecosystem functions across biomes. Nature Ecology and Evolution 2020;4(2):210-20.

Du H, Hu F, Zeng F, Wang K, Peng W, Zhang H, et al. Spatial distribution of tree species in evergreen-deciduous broadleaf karst forests in Southwest China. Scientific Reports 2017;7(1):1-9.

Elliott S, Navakitbumrung P, Kuarak C, Zangkum S, Anusarnsunthorn V, Blakesley D. Selecting framework tree species for restoring seasonally dry tropical forests in Northern Thailand based on field performance. Forest Ecology and Management 2003;184(1-3):177-91.

Fagundes M, Weisser W, Ganade G. The role of nurse successional stages on species-specific facilitation in drylands: Nurse traits and facilitation skills. Ecology and Evolution 2018;8(10):5173-84.

Food and Agriculture Organization of the United Nation (FAO), United Nation Environment Programme (UNEP). The State of the World’s Forests 2020: Forests, Biodiversity and People. Rome, Italy: FAO; 2020.

Geist HJ, Lambin EF. Proximate causes and underlying driving forces of tropical deforestation tropical forests are disappearing as the result of many pressures, both local and regional, acting in various combinations in different geographical locations. BioScience 2002;52(2):143-50.

Good SP, Noone D, Bowen G. Hydrologic connectivity constrains partitioning of global terrestrial water fluxes. Science 2015;349(6244):175-7.

Goodale UM, Ashton MS, Berlyn GP, Gregoire TG, Singhakumara BMP, Tennakoon KU. Disturbance and tropical pioneer species: Patterns of association across life history stages. Forest Ecology and Management 2012;277(1):54-66.

Gravel D, Canham CD, Beaudet M, Messier C. Shade tolerance, canopy gaps and mechanisms of coexistence of forest trees. Oikos 2010;119(3):475-84.

Gustafsson N, Culley S, Ashdown G, Owen DM, Pereira PM, Henriques R. Fast live-cell conventional fluorophore nanoscopy with ImageJ through super-resolution radial fluctuations. Nature Communications 2016;7(1):Article No. 12471.

Hansen MC, DeFries RS. Detecting long-term global forest change using continuous fields of tree-cover maps from 8-km advanced very high resolution radiometer (AVHRR) data for the years 1982-99. Ecosystems 2004;7(7):695-716.

Hooker TD, Compton JE. Forest ecosystem carbon and nitrogen accumulation during the first century after agricultural abandonment. Ecological Applications 2003;13(2):299-313.

Kamyo T. Gep-Informatics Modeling on Tropical Seasonal Forest Dynamics in Mae Klong Watershed Research Station, Kanchanaburi Province [dissertation]. Bangkok, Kasetsart University; 2016.

Kamyo T, Thinkampaeng S, Panuthai S, Tanaka H, Marod D. Natural forest regeneration in abandoned areas in Mae Klong Watershed Research Station Thong PhaPhoom District, Kanchanaburi Province. Proceedings of the 2nd Thai Forest Ecological Research Network Conference; 2013 Jan 24-26; Maejo University, Chiangmai: Thailand; 2013 (in Thai).

Kamyo T, Marod D, Pattanakiat S, Suksawang S, Panuthai S. Land cover changes in tropical seasonal forests at Mae Klong head watershed, Kanchanaburi Province, Thailand. Maejo

International Journal of Science and Technology 2016; 10(3):304-12.

Keeley JE, Bond WJ. Mast flowering and semelparity in bamboos: The bamboo fire cycle hypothesis. The American Naturalist 1999;154(3):383-91.

Khamyong N, Wangpakapattanawong P, Chairuangsri S, Inta A, Tiansawat P. Tree species composition and height-diameter allomery of three forest types in northern Thailand. Chiang Mai University Journal Of Natural Sciences 2018;17(4):289-306.

Klemick H. Shifting cultivation, forest fallow, and externalities in ecosystem services: Evidence from the Eastern Amazon. Journal of Environmental Economics and Management 2011;61(1):95-106.

Krebs CJ. Ecology: The Experimental Analysis of Distribution and Abundance. New York, USA: Harper Collins Publishers; 1994.

Kutintara U, Marod D, Takahashi M, Nakashizuka T. Growth and dynamics of bamboos in a tropical seasonal forest. In: The International Workshop on the Changes of Tropical Forest Ecosystems by El Niño and Others. Bangkok, Thailand: National Research Council; 1995.

Lacerda AEB, Kellermann B. What is the long-term effect of bamboo dominance on adult trees in the Araucaria Forest? A comparative analysis between two successional stages in southern Brazil. Diversity 2019;11(9):Article No. 165.

Larpkern P, Moe SR, Totland Ø. Bamboo dominance reduces tree regeneration in a disturbed tropical forest. Oecologia 2011; 165:161-8.

Laurance WF. Have we overstated the tropical biodiversity crisis? Trends in Ecology and Evolution 2007;22(2):65-70.

Lebrija-Trejos E, Pérez-García EA, Meave JA, Poorter L, Bongers F. Environmental changes during secondary succession in a tropical dry forest in Mexico. Journal of Tropical Ecology 2011;27(5):477-89.

Leishangthem D, Singh MR. Tree diversity, distribution and population structure of a Riparian Forest from certain zones along the Dikhu River in Nagaland, India. Journal of Forest and Environmental Science 2018;34(1):31-45.

Lepore M, Arellano G, Condit R, Davies S, Detto M, Gonzales-Akre E, et al. Fgeo: Analyze forest diversity and dynamics [Internet]. 2019 [cited 2021 May 7]. Available from: https://CRAN.R-project.org/package=fgeo.

Lewis SL, Edwards DP, Galbraith D. Increasing human dominance of tropical forests. Science 2015;349(6250):827-32.

Mabry CM, Fraterrigo JM. Species traits as generalized predictors of forest community response to human disturbance. Forest Ecology and Management 2009;257(2):723-30.

Marod D. Secondary Successional Pattern in Mixed Deciduous Forest of Mae Klong Watershed Research Station Changwat Kanchanavuri [dissertation]. Bangkok, Kasetsart University; 1995 (in Thai).

Marod D, Duengkae P, Sangkaew S, Racharak P, Suksavate W, Uthairatsamee S, et al. Population structure and spatial distribution of tree species in lower Montane Forest, Doi Suthep-Pui National Park, Northern Thailand. Environment and Natural Resources Journal 2022;20(6):644-63.

Marod D, Hermhuk S, Sungkaew S, Thinkampheang S, Kamyo T, Nuipakdee W. Species composition and spatial distribution of dominant trees in the forest ecotone of a mountain ecosystem, northern Thailand. Environment and Natural Resources Journal 2019;17(3):40-9.

Marod D, Kutintara U. Forest Ecology. Bangkok: Department of Forest Biology, Faculty of Forestry; 2009 (in Thai).

Marod D, Kutintara U, Yarwudhi C, Tanaka H, Nakashisuka T. Structural dynamics of a natural mixed deciduous forest in western Thailand. Journal of Vegetation Science 1999; 10(6):777-86.

Marod D, Kutintara U, Tanaka H, Nakashizuka T. The effects of drought and fire on seed and seedling dynamics in a tropical seasonal forest in Thailand. Plant Ecology 2002;161:41-57.

Marod D, Kutintara U, Tanaka H, Nakashizuka T. Effects of drought and fire on seedling survival and growth under contrasting light conditions in a seasonal tropical forest. Journal of Vegetation Science 2004;15(5):691-700.

Marod D, Lamthai A, Duengkae P, Pattanavibool A. Vegetation structure and floristic composition along the edge of Montane Forest and agricultural land in Um Phang Wildlife Santuary, Western Thailand. Agriculture and Natural Resources 2012; 46(2):162-80.

Matsuo T, Martínez-Ramos M, Bongers F, van der Sande MT, Poorter L. Forest structure drives changes in light heterogeneity during tropical secondary forest succession. Journal of Ecology 2021;109(8):2871-84.

Miles L, Newton AC, DeFries RS, Ravilious C, May I, Blyth S, et al. A global overview of the conservation status of tropical dry forest. Journal of Biogeography 2006;33(3):491-505.

Mohandass D, Hughes AC, Mackay B, Davidar P, Chhabra T. Floristic species composition and structure of a mid-elevation tropical montane evergreen forests (sholas) of the western ghats, southern India. Tropical Ecology 2016;57(3):533-43.

Mondoni A, Orsenigo S, Abeli T, Rossi G, Brancaleoni L, Corli A, et al. Plant regeneration above the species elevational leading edge: Trade-off between seedling recruitment and plant production. Frontiers in Ecology and Evolution 2020;8:Article No. 572878.

Phumphuang W, Marod D, Sungkaew S, Thinkampaeng S. Forest dynamics and tree distribution patterns in dry evergreen forest, northeastern, Thailand. Environment and Natural Resources Journal 2018;16(2):58-67.

Poorter L, Rozendaal DM, Bongers F, Almeida DJS, Álvarez FS, Andrade JL, et al. Functional recovery of secondary tropical forests. Proceedings of the National Academy of Sciences 2021;118(49):e2003405118.

Pothasin P, Compton SG, Wangpakapattanawong P. Riparian Ficus tree communities: The distribution and abundance of riparian fig trees in Northern Thailand. PLoS ONE 2014;9(10):e108945.

Quesada M, Stoner KE. Threats to the conservation of the tropical dry forest in Costa Rica. In: Frankie GW, Mata A, Vinson SB, editors. Biodiversity Conservation in Costa Rica: Learning the Lessons in a Seasonal Dry Forest. Berkeley: University of California Press; 2004. p. 266-80.

R Core Team. A language and environment for statistical computing, R Foundation for Statistical Computing [Internet]. 2017 [cited 2020 Jun 15]. Available from: http://www.R-project.org/.

Rong L, Duan X, Feng D, Zhang G. Soil moisture variation in a farmed dry-hot valley catchment evaluated by a redundancy analysis approach. Water 2017;9(2):Article No. 92.

Rother DC, Pizo MA, Siqueira T, Rodrigues RR, Jordano P.

Community-wide spatial and temporal discordances of seed-seedling shadows in a tropical rainforest. PLoS ONE 2015;10(4):e0123346.

Rueangket A, Duengkae P, Thinkhampang S, Marod D. Utilization of fruit by frugivores in lower montane forest at Doi Suthep-Pui National Park, Chiang Mai Province. Agriculture and Natural Resources 2019;53(5):457-64.

Sanchez-Azofeifa GA, Quesada M, Calvo J, Rodriguez JP, Nassar J, Garvin T, et al. Research priorities for tropical secondary dry forests. Biotropica 2005;37:477-85.

Sangsupan HA, Hibbs DE, Withrow-Robinson BA, Elliott S. Effect of microsite light on survival and growth of understory natural regeneration during restoration of seasonally dry tropical forest in upland northern Thailand. Forest Ecology and Management 2021;489:Article No. 119061.

Sann B, Kanzaki M, Ohta S. Vegetation patterns and species-filtering effects of soil in secondary succession in a tropical dry forest in central Myanmar. Journal of Tropical Ecology 2016;32(2):116-24.

Sasunti A, Asanog L. Tree Species Regeneration in Forest Restoration Area by Economic Tree at Nan Watershed, Nan Province [dissertation]. Chiang Mai, Maejo University; 2021.

Scheper AC, Verweij PA, Kuijk VM. Post-fire forest restoration in the humid tropics: A synthesis of available strategies and knowledge gaps for effective restoration. Science of the Total Environment 2021;771:Article No. 144647.

Sellan G, Thompson J, Majalap N, Brearley FQ. Soil characteristics influence species composition and forest structure differentially among tree size classes in a Bornean heath forest. Plant and Soil 2019;438(1):173-85.

Shannon CE, Weaver W. The Mathematical Theory of Communication. Illinois, United States of America: University of Illinois Press; 1949.

Shumi G, Dorresteijn I, Schultner J, Hylander K, Senbeta F, Hanspach J, et al. Woody plant use and management in relation to property rights: A social-ecological case study from southwestern Ethiopia. Ecosystems and People 2019; 15(1):303-16.

Smitinand T. Thai Plant Names. Bangkok, Thailand: Department of National Parks, Wildlife and Plant Conservation; 2014 (in Thai).

Soil Science Division Staff. Soil Survey Manual: United States Department of Agriculture Handbook No. 18. USA: United States Department of Agriculture; 2017.

Staelens J, Nachtergale L, Schrijver DA, Vanhellemont M, Wuyts K, Verheyen K. Spatio-temporal litterfall dynamics in a 60-year-old mixed deciduous forest. Annals of Forest Science 2011;68:89-98.

Suksawang S. Site Overview: Thong Pha Phoom Study Site. Bangkok, Thailand: Royal Forest Department; 1993.

Sullivan MJ, Talbot J, Lewis SL, Phillips OL, Qie L, Begne SK, et al. Diversity and carbon storage across the tropical forest biome. Scientific Reports 2017;7(1):Article No. 39102.

Swinfield T, Afriandi R, Antoni F, Harrison RD. Accelerating tropical forest restoration through the selective removal of pioneer species. Forest Ecology and Management 2016; 381:209-16.

Takahashi M, Kutintara U, Eaidthong W, Kobayashi S. Changes of the vegetation pattern in different successional stages. Proceedings of the International Workshop on the Changes of Tropical Forest Ecosystems by El Niño and Others; 1995 Feb 7-10; Kanchanaburi: Thailand; 1995.

Takahashi M, Marod D, Panuthai S, Hirai K. Carbon cycling in teak plantations in comparison with seasonally dry tropical forests in Thailand. In: Blanco JA, Lo YH, editors. Forest Ecosystems More Than Just Trees. Rijeka: InTech; 2012. p. 209-30.

Thein HM, Kanzaki M, Fukushima M. Structure and composition of a teak-bearing forest under the Myanmar Selection System: impacts of logging and bamboo flowering. Southeast Asian Studies 2007;45(3):303-16.

Van Hall RL, Cammeraat LH, Keesstra SD, Zorn M. Impact of secondary vegetation succession on soil quality in a humid Mediterranean landscape. Catena 2017;149:836-43.

Wang J, Wang H, Cao Y, Bai Z, Qin Q. Effects of soil and topographic factors on vegetation restoration in opencast coal mine dumps located in a loess area. Scientific Reports 2016;6(1):1-11.

Wang XY, Ling HB, Xu HL, De Pan C, Yuan KY. Relationships between plant communities and environmental factors in an extremely arid area: A case study in China. Polish Journal of Environmental Studies 2019;28(1):359-70.

Wright SJ. Tropical forests in a changing environment. Trends in Ecology and Evolution 2005;20(10):553-60.

Yarwudhi C, Tanaka N, Kobayashi S, Marod D, Kutintara U, Tabaka H, et al. Regeneration dynamics of tree after the simultaneous flowering and death of undergrowing bamboo in a mixed deciduous forest, western Thailand. Proceedings of the International Workshop on the Responses of Tropical Forest Ecosystem to Long Term Cyclic Climate Changes; 2000 Jan 24-27; Kanchanaburi: Thailand; 2000.

Zhang ZH, Hu G, Ni J. Effects of topographical and edaphic factors on the distribution of plant communities in two subtropical karst forests, Southwestern China. Journal of Mountain Science 2013;10(1):95-104.

Zhao H, Wang QR, Fan W, Song GH. The relationship between secondary forest and environmental factors in the southern Taihang Mountains. Scientific Reports 2017;7(1):Article No. 16431.