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**Effects of Fire on Diversity and Aboveground Biomass of Understory Communities in Seasonally Dry Tropical Forest in Western Thailand**

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% Abstract (Do not insert blank lines, i.e. \\)

\abstract{Fire is a necessary disturbance in tropical deciduous forests, as it helps clear the understory community and allow regeneration of grasses and forbs for local wildlife. The Huai Kha Khaeng Wildlife Sanctuary (HKK) and The Huai Thab Salao-Huai Rabum Non-Hunting Area (HTS) are parts of a few places in Southeast Asia with the deciduous forests. However, this area was heavily logged up until 1989, followed by a long period of fire suppression. The consequences of these changes on understory communities have not been investigated. Therefore, the current study aimed to examine the understory communities and their aboveground biomass before and after the annual prescribed burns in HKK and HTS. Understory plant composition and biomass were surveyed in November 2018 (before the fire) and May 2019 (three months after the fire) in 128 temporary plots, covering of deciduous dipterocarp forest, mixed deciduous forest, mixed deciduous forest with bamboo, and open area. We identified a total of 480 understory species, including 37 grass species, 214 forb species, 73 shrub species, 153 tree seedling species and three species of bamboo in the study plots. Grasses in the DDF plots were at 72.79 ± 22.41 kg ha$^{-1}$, accounting for only ten percent of the understory plants in the plots. The understory community in the DDF plots was dominated by shrubs and tree seedlings of competing species, especially after the fire. The results suggested that past logging activities and long-term fire suppression had reduced the number of mature key dipterocarp forests and hindered the regeneration of grasses and forbs. Maintaining the structure of dipterocarp forests and sufficient food sources for the local wildlife species will require more active habitat management of the study areas.}

% **Keywords**

\keyword{deciduous dipterocarp forest; fire suppression; understory plants; understory succession}

**\section{Introduction}**

Tropical deciduous forests stand out among the other biomes, for their high biodiversity and unique floral composition, despite its relatively small cover of the Earth surface at 2.85{$\%$} \cite{RN10, RN17}. In this type of forest, understory communities change drastically with fluctuating seasonal microclimates in dry and wet seasons \cite{RN35, RN37} making them more vulnerable than their canopy tree community \cite{RN20}. Understory communities can be affected by abiotic factors, such as soil properties and water availability, and biotic factor, such as light competition among the species \cite{RN35, RN37}. Disturbances can also affect the understory community more dramatically than the canopy tree. In dry forests, fire is a regular disturbance in the tropical deciduous forests, and the native species of herbaceous plants usually have adaptation to withstand the fire \cite{RN42, RN50, RN1}.

Understory communities in seasonally dry tropical forests are mostly consisted of many grasses (Poaceae), forbs, shrubs, and tree seedlings \cite{RN50, RN47, RN37}. Many of these species can resprout rapidly after the fire \cite{RN27, RN7}. Since the beginning of human colonization in Southeast Asia, these fires are frequently initiated by humans for forest clearing, hunting, farming, and logging. In many protected areas in Thailand, the forests have also experienced regular prescribed burns. These fires are usually low-intensity ground fires which directly impact the understory communities in seasonally dry tropical forests \cite{RN6, RN51}.

The Huai Kha Khaeng Wildlife Sanctuary (HKK) and The Huai Thab Salao-Huai Rabum Non-Hunting Area (HTS) in Western Thailand is a home to one of the largest patches of contiguous lowland seasonally dry tropical forests in the country \cite{RN40, RN48}. These deciduous forests produce forages, mostly through understory herbaceous for many large mammal species. Since the end of logging activities in 1989, the plant community in these seasonally dry forests are undergoing successions \cite{RN15, RN32}. Between 1990-2002, any form of fires was actively suppressed in the Wildlife Sanctuary and its surroundings \cite{RN39}, and since 2002, annual early prescribed burns were administered in January to February \cite{RN22}. These unusual fire control regimes must have impact on assembly and succession of the understory community in the area.

In theory, a forested area experiences a low-intensity fire will maintain their canopy trees, but most of the understory species should be eliminated immediately after the fire \cite{RN36}. A secondary succession should follow with the light-demanding species, such as grasses and forbs. They should become more abundant for a period of time, before the shade-tolerant species takes over \cite{RN9, RN12}. This period with grasses as dominant life form is critical as a food source of herbivore species and is often maintained in many protected areas to ensure sufficient food sources for the herbivore species \cite{RN57}. However, our study area has experienced a unique fire regime and land use history that alter the composition of the understory plants from a typical deciduous dipterocarp forest. Fire suppression can lead to accumulation of fuel loads and alter the composition of the understory and tree communities. In some cases, litter accumulation can become an obstacle to the establishment of tree seedlings and other understory species, which will irreversibly change the forest structure \cite{RN56, RN55}. It should be of interest for ecologists and land managers to understand the effect of low-intensity fire in the study area with a decade-long fire suppression. It is expected that a low-intensity fire in our study area would remove some biomass and alter the species composition. The effects of the fire will likely differ among the forest types and life forms as well.

Previous studies about the understory community in HKK focused on the aboveground biomass to determine the amount of fuel on the forest floor \cite{RN46, RN50, RN51}. Only a few studies have examined understory community and temporal variation of aboveground biomass \cite{RN52, RN23, RN18, RN45}. We found no report on the identity of these understory species and their individual contribution to the aboveground biomass of the seasonally dry forest in HKK. Therefore, the objectives of this study were 1) to determine the species composition and its aboveground biomass and 2) to compare the changes in aboveground biomass of understory plants before and after prescribed burns in the study area. We used systematic samplings to collect aboveground biomass and voucher specimens to identify them to the species level. These data will provide insights for the forest and wildlife habitat managers in their management of forest structure, fire control, and availability of natural forage in the seasonally dry tropical forest \cite{RN29, RN2, RN30}.

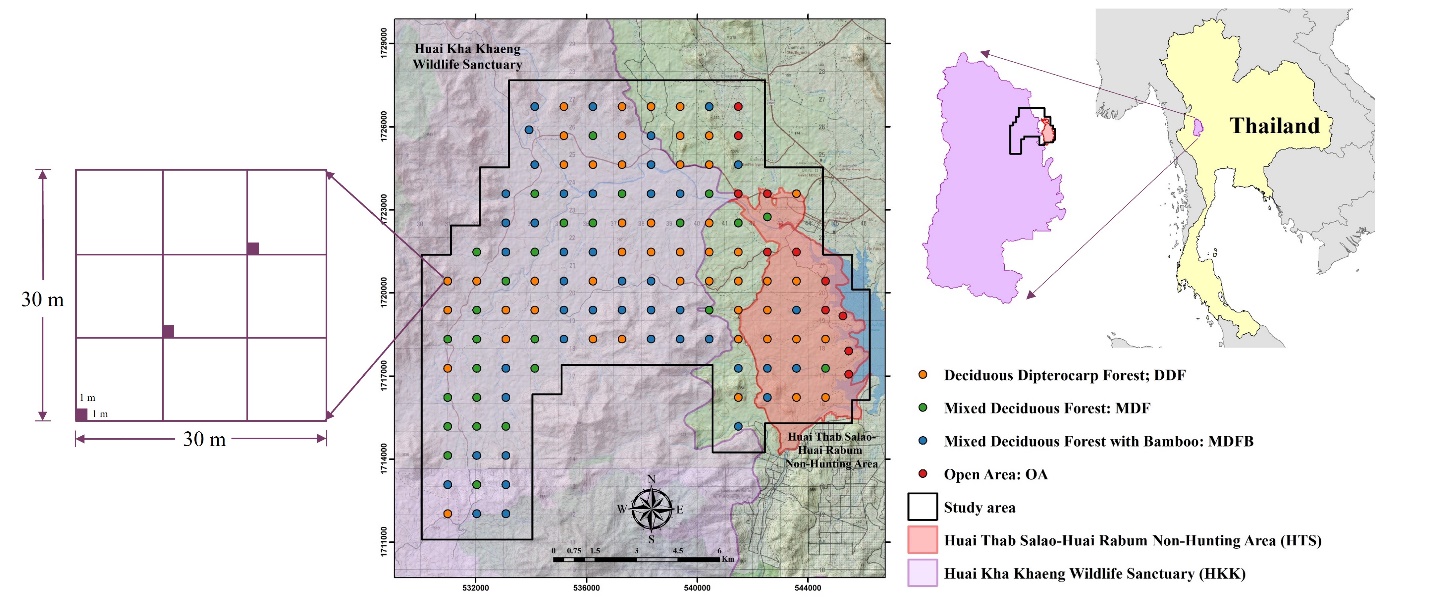
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**\section{Materials and Methods}**

**\subsection{Study Site}**

HKK is located in Uthai Thani Province in Thailand, covering around 2,780 km$^{2}$ \cite{RN5}. HTS, with the area of 26 km$^{2}$, is adjacent to the east of HKK. This natural vicinity is considered the “meeting points” of flora and fauna from multiple biogeographical realms, including Sino-Himalayan, Sundaic, Indo-Burmense and Indo-Chinese regions. HKK is a part of the UNESCO’s World Heritage site, Thungyai-Huai Kha Khaeng Wildlife Sanctuaries, established in 1991 \cite{RN48}. The study site is located on the northeastern side of HKK and its buffer, covering about 173 km$^{2}$ of undulating valleys, including Nang Rum Valley and Thab Salao Valley, at 153-601 m above sea level \cite{RN33} (Figure \ref{Fig\_1}). HKK and HTS are two adjacent official protected areas managed by different policies under the “Wild Animal Reservation and Protection Act, B. E. 2562 (2019)”. HKK focuses on strict preservation and protection, while HTS applies a more relaxed measures for sustainable and participatory uses of local community.

The study area experiences a distinct dry period of 5-6 months between November and April of the following year. The 19-year average (during 2001-2019) of weather conditions are as follows. The annual average temperature at 27.10$^\circ C$ with the lowest temperature at 16.23$^\circ C$ in January and the highest at 37.05$^\circ C$ in April. The annual total precipitation is on average 1,462.83 mm, and the relative humidity is on average 79.95\textbf{$\%$} \cite{RN21}. More than 75\textbf{$\%$} of the study site are classified as “deciduous forest,” including two subtypes: Deciduous Dipterocarp Forest (aka Dry Dipterocarp Forest) and Mixed Deciduous Forest \cite{RN5, RN6}.



**Figure 1** The 128 sample plots systematically located on the border of the Huai Kha Khaeng Wildlife Sanctuary and the Huai Thab Salao - Huai Rabum Non-Hunting Area, Western Thailand

**\subsection{Historical record}**

In 1964, the Huai Kha Khaeng-Thab Salao Valleys were declared a “National Forest”. During this time, the logging in natural forests were still allowed. Even with the establishment of HKK in 1972, trees were regularly logged from this area through 1987 \cite{RN15}. It is not until 1989 when the Thai Government no longer granted a concession for logging in national forests \cite{RN32}. In 1998, a major El Niño-Southern Oscillation (ENSO) event was observed worldwide, which resulted in a high-intensity fire in the Huai Kha Khaeng-Thab Salao forests. A majority of trees and tree seedlings were decimated over a large expanse of forests \cite{RN1}. Such impacts from fire raised concerns among the governmental officials and led to a strict “fire prevention program.” Under this program, the Thai Royal Forest Department established five wildfire prevention stations around the Sanctuary to completely suppress all the forest fires, big and small. The fire suppression program lasted until around 2002, where the complete lack of fires in this area started to show the impact in the disappearance of open areas in the deciduous dipterocarp forest that normally provide forages for large herbivores in the area. Since then, the prescribed burns (early burning) have been administered in January to February every year to reduce the fuel loads and prevent the spread of the fire into the evergreen forests in the mountainous areas nearby \cite{RN39, RN22} (Figure \ref{Fig\_2}).

A picture containing tree, plant, forest, wooded

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**Figure 2** Annual Ground fires with low intensity usually caused by prescribed burning in Seasonally Dry Tropical Forest during January to February. Photo by: Khao Nang Ram Wildlife Research Station, Department of National Parks, Wildlife and Plant Conservation.

**\subsection{Data Collection}**

**\subsubsection{Understory Community}**

A total of 128 temporary plots were chosen systematically to be 1 km apart, covering the 173 km$^{2}$ of Thab Salao Valley (Figure \ref{Fig\_1}). Each plot was 30 × 30 m$^{2}$. These plots were classified into their respective forest types according to the dominant species as followed: Deciduous Dipterocarp Forest (DDF), Mixed Deciduous Forest (MDF), Mixed Deciduous Forest with Bamboo (MDFB), and Open Area (OA). During the study, the prescribed burning conducted by the forest rangers of HKK was between 22 February to 10 March 2019.

Each 30 × 30 m$^{2}$ plot was further divided into nine 10 × 10 m$^{2}$ subplots. In each subplot, the canopy cover was estimated using a densiometer. Three 1 × 1 m$^{2}$ plots were laid out at the lower left corner of diagonal subplots (Figure \ref{Fig\_1}) to destructively sample all understory plants within. The collected plant specimens were classified into five groups according to their life forms, using a modified definition from \citet{RN30}: 1) Graminoids (all Cyperaceae and Poaceae, except for bamboos), 2) forbs, 3) bamboo seedlings, 4) shrubs, and 5) tree seedlings. The life forms focus on the forage plants. Species were grouped based on the woodiness and food preference by large herbivore species. In this study, the “tree” life form included tree seedlings (shorter than 1.30 m) and saplings (1.30 – 2 m tall, and diameter at breast height less than 4.5 cm). Each specimen was identified to the smallest taxonomic level as possible, as most of the specimens lacked flowers necessary for species identification. The voucher specimens were deposited at Faculty of Forestry, Kasetsart University.

**\subsubsection{Aboveground Biomass Measurement and Analysis}**

All understory plants collected from 1 × 1 m$^{2}$ plots were removed by cutting the plants right by the ground. Then, the samples for each species were dried at 70$^\circ C$ in a hot oven for 48 hours before weighting for their dry mass. The aboveground biomass (AGB) was measured twice 1) prior to prescribed burn in November-December 2018, and 2) at three months after the burn in May-June 2019 to allow some regeneration of understory plants in the plot. AGB before and after the fires in each life form was compared separately for burned (n = 100) and unburned plots (n = 28), using the Wilcoxon rank sum test \cite{RN19}.

To discern the impact of forest fire on species composition of understory, a permutational multivariate analysis of variance (PERMANOVA) was performed on the community matrix on the burned plots, using the time (before/after the fire), the forest types, and their interaction as the explanatory variables. The matrix excluded the data from rare species (found in less than 20 plots) and the plots from Open Area (OA), as they contained a completely different set of herbaceous species. The analysis was performed at 9,999 permutations within each forest type, using the function “adonis2” in the “vegan” package (xxxx, xxxx). To visualize the results, non-metric multidimensional scaling (NMDS) was performed on the community matrix with the function “metaMDS” in “vegan” package, using the Bray-Curtis distance at 1,000 maximum iterations. The first two NMDS axes and the convex hulls for each forest type before and after the fire were drawn. The Similarity Percentage (SIMPER) analysis was also performed to compare the abundance of each species the before/after fire in the burned plots, as well as its contribution to the overall Bray-Curtis dissimilarity index (XXX). This part of analysis was computed using the function “simper” in the “vegan” package (XXX).

Additionally, the seedling density of some species in deciduous dipterocarp forest was analyzed to infer about the future forest structure, because we observed the increasing number of competing non-native species that may colonize the area and render the forest structure unsuitable for the livelihood of local herbivore species. This analysis will allow us to determine ways in which we can preserve the original composition of deciduous dipterocarp forest. All statistical analyses were performed in R version 4.1.2 and manipulate the database by using “tidyverse” package \cite{RN53}.

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**\section{Results}**

**\subsection{Understory species composition by forest types}**

The 128 systematic plots covered of Deciduous Dipterocarp Forest (DDF, n= 48), Mixed Deciduous Forest (MDF, n= 27), Mixed Deciduous Forest with Bamboo (MDFB, n= 44), and Open Area (OA, n= 9). We identified a total of 480 understory species, including 37 grass species, 214 forb species, 73 shrub species, 153 tree species and 3 species of bamboo, were found in the study plots (Table S1). From a total of 128 plots, 100 plots were impacted by the fire and the other 28 plots remained unaffected. Here we reported understory plant composition according to the following four forest types (Table \ref{Table\_1}). The dominant understory species, ranked by biomass, and the common species, ranked by observed frequency of given species found in the burned plots, presented in Table \ref{Fig\_2} and Table \ref{Fig\_3}, respectively. In terms of the effect of prescribed fire on species composition, the PERMANOVA showed that fire and forest type significantly affected the species composition (Ffire = 3.35, Pfire = 0.0001; Fforest type = 8.21, Pforest type = 0.001), while the interaction term was not significant (F = 1.18, P = 0.15). When testing by given forest types, the PERMANOVA indicated that the prescribed fire significantly affected the species communities of DDF (F = 1.58, P = 0.05), MDF (F = 2.07, P = 0.001) and MDFB (F = 2.04, P = 0.002) (Figure **3**). The results were consistent with the hypotheses that the fire would alter the species composition, but the effect of the fire did not vary among the forest types, as the forest types already had the different composition to begin with.

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**Figure XX** Non-metric Multidimensional Scaling (NMDS) plots with the first two axes, illustrating species composition for each forest type before and at three months after the prescribed burn.

Before the fire (November 2018, n= 128), we identified a total of 403 species from 293 genera and 81 families (see Table S1). Fabaceae was the family with the largest number of species, followed by Poaceae, Malvaceae, Rubiaceae, and Cyperaceae, respectively. For the burned plots in DDF, \textit{Polyalthia debilis} had the highest AGB (75.92 ± 43.70 kg ha$^{-1}$) (Table \ref{Fig\_2} and Table S2), whereas \textit{Streptocaulon juventas} was the most common species (Table \ref{Fig\_3} and Table S2). In MDF, \textit{Cyrtococcum accrescens} had the highest biomass at 74.46 ± 21.09 kg ha$^{-1}$ (Table \ref{Fig\_2} and Table S2), while \textit{Cyrtococcum accrescens} was the most common species (Table \ref{Fig\_3} and Table S2). In MDFB, \textit{Helicteres isora} had the highest biomass at 40.20 ± 21.89 kg ha$^{-1}$ (Table \ref{Fig\_2} and Table S2), while \textit{Commelina} cf. \textit{paludosa} was the most common species (Table \ref{Fig\_3} and Table S2). In OA, more than 80\textbf{$\%$} of understory species were graminoids and forbs. The species with the highest biomass included \textit{Paspalum notatum}, \textit{Euploca strigosa}, and \textit{Eragrostis montana} (Table \ref{Fig\_2} and Table S2).

At three months after the fire (June 2019, n= 128), a total of 388 species from 264 genera and 79 families were identified (see Table S1). Fabaceae still had the highest number of species, followed by Poaceae, Malvaceae, Lamiaceae, and Apocynaceae, respectively. The most diverse understory community was found in DDF, followed by MDFB, MDF and OA, respectively (Table \ref{Fig\_1}). The total number of species for each forest type were similar before and after the fire (Table \ref{Fig\_1}). For the burned plots in DDF and MDF, \textit{Croton hutchinsonianus} became more common species in the plots. For MDFB, \textit{Alangium indochinense} became more abundant at 36.30 ± 34.69 kg ha$^{-1}$. In OA, \textit{Sida cordifolia} colonized the area very densely, while biomass of graminoid and forb species reduced substantially (Table \ref{Fig\_2}, Table \ref{Fig\_3}, and Table S2).

To determine the species that contributed to the observed change in species composition and biomass, the SIMPER analysis was performed and showed that ten understory species (P < 0.05) contributed significantly to the overall dissimilarity in biomass before and after the fire, including CROTHU, CYRTAC, CURCSP1 GLOBSP1, ALBIOD, CAYRTR, OPLICO, ACRARA, CHROOD, AMPHMA, HELIAN and CYANCR. The lists of significant species in overall forest types and each forest type were shown in Table S33. Notably, for the burned plots in DDF and MDF, tree seedlings of \textit{Croton hutchinsonianus} had the highest contribution to the observed change after the fire.

**\subsection{Canopy cover}**

In the burn plots, the average canopy cover before the fire was 70.68 ± 1.36\textbf{$\%$} (mean ± 1 standard error) with the MDF plots having the highest canopy cover at 75.38 ± 1.37\textbf{$\%$}, and the OA plots being completely open (0\textbf{$\%$} cover). After the fire, the average canopy cover was at 68.37 ± 1.38\textbf{$\%$}, slightly lower than that before the fire. The MDFB plots had the highest canopy cover at 72.73 ± 1.99\textbf{$\%$}, and the OA plots had the lowest cover at 5.64 ± 5.64\textbf{$\%$}. The canopy covers before and after the fire were not significantly different (\textit{W} = 4378.5, \textit{p} = 0.129, Table \ref{Fig\_1}).

In the unburned plots, the average canopy cover before and after the fire were at 59.47 ± 5.51\textbf{$\%$} and 57.92 ± 5.25\textbf{$\%$}, respectively. Obviously, in the unburned areas, the OA plots had higher canopy cover than that of the burned areas. The canopy covers before and after the fire were also not significantly different (\textit{W} = 351.0, \textit{p} = 0.507, Table \ref{Table\_1}).

**\subsection{Aboveground Biomass of Understory Plants}**

For the plots in the burned areas, AGB of understory plants was at 715.39 ± 51.33 kg ha$^{-1}$ (mean ± 1 standard error) prior to the fire in November-December 2018. The average AGB significantly decreased to 587.51 ± 58.99 kg ha$^{-1}$ after the fire in May-June 2019 (\textit{W} = 6097, \textit{p} = 0.007). Notably, AGB decreased significantly after the fire, especially that in MDFB (\textit{W} = 751, \textit{p} = 0.034 , Table \ref{Table\_4}). When considering each life form separately, we found that AGB of bamboos and tree seedlings showed no significant increase (\textit{W} = 4851 and 5260.5, \textit{p} > 0.05, Figure \ref{Fig\_3}, Table S3), whereas that of forbs and grasses showed a distinct decrease (\textit{W} = 6238, \textit{p} < 0.05, Figure \ref{Fig\_3}, Table S3). Estimated AGB and water content of individual species of understory based on the 128 sample plots were reported in Table S1.

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**Figure 3** Dry above ground biomass (AGB) of understory plants categorized by life forms before fire, and at three months after fire. An asterisk indicates significant difference between before and after the fire, and “ns” indicated no significant difference based on the Wilcoxon rank sum test (Significant codes: \*\*\*< 0.001, \*\* < 0.01, \*< 0.05).

**Table 1** Mean of canopy cover and number of species found in particular forest types before and at three months after fire in 2019.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Forest types\*** | **No. of plot** | **Total Number of species** | | **% Canopy Cover (± 1 SE)** | | **Significant Difference** | |
| **Before fire**  **(Nov-Dec 2018)** | **After fire**  **(May-Jun 2019)** | **Before fire**  **(Nov-Dec 2018)** | **After fire**  **(May-Jun 2019)** | **W\*\*** | **p-value** |
| **Burned plots (burned in January 2019, n =100)** | | | | | |  |  |
| DDF | 41 | 213 | 219 | 67.98 ± 1.62 | 69.08 ± 1.45 | 923 | 0.447 |
| MDF | 23 | 159 | 169 | 75.38 ± 1.37 | 66.08 ± 2.10 | 120 | 0.001 |
| MDFB | 34 | 195 | 188 | 74.91 ± 1.212 | 72.73 ± 1.99 | 553 | 0.764 |
| OA | 2 | 22 | 13 | 0.00 ± 0.00 | 5.64 ± 5.64 | 3 | 0.617 |
| All forest types | 100 | 356 | 330 | 70.68 ± 1.36 | 68.37 ± 1.38 | 4378.5 | 0.129 |
| DDF | 7 | 92 | 87 | 70.45 ± 3.07 | 67.39 ± 3.28 | 18 | 0.456 |
| MDF | 4 | 51 | 56 | 75.24 ± 4.66 | 73.29 ± 2.37 | 7 | 0.886 |
| MDFB | 10 | 111 | 110 | 75.66 ± 1.42 | 73.03 ± 3.14 | 40 | 0.481 |
| OA | 7 | 74 | 58 | 16.32 ± 10.47 | 18.10 ± 10.34 | 29 | 0.595 |
| All forest types | 28 | 240 | 229 | 59.47 ± 5.51 | 57.92 ± 5.25 | 351 | 0.507 |

**\***DDF = Deciduous Dipterocarp Forest, MDF = Mixed Deciduous Forest, MDFB = Mixed Deciduous Forest with Bamboos, OA = Open Area.

\*\**W* = Wilcoxon value based on the Wilcoxon rank sum test

**Table 2** Five Dominant species of understory plants found in the burned plots across different forest types between before and at three months after fire.

| **Forest types\*** | **Before fire (Nov-Dec 2018)** | | | |  | **After fire (May-Jun 2019)** | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Botanical names** | **Life form** | **AGB (kg ha-1)** | **Obs Freq** |  | **Botanical names** | **Life form** | **AGB (kg ha-1)** | **Obs Freq** |
| DDF | *Polyalthia debilis* | Shrub | 75.92 ± 43.70 | 17 |  | *Croton hutchinsonianus* | Tree | 120.14 ± 40.23 | 21 |
| (n = 41) | *Helicteres angustifolia* | Shrub | 74.51 ± 27.43 | 16 |  | *Shorea obtusa* | Tree | 56.43 ± 40.42 | 9 |
|  | *Croton hutchinsonianus* | Tree | 52.09 ± 21.89 | 18 |  | *Phyllodium insigne* | Shrub | 34.48 ± 14.76 | 10 |
|  | *Shorea obtusa* | Tree | 43.04 ± 23.57 | 9 |  | *Polyalthia debilis* | Shrub | 31.05 ± 11.35 | 19 |
|  | *Phyllodium insigne* | Shrub | 40.46 ± 13.90 | 11 |  | *Dillenia obovata* | Tree | 27.13 ± 17.16 | 8 |
| MDF | *Cyrtococcum accrescens* | Grass | 74.46 ± 21.09 | 17 |  | *Croton hutchinsonianus* | Tree | 114.95 ± 36.17 | 14 |
| (n = 23) | *Dendrolobium rugosum* | Shrub | 58.31 ± 27.27 | 11 |  | *Polyalthia debilis* | Shrub | 102.88 ± 89.57 | 7 |
|  | *Chromolaena odorata* | Forb | 57.31 ± 32.29 | 9 |  | *Harrisonia perforata* | Shrub | 70.17 ± 64.61 | 4 |
|  | *Croton hutchinsonianus* | Tree | 51.24 ± 24.02 | 10 |  | *Dendrolobium rugosum* | Shrub | 35.05 ± 22.33 | 8 |
|  | *Helicteres isora* | Shrub | 46.68 ± 32.22 | 6 |  | *Caesalpinia* sp.1 | Shrub | 27.64 ± 27.23 | 2 |
| MDFB | *Helicteres isora* | Shrub | 40.20 ± 21.89 | 5 |  | *Alangium indochinense* | Tree | 36.30 ±34.69 | 6 |
| (n = 34) | *Cyrtococcum accrescens* | Grass | 34.79 ±11.69 | 17 |  | *Thyrsostachys siamensis* | Bamboo | 20.89 ± 17.29 | 3 |
|  | *Ottochloa nodosa* | Grass | 26.47 ± 9.46 | 21 |  | *Berrya mollis* | Tree | 15.69 ± 15.69 | 1 |
|  | *Chromolaena odorata* | Forb | 21.93 ± 8.80 | 11 |  | *Sterculia guttata* | Tree | 14.17 ± 8.67 | 8 |
|  | *Polyalthia debilis* | Shrub | 20.64 ± 9.19 | 5 |  | *Xylia xylocarpa* | Tree | 13.77 ± 13.23 | 3 |
| OA | *Paspalum notatum* | Grass | 458.33 ± 134.67 | 2 |  | *Sida cordifolia* | Shrub | 949.02 ± 942.36 | 2 |
| (n = 2) | *Euploca strigosa* | Forb | 267.83 ± 252.17 | 2 |  | *Mimosa pigra* | Shrub | 29.33 ± 23.67 | 2 |
|  | *Eragrostis montana* | Grass | 142.33 ± 113.33 | 2 |  | *Sida acuta* | Shrub | 21.33 ± 21.33 | 1 |
|  | *Cyperus isolepis* | Grass | 135.83 ± 54.17 | 2 |  | *Scoparia dulcis* | Forb | 20.67 ± 17.33 | 2 |
|  | *Amaranthus spinosus* | Forb | 131.67 ± 130.67 | 2 |  | *Tephrosia purpurea* | Forb | 12.83 ± 1.83 | 2 |

**Table 3** Five Common species of understory plants found in the burned plots across different forest types between before and at three months after fire.

| **Forest types\*** | **Before fire (Nov-Dec 2018)** | | | |  | **After fire (May-Jun 2019)** | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Botanical names** | **Life form** | **AGB (kg ha-1)** | **Obs Freq** |  | **Botanical names** | **Life form** | **AGB (kg ha-1)** | **Obs Freq** |
| DDF | *Streptocaulon juventas* | Forb | 8.70 ± 2.05 | 26 |  | *Setaria parviflora* | Grass | 13.75 ± 3.46 | 29 |
| (n = 41) | *Shorea siamensis* | Tree | 18.29 ± 8.92 | 21 |  | *Streptocaulon juventas* | Forb | 7.51 ± 1.65 | 28 |
|  | *Setaria parviflora* | Grass | 20.85 ± 11.30 | 19 |  | *Cyanotis burmanniana* | Forb | 0.79 ± 0.26 | 25 |
|  | *Croton hutchinsonianus* | Tree | 52.09 ± 21.89 | 18 |  | *Croton hutchinsonianus* | Tree | 120.14 ± 40.23 | 21 |
|  | *Uvaria ferruginea* | Shrub | 21.48 ± 10.23 | 18 |  | *Polyalthia debilis* | Shrub | 31.05 ± 11.35 | 19 |
| MDF | *Cyrtococcum accrescens* | Grass | 74.46 ± 21.09 | 17 |  | *Ottochloa nodosa* | Grass | 16.45 ± 7.18 | 17 |
| (n = 23) | *Dendrolobium rugosum* | Shrub | 58.31 ± 27.27 | 11 |  | *Croton hutchinsonianus* | Tree | 114.95 ± 36.17 | 14 |
|  | *Ottochloa nodosa* | Grass | 17.21 ± 6.45 | 11 |  | *Cayratia trifolia* | Forb | 1.55 ± 0.81 | 13 |
|  | *Croton hutchinsonianus* | Tree | 51.24 ± 24.02 | 10 |  | *Senegalia comosa* | Shrub | 7.17 ± 4.10 | 9 |
|  | *Senegalia comosa* | Shrub | 8.24 ± 4.64 | 10 |  | *Commelina* cf. *paludosa* | Forb | 2.83 ± 0.97 | 9 |
| MDFB | *Commelina* cf. *paludosa* | Forb | 3.80 ± -0.91 | 26 |  | *Commelina* cf. *paludosa* | Forb | 4.99 ± 1.16 | 26 |
| (n = 34) | *Ottochloa nodosa* | Grass | 26.47 ± 9.46 | 21 |  | *Ottochloa nodosa* | Grass | 9.38 ± 3.47 | 17 |
|  | *Cyrtococcum accrescens* | Grass | 34.79 ± 11.69 | 17 |  | *Kaempferia* sp.1 | Forb | 1.02 ± 0.41 | 16 |
|  | *Globba* sp.1 | Forb | 1.90 ± 0.90 | 17 |  | *Cayratia trifolia* | Forb | 1.07 ± 0.39 | 15 |
|  | *Oplismenus compositus* | Grass | 9.56 ± 4.16 | 12 |  | *Zingiber zerumbet* | Forb | 3.03 ± 1.34 | 14 |
| OA | *Paspalum notatum* | Grass | 458.33 ± 134.67 | 2 |  | *Sida cordifolia* | Shrub | 949.02 ± 942.36 | 2 |
| (n = 2) | *Euploca strigosa* | Forb | 267.83 ± 252.17 | 2 |  | *Mimosa pigra* | Shrub | 29.33 ± 23.67 | 2 |
|  | *Eragrostis montana* | Grass | 142.33 ± 113.33 | 2 |  | *Scoparia dulcis* | Forb | 20.67 ± 17.33 | 2 |
|  | *Cyperus isolepis* | Grass | 135.83 ± 54.17 | 2 |  | *Tephrosia purpurea* | Forb | 12.83 ± 1.83 | 2 |
|  | *Amaranthus spinosus* | Forb | 131.67 ± 130.67 | 2 |  | *Alternanthera sessilis* | Forb | 8.50 ± 5.50 | 2 |

For the plots in the unburned area, the average AGB was at 1,045.50 ± 150.24 kg ha$^{-1}$ prior to the fire with the OA plot having the highest biomass, followed by MDF, MDFB, and DDF, respectively (Table \ref{Table\_4}). After the fire, the average AGB was at 1,143.68 ± 223.11 kg ha$^{-1}$, which showed a slight increase but did not differ significantly from that before the fire (\textit{W} = 408, \textit{p} = 0.801, Table \ref{Table\_4}). The OA plots had the highest biomass, followed by the MDFB, DDF, and MDF plots. The biomass increased slightly from before the fire in the DDF and OA plots and decreased slightly in the MDF and MDFB plots. This result not only found the no significant between before and after forest fire, but also found no significant difference was found in the AGB for each life form (\textit{p} > 0.05, Figure \ref{Fig\_3}, Table S3).

**Table 4** Mean of AGB of understory plants in different forest types before and at three months after fire.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Forest types\*** | **No. of plot** | **AGB (kg ha-1 ± 1SE)** | | **Significant Difference** | |
| **Before fire**  **(Nov-Dec 2018)** | **After fire**  **(May-Jun 2019)** | ***W\*\**** | **p -value** |
| **Burned plots (burned in February 2019)** | | | | | |
| DDF | 41 | 803.79 ± 85.82 | 707.08 ± 92.62 | 738 | 0.346 |
| MDF | 23 | 718.64 ± 101.28 | 679.27 ± 150.59 | 192 | 0.114 |
| MDFB | 34 | 544.23 ± 67.78 | 352.37 ± 59.50 | 405 | 0.034 |
| OA | 2 | 1,775.42 ± 221.92 | 1,078.52 ± 945.86 | 2 | 1.000 |
| All forest types | 100 | 715.39 ± 51.33 | 587.51 ± 58.99 | 3903 | 0.007 |
| **Unburned plots (unaffected by 2019 fire)** | | | | | |
| DDF | 7 | 638.30 ± 221.08 | 965.05 ± 300.27 | 32 | 0.383 |
| MDF | 4 | 1,178.17 ± 398.32 | 939.09 ± 279.68 | 6 | 0.686 |
| MDFB | 10 | 974.95 ± 218.87 | 466.60 ± 128.25 | 26 | 0.075 |
| OA | 7 | 1,477.67 ± 384.46 | 2,406.46 ± 603.36 | 33 | 0.318 |
| All forest types | 28 | 1,045.50 ± 150.24 | 1,143.68 ± 223.11 | 376 | 0.801 |

**\***DDF = Deciduous Dipterocarp Forest, MDF = Mixed Deciduous Forest, MDFB = Mixed Deciduous Forest with Bamboos, OA = Open Area.

\*\**W* = Wilcoxon value based on the Wilcoxon rank sum test

**\subsection{Variation in Biomass by Life Forms}**

Regarding the burned plots (n = 100), after the fire in the DDF plots, the biomass of forbs decreased significantly from that before the fire (\textit{W} = 1062, \textit{p} = 0.004, Table S4), while the changes in the other life forms were not significant. In the MDF plots, the grass biomass decreased significantly from that before the fire (\textit{W} = 411, \textit{p} = 0.001, Table S4), while the changes in the other life forms were not significant. In the MDFB plots, the biomasses of grass showed significant decreases from those before the fire (\textit{W} = 769, \textit{p} = 0.019, Table S4) and were not found significant changes were detected in the others life forms. Finally, in the OA plots, bamboos and tree seedlings were not found in the sampling plots. Forb and grass biomasses showed no significant decreases after the fire, while the shrub biomass showed a no significant increase after the fire (\textit{W} = 3.0, \textit{p} > 0.05, Figure \ref{Fig\_4}, Table S4).

Chart, bar chart

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**Figure 4** Dry aboveground biomass (AGB) of understory plants categorized by life forms in different forest types of the burned plots before fire and at three months after fire. An asterisk indicates significant difference between before and after the fire, and “ns” indicated no significant difference based on the Wilcoxon rank sum test (Significant codes: \*\*\*< 0.001, \*\* < 0.01, \*< 0.05).

**\subsection{Aboveground biomass of key species of deciduous dipterocarp forests}**

DDF are a unique ecosystem in Southeast Asia and currently experiencing a rapid decline due to land conversion and invasive species. To highlight potential changes in DDF forest structures (n = 48), seedlings biomass and density for some key species were calculated. The results showed that the seedlings of key native species (\textit{Dipterocarpus} spp. and \textit{Shorea} spp.) were low in AGB and density especially after forest fire, compared to the competing species, \textit{Croton hutchinsonianus} (Table \ref{Table\_5}).

**Table 5** Average AGB and density of tree seedlings of some key species in deciduous dipterocarp forest (n=48).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Species** | **AGB (kg ha-1 ± 1SE)** | | **Density (stem/ha ± 1SE)** | |
| **Before fire**  **(Nov-Dec 2018)** | **After fire**  **(May-Jun 2019)** | **Before fire**  **(Nov-Dec 2018)** | **After fire**  **(May-Jun 2019)** |
| *Croton hutchinsonianus* | 45.72 ± 18.84 | 105.00 ± 34.79 | 6,736.11 ± 1,912.92 | 15,138.89 ± 4,138.75 |
| *Dipterocarpus obtusifolius* | 0.00 ± 0.00 | 16.06 ± 10.95 | 0.00 ± 0.00 | 1,041.67 ± 666.93 |
| *Dipterocarpus tuberculatus* | 0.65 ± 0.65 | 1.94 ± 1.94 | 69.44 ± 69.44 | 277.78 ± 277.78 |
| *Shorea obtusa* | 41.51 ± 20.55 | 16.06 ± 10.95 | 7,430.55 ± 3,271.05 | 4,722.22 ± 1,788.77 |
| *Shorea siamensis* | 16.31 ± 7.66 | 14.97 ± 6.71 | 14,097.22 ± 3,395.17 | 7,083.33 ± 1,608.39 |

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**\section{Discussion}**

**\subsection{Effects of fire on understory biomasses}**

The fire in the study area in 2019 resulted in significant changes in species richness and composition of understory plants across different forest types (Table \ref{Table\_2}, Table \ref{Table\_3}). The changes in the understory biomass, relatively similar levels canopy cover pre- and post-fire suggested the fire must be of low intensity, which is typical to this study area. The biomass of tree seedlings increased in the burned plots for all forest types (Figure \ref{Fig\_3}, Figure \ref{Fig\_4}), suggesting that a low-intensity fire may help promoting regeneration of tree seedlings (Figure \ref{Fig\_5}, Figure S1, S2 and S3). The low-intensity fire also significantly suppressed the biomasses of forbs, grasses, and shrubs (Figure \ref{Fig\_3}, Figure \ref{Fig\_4}, Figure S1, S2 and S3).

The increase in tree seedling density is particularly concerning for DDF plots, as the regenerating seedlings came from competing species instead of the typical characteristic species of \textit{Dipterocarpus} and \textit{Shorea} (Bunyavejchewin, 1983). One of the competing species, \textit{Croton hutchinsonianus}, is typically a pioneer species that can thrive under a thick canopy cover \cite{RN11}. The biomass and density of \textit{C. hutchisonianus} seedlings were high before the fire, and they became significantly more prominent after the fire, while the typical DDF species, such as \textit{Shorea siamensis}, experience a significant decrease in density after the fire (Table \ref{Table\_5}). These results suggested that the regenerating populations of Dipterocarpaceae were in decline in the DDF plots, and the current stand may be replaced by other species. The lack of typical DDF species may lead to the change in successional trajectories \cite{RN28} and eventually result in a loss of deciduous dipterocarp forest from the study area. This situation is similar to the Oak-hickory bottleneck in Southern Indiana, USA. The lack of seedlings and saplings of oak and hickory potentially changed structure and species composition of the forest stands. The typical oak-hickory stands have been replaced by shade-tolerant species in upper canopy layers \cite{RN54}.

**\subsection{The 30-year succession after logging}**

The current understory community structure in the study area is likely to the result of a secondary succession after the end of logging thirty years ago \cite{RN15}. The logging activity had extracted a large number of mature trees from the forests, as the area now contains only 3.7 ± 0.9 tree ha$^{-1}$ for the dipterocarp trees with DBH of 50 cm and greater (Kulpattanapreecha, \textit{personal comm}). The initial succession was probably led by the establishment of light demanding species, such as grasses, forbs, some shrubs, and pioneer trees species \cite{RN9}. In DDFs, fire is necessary for clearing the understory vegetation and maintaining the forest structure \cite{RN22}. However, the fire suppression between 1988-2001 \cite{RN22} facilitated the establishment of shrubs and tree seedlings and consequently prevented the growth and regeneration of light demanding species and grasses \cite{RN12}. Moreover, the increased canopy cover can reduce the available light on the forest floor, allowing shade tolerant shrubs and tree seedlings to flourish \cite{RN13, RN16, RN41, RN14}. Even though the prescribed burns were performed after 2001 \cite{RN22}, the understory community is still dominated by tall shrubs and tree seedlings (Figure \ref{Fig\_3}). These lifeforms are more tolerant to low-intensity ground fires and likely to stay on after the prescribed burns. The observed community differs from the typical understory community in DDFs where grasses (Poaceae) are supposed to be the dominant life form \cite{RN4, RN46, RN23, RN1, RN37, RN24}. In the current study, only ten percent of all understory plants were grasses, while DDFs in the vicinity had a higher percentage of grasses, between 39-52\textbf{$\%$} \cite{RN52, RN23}. The proportion and biomass of grass in this study is similar to another study in the unburned plots of a DDF \cite{RN50} (Table \ref{Table\_6}). The comparison with the previous studies demonstrates that the understory community of our study area is likely to be the result of natural generation of shade tolerant species and continuous fire suppression.

A forest of trees

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**Figure 5** Understory communities in Deciduous Dipterocarp Forest (DDF). a) a DDF burned plot before prescribed burning (November-December 2018), b) a DDF burned plot at three months after prescribed burning (May-June 2019), c) a DDF unburned plot before prescribed burning (November-December 2018), and d) a DDF unburned plot at three months after prescribed burning (May-June 2019).

**Table 6** Aboveground biomass of grass and all of understory plants in this study and the previous studies.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Grass biomass (kg ha-1)** | **Overall understory biomass (kg ha-1)** | **Forest types\*** | **Location** | **Source** |
| 72.79 ± 22.41 | 779.65 ± 79.60 | DDF | Thailand | This study (before fire) |
| 519.50 | 1,338.60 | DDF | Thailand | Wanussakul (1989) in *Shorea siamensis* Stand (November) |
| 680.00 | 1,295.00 | DDF | Thailand | Kanjanavanit (1992) in November |
| 85.90 ± 11.50 | 3,803.40 | DDF | Thailand | Wanthongchai *et al.* (2008) in unburned site |
| 236.00 ± 61.30 | 3,328.00 | DDF | Thailand | Wanthongchai *et al.* (2008) in rarely burned site |
| 947.20 ± 135.20 | 1,448.80 | DDF | Thailand | Wanthongchai *et al.* (2008) in frequency burned site |
| 1,930 | 2,620.00 | DDF | Thailand | Himmapan & Kaitpraneet (2008) |
| 588.00 | - | SDTF | India | Mondal & Sukumar (2016) |
| 106.64 ± 14.41 | - | DDF | Vietnam | Nguyen (2017) |

**\subsection{Management implication}**

The results of our 128 systematic plots across the study area showed an unusually high level of canopy cover (about 70\textbf{$\%$}) and the dense understory community of shrubs and tree seedings. The observed forest structure is likely to be the results of the low-intensity fires that were not sufficient to remove the woody understory and allow regeneration of forbs and grasses (Table \ref{Table\_2}). Without a proper management of fire regime, the study area is less likely to return to the open DDFs where abundance of forbs and grasses provide forage for local mammal species \cite{RN36, RN43, RN3, RN12, RN28, RN8}.

Frequent prescribed burns are shown to be effective in regenerating grasses in the understory layer \cite{RN36, RN50, RN49}. However, the current study showed that the ongoing annual prescribed burns in the HKK wildlife sanctuary was not sufficient for grass regeneration. \citet{RN1} reported that the intensity of fire in the DDF in Uthai Thani Province, where the study site is located, was at 111 kWm$^{-1}$, which was lower than the proposed intensity for grass regeneration at 361 kWm$^{-1}$ \cite{RN51}. The observed low-intensity fire is probably the results of the low fuel load, especially that from grasses, during the burning season \cite{RN23, RN49}. Therefore, a higher intensity fire should be occasionally administered during the prescribed burns (such as late burning) to ensure the regeneration of grasses and forbs in the future.

Apart from regenerating grass biomass in the area, increasing the sapling density of dipterocarp species should also be a priority. Several silvicultural techniques, such as planting of target species and canopy thinning, can help maintain the composition and structure of DDF \cite{RN26, RN38}. Managing this piece of forest in HKK and HTS will help slowing down the disappearance of DDFs, as well as maintain a bountiful habitat for local wildlife species.

For the study limitation, the current study is based on a set of temporary plots which could generate data for only one season. It is sufficient for estimating the biomass over a large area. However, to fully address ecological questions and temporal dynamics of the plants, the establishment of permanent plots in this area will be required.

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**\section{Conclusions}**

Unregulated timber logging and forest fire suppression in the past resulted in the observed diversity of understory plant communities of seasonally dry forests in the study area at present. Annual low-intensity ground fire from prescribed and crop burns directly affected species composition and biomass of understory across various forest types. Rather than seedlings of dominant dipterocarp species, pioneer species of shrub and tree seedlings benefited more from ground fires, as their biomass and abundance increased after the fire. In the burned areas, even though the ground fire significantly impacted the understory biomass in general, the plots in DDF and MDF did not show significant differences in aboveground biomass comparing prior and after fire. Our results showed that low-intensity fire from annual prescribed burns could not promote regeneration and establishment of grasses, forbs, and tree seedlings of dipterocarp species, especially \textit{Shorea siamensis} and \textit{S. obtusa} in DDF plots. The low abundances of these life forms in DDF highlights the need to enhance forage plants for large herbivores and restore dipterocarp trees in this forest. The information from the study can help decision makers manage the secondary DDFs in HKK and HTS.

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\authorcontributions{S.P. and N.P. originated the idea. N.P., S.P. and K.D. participated in the design of the study. K.D., N.P. and S.P. performed the field work and data collection. S.S., A.T., K.D., E.K. and N.P. identified understory species to taxonomic levels. S.P., K.D. and N.P. analyzed the data, S.P., K.D., N.P. and E.K. wrote the article. N.P. and S.P. edited the manuscript. S.P., E.K. and N.P. rechecked and revised the English version of the manuscript. All authors read and approved the final manuscript and agree to authorship and submission of the manuscript for peer review.}

\funding{This research grant was funded by National Science and Technology Development Agency (NSTDA), Thailand (contract number FDA-CO-2563-12498-TH) and the United Nations Development Programme (UNDP) in Thailand (contract reference: RPA/UNDP/CO/66/2018).}

\acknowledgments{We acknowledge the support received from Department of National Parks, Wildlife and Plant Conservation, and the Royal Forest Department gave the permission to work in the site and facilitated the research data collection. We would like to thank Uthai Thani Province for various supports. Additionally, we wish to thank various people who have contributed to data collection and valuable, constructive recommendations on this project.}

\institutionalreview{Not applicable}

\informedconsent{Not applicable}

\dataavailability{The data that support the findings of this study are available from the corresponding author upon request.}

\conflictsofinterest{The authors declare no conflict of interest.}

Table S33 The list of significant species contributing to the change in species composition before forest fire and at three months after forest fire.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | Species | Contribution | Abundance before fire | Abundance after fire | P |
| Overall forest types (n = 97) |  |  |  |  |  |
| CROTHU | CROTHU | 0.029 | 0.016 | 0.049 | 0.01 |
| CYRTAC | CYRTAC | 0.028 | 0.055 | 0.002 | 0.01 |
| CURCSP1 | CURCSP1 | 0.023 | 0.041 | 0.009 | 0.01 |
| GLOBSP1 | GLOBSP1 | 0.02 | 0.035 | 0.009 | 0.01 |
| ALBIOD | ALBIOD | 0.018 | 0.006 | 0.032 | 0.03 |
| CAYRTR | CAYRTR | 0.017 | 0.012 | 0.026 | 0.02 |
| OPLICO | OPLICO | 0.016 | 0.028 | 0.006 | 0.01 |
| ACRARA | ACRARA | 0.015 | 0 | 0.029 | 0.01 |
| CHROOD | CHROOD | 0.014 | 0.02 | 0.01 | 0.05 |
| AMPHMA | AMPHMA | 0.012 | 0.015 | 0.009 | 0.04 |
| HELIAN | HELIAN | 0.011 | 0.019 | 0.003 | 0.01 |
| CYANCR | CYANCR | 0.008 | 0 | 0.016 | 0.01 |
| Deciduous Dipterocarp Forest (DDF) |  |  |  |  |  |
| CROTHU | CROTHU | 0.04 | 0.017 | 0.072 | 0.04 |
| GLOBSP1 | GLOBSP1 | 0.028 | 0.052 | 0.008 | 0.03 |
| ACRARA | ACRARA | 0.027 | 0 | 0.054 | 0.01 |
| CURCSP1 | CURCSP1 | 0.021 | 0.038 | 0.008 | 0.01 |
| HEDYOV | HEDYOV | 0.009 | 0.018 | 0.002 | 0.04 |
| CYRTAC | CYRTAC | 0.005 | 0.009 | 0 | 0.02 |
| Mixed Deciduous Forest (MDF) |  |  |  |  |  |
| AMPHMA | AMPHMA | 0.004 | 0.009 | 0 | 0.03 |
| CROTHU | CROTHU | 0.037 | 0.02 | 0.071 | 0.04 |
| CAYRTR | CAYRTR | 0.025 | 0.005 | 0.047 | 0.02 |
| ACRARA | ACRARA | 0.004 | 0 | 0.008 | 0.05 |
| CYANCR | CYANCR | 0.005 | 0 | 0.011 | 0.01 |
| CYRTAC | CYRTAC | 0.068 | 0.136 | 0 | 0.01 |
| Mixed Deciduous Forest with Bamboo (MDFB) |  |  |  |  |  |
| AMPHMA | AMPHMA | 0.014 | 0.028 | 0.002 | 0.02 |
| CURCSP1 | CURCSP1 | 0.03 | 0.055 | 0.01 | 0.04 |
| STERGU | STERGU | 0.018 | 0.002 | 0.035 | 0.04 |
| OPLICO | OPLICO | 0.025 | 0.045 | 0.009 | 0.04 |
| SETAPA | SETAPA | 0.003 | 0 | 0.006 | 0.01 |
| CHROOD | CHROOD | 0.009 | 0.017 | 0.001 | 0.01 |
| ACRARA | ACRARA | 0.006 | 0 | 0.013 | 0.03 |
| ALBIOD | ALBIOD | 0.032 | 0.004 | 0.063 | 0.02 |
| CYANCR | CYANCR | 0.016 | 0 | 0.031 | 0.01 |
| DIOSSP1 | DIOSSP1 | 0.038 | 0.008 | 0.07 | 0.05 |
| CYRTAC | CYRTAC | 0.029 | 0.056 | 0.004 | 0.02 |