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Determinants of Composition, Diversity and Structure in a Seasonally Dry Forest in Myanmar

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ရာသီအလိုက်ခြောက်သွေ့တော့များ၏ composition, diversity နှင့် structure များရှင်သန်ပေါက်ရောက်မှုအတွက် ဆုံးဖြတ်ပေးသည့်အရာများ

သီရိတိုးခိုင်၊ ဦးစီးအရာရှိ

စာတမ်းအကျဉ်း

ရာသီအလိုက် ရွက်ပြတ်တောခြောက်ဂေဟစနစ်ကို အရှေ့တောင်အာရှနိုင်ငံများတွင် အများ အပြားတွေ့ရလေ့ရှိပါသည်။ ၎င်းတောအမျိုးအစားများကို သစ်တောဂေဟဗေဒစနစ် (သို့မဟုတ်) ဆာဗားနားဂေဟဗေဒစနစ်တွင် ပါဝင်နေသလားဆိုသည့်မှာ အငြင်းပွားစရာအဖြစ် ယနေ့အထိ ဖြစ်ပွားဆဲဖြစ်ပါသည်။ ရွက်အုပ် (၆၀)ရာခိုင်နှုန်းနှင့်အထက် အောက် ပေါင်းမြက် တွင် C_4 မြက်များ ပါဝင်မှုအများဆုံးဖြစ်ပြီး မီးမကြာခဏ လောင်ကျွမ်းနေသည့် ဂေဟဗေဒစနစ်ကို ဆာဗားနား ဂေဟစနစ်ဟုသတ်မှတ်ပြီး ရွက်အုပ်(၇၀)ရာခိုင်နှုန်းနှင့် အထက် အောက်ပေါင်း မြက်တွင် C_3 မြက်များ ပါဝင်မှုအများဆုံးဖြစ်ပြီး မီးလောင်ကျွမ်းမှု နည်းပါးသော ဂေဟဗေစနစ် ကို သစ်တောဂေဟ ဗေဒစနစ်ဟု အပင်ဂေဟဗေဒကျွမ်းကျင် ပညာရှင်များက သတ်မှတ်ကြပါသည်။ ဤသုတေသသနသည် မဟာသိပ္ပံကျမ်းမှ ကောက်နုတ်ထားသော သုတေသနစာတမ်း ဖြစ်ပြီး သုတေသနလုပ်ငန်းကို အင်တိုင်းမြင့် (Community) ၊ အင်တိုင်းနိမ့် (Community) နှင့် ရွက်ပြတ် ရောနှော (Community) များ ပါဝင်ပေါက်ရောက်သော အပူပိုင်းဒေသ၊ မကွေးတိုင်းဒေသကြီး၊ ရွှေဘိုခရိုင်၊ ချပ်သင်းတောရိုင်းတိရစ္ဆာန်ဘေးမဲ့တောတွင် ဆောင်ရွက်ခဲ့ပါသည်။ နမူနာကောက် အကွက် အရွယ်အစားမှာ (၅၀မီတာx၅၀မီတာ) ဖြစ်ပြီး ထိုအကွက်တွင် ရင်စို့လုံးပတ် ၅ စင်တီ မီတာနှင့်အထက်အပင်ကြီးများအားလုံး၏ basal area, abundance, richness များ၊ အောက်ပေါင်း အပင်ပျော့ အပင်ငယ်များ၏ percentage cover, abundance ,richness များ ကောက်ယူပြီး အပင်ပျော့ အပင်ငယ်များတွင် C_3/C_4 မျိုးစိတ် အမျိုးအစားအား ထပ်မံ ခွဲခြားထားပါသည်။ အပင်များသည် မိမိပတ်ဝန်းကျင်ရှိ ပတ်ဝန်းကျင်အခြေအနေများကို မှီခိုပြီး ရှင်သန်ပေါက်ဖွားကြီးထွားမှု ဖြစ်သည့် အတွက် ရွက်အုပ်အနေအထား၊ မြေဆီလွှာနှင့် မီးလောင်မ အခြေအနေများကို environmental data အနေဖြင့် ကောက်ယူစုဆောင်းခဲ့ပါသည်။ (၂၀၀၁–၂၀၁၇)ခုနှစ်အထိ Study Area၏ မီးလောင်မှုအခြေ အနေပြမြေပုံအား ဂြိုလ်ထုဓါတ်ပုံ (MODIS)မှ ဖမ်းယူထားသော (၁၇)နှစ်အတွင်း မီးလောင်မှု အချက်အလက်များကို အခြေခံ၍ ထုတ်လုပ်ထားပြီး study plot ရွေးရာတွင် ၎င်းမြေပုံကို အခြေခံ၍ရွေးချယ်ထားသည့်အတွက် မီးလောင်မှုအခြေအနေ သတင်း အချက်အလက်အား စုဆောင်း ပြီးဖြစ်ပါသည်။ သုတေသန လုပ်ကွက်များကို Community တစ်ခုလျှင် (၅) ကွက်နှုန်းဖြင့် စုစုပေါင်း Community (၃) ခုတွင် (၁၅) ကွက် (5 replications) ဖြင့် ဆောင်ရွက်ခဲ့ပါသည်။ မီးလောင်ကျွမ်းမှုကို Community (၃)ခုလုံးတွင်တွေ့ရပြီး မြေဆီလွှာ အခြေ

အနေသည် ရွက်ပြတ်ရောနှောတောတွင် ကျန်တော အမျိုးအစား(၂)မျိုးထက် ပိုမိုကောင်းမွန်နေကြောင်း တွေ့ရပါသည်။ အင်တိုင်းနိမ့် Community ၏ ရွက်အုပ်အနေအထားသည် အပွင့်လင်းဆုံးဖြစ်ပြီး အလင်းရောင်ကြိုက်သော မြက်အမျိုး အစားများ C_4 များ အများဆုံးပါဝင်နေသည့် အတွက် ဆာဗာနားဂေဟဗေဒစနစ်ဖြစ်ပြီး ရွက်ပြတ်ရောနှော Community သည် ရွက်အုပ် အနေအထား အနည်းငယ်ပိတ်၍ အရိပ်ကြိုက်သော C_3 များ အများဆုံး ပါဝင်နေသည့်အတွက် သစ်တောအမျိုးအစား တစ်ခု၏ ဂေဟဗေဒစနစ် ဖြစ်ကြောင်း ဤသုတေသနပြုလုပ်ချက်မှ သိရှိရပါသည်။ အင်တိုင်းမြင့် Communityသည် ဆာဗားနား ဂေဟဗေဒစနစ်နှင့် သစ်တော အမျိုးအစားဂေဟဗေဒ စနစ်(၂)မျိုးစလုံး၏ ဝိသေသလက္ခဏာများဖြစ်သော ရွက်အုပ် အနေအထား အနည်းငယ်ပိတ်ခြင်းနှင့် C_4 များပါဝင်မှုမှာ များပြားနေသည့် အစရှိသော ဝိသေသလက္ခဏာများကို ယှဉ်တွဲ၍တွေ့ရပါသည်။ အာရှဒေသတွင် မြေဆီလွှာ အခြေအနေသည် community အမျိုးအစားပြောင်းလဲခြင်း (transition) ကို ထိန်းချုပ်သည် ဆိုသော်လည်း အာဖရိကနှင့် အမေရိကန်တောင်ပိုင်းတို့တွင် တွေ့ရမြဲတွေ့ရလေ့ရှိသော ထင်ရှား ပြတ်သားသော ဆာဗားနား–သစ်တော ပြောင်းလဲခြင်း (transition) တွေ့ရခြင်း မရှိကြောင်းကို ဤသုတေသန စာတမ်းမှသိရှိရပါသည်။

Determinants of Composition, Diversity and Structure in a Seasonally Dry Forest in Myanmar

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Abstract

Seasonally dry forest with a deciduous tree canopy is the widespread ecosystem in Southeast Asia. Debate continues about whether this vegetation is forest or savanna. Savannas have tree cover < 60%, C_4-dominated ground vegetation, and frequent fires. Forests have tree cover > 70%, C_3-dominated ground vegetation, and infrequent fires. Co-occurrence of these biomes has been explained as follows: 1. Fire-grass and shade-tree positive feedbacks promote alternate stable states of savannas or forests under the same climate and soil conditions. 2. Fine-scale soil characteristics differentiate plant growth rates and determine whether trees can overcome fires.

We studied three community types previously identified in seasonally dry forests in Myanmar, High Indaing, Low Indaing (both types of deciduous Dipterocarp-dominated forest) and Mixed Deciduous Forest (a community usually dominated by non-Dipterocarp species). We wanted to know whether their herbaceous layer communities were also compositionally distinctive, whether their structure (tree cover %, abundance of C_4 plants) identified them as savannas or forests, whether they differed with respect to soil nutrients, and fire frequency. We sampled fifteen 50 m x 50 m plots thought to represent the 3 community types (5 plots of each community type). In each plot we measured basal area, abundance and richness of trees with DBH $\geq$ 5 cm, and percentage cover, abundance and richness of herbaceous layer species, and classified each species as C_3/C_4. We estimated tree cover along four 50 m line transects recording canopy openness/closure every 1 m. We pooled six 0 - 15 cm soil cores to estimate soil parameters (N, P, K, pH). We recorded fire frequency in each plot using MODIS fire products for 2001-2017.

We found that tree, herbaceous-layer and combined compositional data generated similar community clusters. Low Indaing had open tree canopies and high abundance of C_4 plants relative to Mixed Deciduous Forest. HI had a wider range of tree covers but also high C_4 abundance. Fire was common in all three communities. Low Indaing could be differentiated from Mixed Deciduous forest by soil K and P (lower for Low Indaing), with High Indaing having intermediate values.

Low Indaing appears to be a type of savanna whereas Mixed Deciduous Forest is a type of forest, but with the propensity to burn based on leaf litter rather than on grass. In our data, HI showed characteristics of both savanna and forest. Although soils underlie the transitions between these Asian communities, they do not show the clear physiognomic boundaries observed in African and South American savanna-forest transitions.

Keywords: Deciduous Dipterocarp Forest, fire, Forest, Chatthin Wildlife Sanctuary, C_4 plants, Savanna, Mixed Deciduous Forest, Soil fertility, Understory plant diversity

Determinants of Composition, Diversity and Structure in a Seasonally Dry Forest in Myanmar

1. Introduction

Seasonally Dry Forests (SDFs) occur on all continents in tropical and sub-tropical zones under monsoonal climates where dry seasons last for at least five months (Miles et al., 2006; Allen et al., 2017; Singh and Chaturvedi, 2018). Monsoonal forests dominated by deciduous canopy trees that are widespread in South and Southeast Asia have been identified as SDFs (Pennington et al., 2009; Bunyavejchewin et al., 2011; Dexter et al., 2015; Slik et al., 2018). There is substantial debate about the biome characterization of the deciduous-dominated forests in South and Southeast Asia (Ratnam et al., 2011; Ashton, 2014): while they have traditionally been classified as 'forest', recent findings argue they possess several characteristics of savannas (Dexter et al., 2015; Ratnam et al., 2011, 2019). This characterization matters because the worldwide SDF biome and other forest biomes are fire-sensitive and are thought to lack functional adaptations for fire (Pennington et al., 2009) and may convert to a savanna-like physiognomy under frequent fire, whereas the savanna biome is adapted to frequent fires and may convert to a forest state under fire suppression (Ratnam et al, 2011). Savannas are characterized by open forest canopies (less than 55-60% tree cover – Hirota et al., 2011; Staver et al., 2011), ground vegetation dominated by C_4 grasses and sedges that require high light conditions for competitive growth (Charles-Dominique et al., 2018), and frequent fires that kill juvenile trees promoting canopy openness and C_4 grasses (Higgins et al., 2000; Nguyen et al., 2019). Forests have closed canopies (above 70% tree cover), infrequent fires, and herbaceous layers dominated by C_3 species, including some C_3 grasses (Charles-Dominique et al. 2018). In humid environments, transitions between forests and savannas can be very abrupt (Hoffmann et al., 2012; Oliveras and Malhi, 2016). Two major explanations for this have been proposed: First, fire-grass and shade-tree positive feedbacks promote alternate stable states of savannas or forests under the same climate and soil conditions (Van Langevelde et al., 2003; Charles-Dominique et al., 2018; Nguyen et al., 2019). This hypothesis assumes that grass is the main fuel for fire. Fire kills or severely reduces biomass of trees creating more space for grasses and maintaining open savannas. Contrastingly, tree canopies reduce light reaching the grasses, thereby suppressing grass growth rates and hence reducing fuel production to support fires, leading to fewer fires and longer intervals for trees to grow that move the system towards forest. Second, fine-scale soil characteristics (soil depth or fertility) differentiate seasonal plant growth potential, that either constrain total standing biomass leading to open savanna communities, or slow annual growth sufficiently that trees cannot overcome endemic fire frequencies (Lloyd et al., 2008; Bond, 2010; Rodriguez-Iturbe et al., 2019). Where soils are deeper or more fertile, trees will grow sufficiently fast to overcome fires and move the system towards forest.

Tree species in Asian SDFs show functional modification for coping with fire, including belowground resource storage, thick bark, and epicormic and subcutaneous meristems

(Ratnam et al. 2011, 2016). Presently fire management in Asian SDFs differs substantially across countries with several countries applying strict fire suppression policies whereas others do not suppress fires at all (Ratnam et al., 2016). Where fire frequencies are high in Southeast Asia most fires are low-intensity ground fires with low flame heights that are set by local people during the middle of the dry season. These fires do not damage adult trees (Stott 1988) but they limit recruitment of tree juveniles into larger stem diameter size-classes (Nguyen et al. 2019). Given the high rainfall usually associated with humid savannas (~ > 900 mm per year), and knowing fire frequencies in other parts of the world for humid savannas are about 1 fire in 3 years (see Hoffmann et al. 2012), we assume that natural fire frequencies in these environments would be high. However, where fires are deliberately suppressed, dead leaf, wood and herbaceous biomass accumulate in the understory over time; these conditions promote crown fires that cause substantial mortality of adult trees (Stott 1988). Fire regimes in Southeast Asian SDF is complex because the landscape is often a mosaic of different forest types. So some areas may burn more frequently than others and the less flammable areas in the landscape may require more extreme drought conditions to burn (Baker and Bunyavejchewin, 2017). Within Southeast Asian deciduous forests, two major plant communities are recognized that are dominated by different deciduous canopy tree species, namely: Deciduous Dipterocarp Forest (dominated by Dipterocarpaceae) and Mixed Deciduous Forest (dominated by a range of families including Anacardiaceae, Combretaceae, Rubiaceae), which both occur at elevations up to 900 m above sea level and with mean annual rainfall of about 890 – 2100 mm (Bunyavejchewin et al. 2011; Khaing, 2013; Ratnam et al., 2016). The communities are interspersed and it is thought that soil types may distinguish their distribution, with mixed deciduous forest occurring on less acidic and more fertile soils, whereas Deciduous Dipterocarp Forest occurs on more acidic, sandy and often shallow soils underlain by laterite (Bunyavejchewin et al., 2011). Whether there are differences in fire frequency between these communities is not well understood.

Little is known about the herbaceous layer communities underlying Southeast Asian SDFs and whether these are associated in a complementary manner to the tree communities. Herb-layer components of Asian deciduous forests are intensively utilized by domestic and wild grazing animals, and also by humans for medicinal plants, food and building materials (Songer et al., 2011). Therefore a better understanding of the diversity and what drives patterns of diversity of herb layers in deciduous forests is warranted. The herb layer of Southeast Asian deciduous forests is often dominated by fire-tolerant and shade-intolerant grass species; many of these are C_4 grasses, but it is visually apparent that the relative proportion of grass biomass versus forb biomass in the understory changes substantially across the deciduous forests (Ashton 2014). From research in other systems it is clear that the relative abundance of grasses versus forbs may reflect fire frequency (more fire = more grass) (Nepolo and Mapaure, 2012), light availability in the understory (more open canopy = more grass) (Charles-Dominique et al., 2018), but we could find scant literature indicating that soil fertility changed the relative abundance of grasses versus forbs (e.g. Craine et al., 2001), though it does affect relative abundance of different C_4 grasses (Fynn et al., 2005).

The actual variation in abundance of C_4 versus C_3 herbs have not been well quantified for Asian SDFs, and the drivers of this variation have not been established. To our knowledge, links between fire, canopy cover, soil properties, and herbaceous diversity, have not been simultaneously investigated, especially in Southeast Asian SDFs.

2. Objectives

We studied composition, richness and structure of tree and herb-layer communities in a seasonally dry forest in central Myanmar.

We wished to explore the following questions:

(1) Do herbaceous communities cluster into different groups in a similar manner to tree species? (2) Are tree and herbaceous clusters differentiated by tree canopy cover, fire frequency, or soil characteristics?

(3) How do tree canopy cover, fire frequency, and soils affect richness and abundance of C_4 grasses?

(4) Using this combined information, is there evidence that some or all communities could be described as savannas or forests?

Since we were trying to establish whether the communities were forests or savannas, we refer to them only as 'communities' for the Methods, Results, and most of the Discussion until we address question (4).

3. Methodology

3.1 Study location

This research was carried out at the Chatthin Wildlife Sanctuary, which is located at the northern edge of central Myanmar's Dry Zone (95°24′ - 95°40′ East, 23°30′ - 23°42′ North). Chatthin Wildlife Sanctuary was established in 1941 and covers an area of 268.2 km². The climate is monsoonal with three seasons: a cool dry season (October - January), a hot dry season (February - May) and a wet season (June - September) (Songer et al., 2011). The annual precipitation ranges from 1270 to 1760 mm and the mean annual temperature is 31°C. During the rainy season, about 60% of the Sanctuary is flooded due to its flat to gently undulating topography with an average elevation of about 200 m. The area burns annually from January to March, due to both human and natural causes (Aung et al., 2004). The soils are mostly alluvial sands and gravels mixed with sandstones (Aung et al., 2004).

Three tree community types are recognized in Chatthin Wildlife Sanctuary: High Indaing, characterized by tall trees, and Low Indaing, characterized by short trees, both dominated by deciduous Dipterocarp species (e.g. *Dipterocarpus tuberculatus*, *Shorea obtusa*, *Shorea siamensis*), and Mixed Deciduous Forest, dominated by non-Dipterocarp deciduous species (Khant, 2017). These are thought to be the three major community types present in Chatthin Wildlife Sanctuary.

3.2 Vegetation Sampling

We established 15 plots that local field staff of Chatthin Wildlife Sanctuary considered to represent the three community subtypes (5 for each type), namely Mixed Deciduous forest (hereafter MD), Low Indaing (LI) and High Indaing (HI) (Figure 1). The field inventory was conducted from July to August 2017 during the rainy season when all deciduous trees were fully leafed.

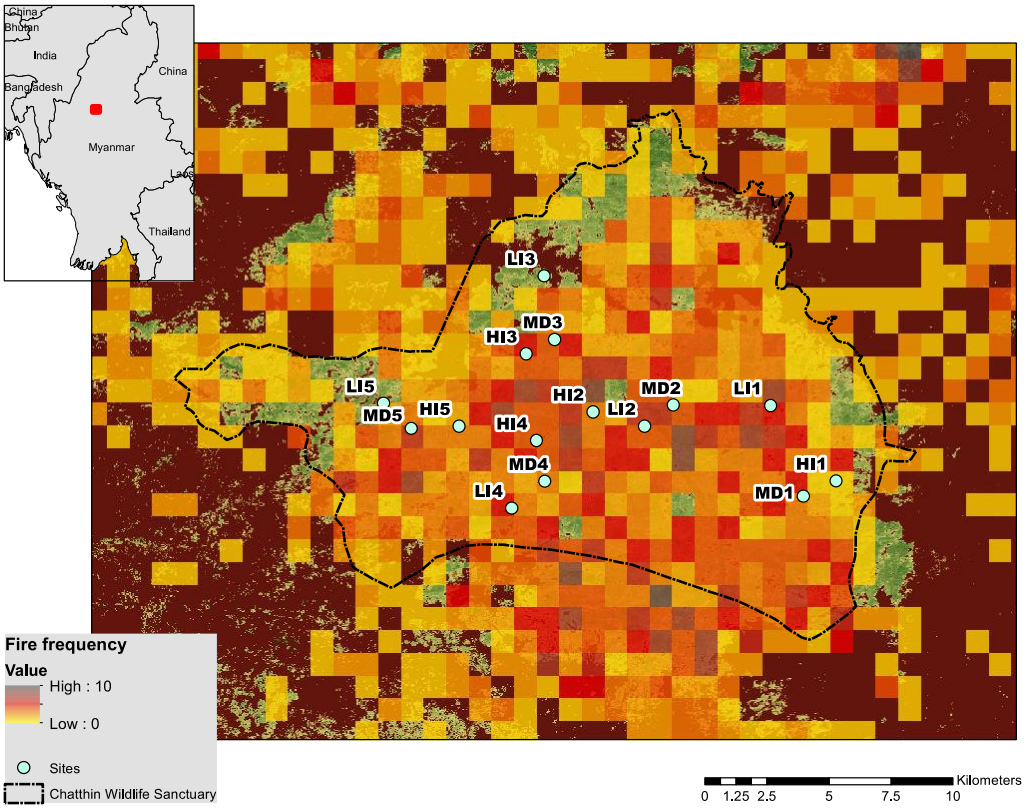

Figure 1. A map of the study area in Chatthin Wildlife Sanctuary, central Myanmar. The map includes fire frequency data based from the MODIS Collection 6's Archive of Active Fires (https://modis.gsfc.nasa.gov/data) and the location of the plots in the study area (HI = High Indaing, LI = Low Indaing, MD = Mixed Deciduous).

At each site a standardized 50 m x 50 m plot design was used to measure plant data (Figure 2). Within the 50 m x 50 m plot, we sampled all trees with a diameter at breast height (DBH) ≥ 5 cm, and measured their DBH (cm), heights (m), basal diameter (below 30 cm above the ground, but above the zone where root widening was apparent), coordinate position, and identified each tree to species. We then established twelve 2 m x 2 m subplots distributed systematically across the 50 m x 50 m square plot. Each subplot was divided in four - 1 m x 1 m quadrats; hence, a total of 48 quadrats per plot. In the top right 1 m x 1 m quadrat, all plant species were recorded, and their individual percentage cover estimated. Then any additional species were identified in the remaining three quadrats, to give the number (for abundance) and identity (for richness) of all species in each sub-plot. The first individual of each new species encountered was dug up, labeled and pressed to aid species identification.

All collected species samples were taken to the Forest Research Institute at Yezin, Myanmar for identification and storage. Juveniles of trees and woody lianas encountered in the herb-layer data collection were recorded but removed from the herb-layer data described here. Woody shrubs not present in the tree data and therefore consigned to the understory, were retained in the herb-layer data. Each identified species of grass (Poaceae) or sedge (Cyperaceae) was classified as C_3 or C_4, following the lists provided in the global database of grass C_3/C_4 photosynthesis compiled by Osborne et al. (2014), and the sedge database complied by Bruhl and Wilson (2007).

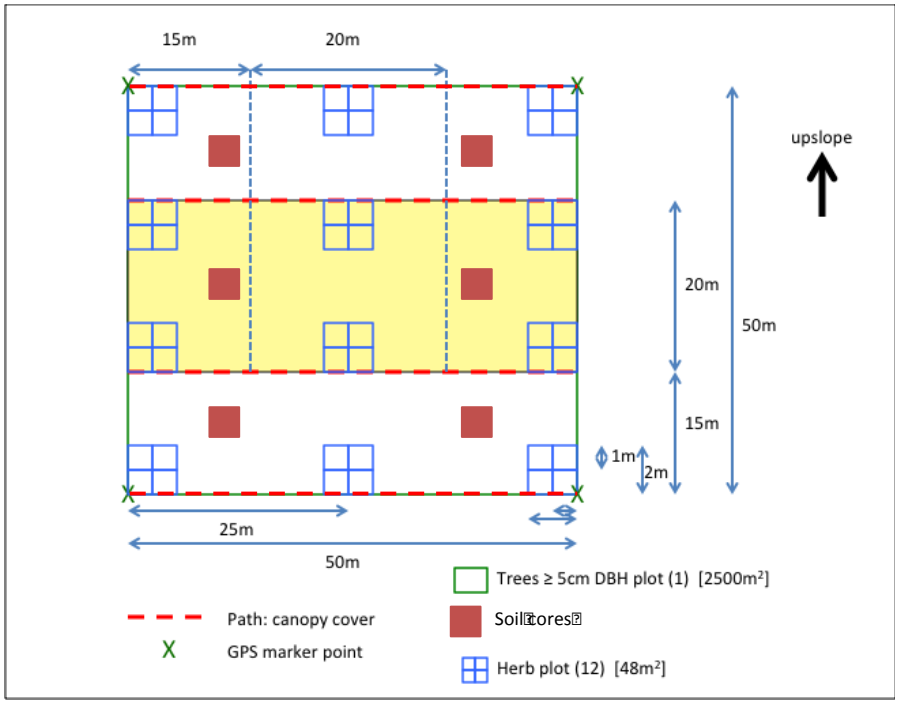

Figure 2. The outer 50 m x 50 m square plot sampling design, where all trees with DBH ≥ 5 cm were measured (Basal circumference, DBH, height). Tree cover was estimated by checking at the interval of 1m, on the four 50 m horizontal transects at 0, 15, 35 and 50 m tape reading along upside in each plot. Within the twelve 2 m x 2 m squares, all herbs were measured by dividing the surface into four 1 m x 1 m squares and counted herb cover on the top-left 1 m x 1 m square of each 2 m x 2 m squares. The orange square represents the soil sampling.

3.3 Environmental data

We measured six environmental variables within each 50 m x 50 m plot, which included four soil chemical properties (N, P, K, and pH), canopy cover and fire frequency. Note that these environmental variables are just a subset of several possible driving factors of plant diversity and structure in Chatthin Wildlife Sanctuary.

Soil chemical properties were derived from six soil samples taken at 0 - 15 cm depth in each plot. Soil samples are mixed for each plot, air-dried then sent to soil laboratory at the Forest Research Institute in Yezin, Myanmar for analysis. Nitrogen, phosphorus and potassium are key macronutrients for plant growth that have been linked to non-forest vegetation (Bond, 2010). Soil pH can affect the accessibility of certain soil nutrients to plants (Kidd and Proctor, 2001).

We estimated tree canopy cover by walking four parallel 50 m lines and checking whether there was overhead canopy at 1 m intervals (thus 51 x 4 = 204 sampling points). To ensure that we were looking vertically we used the height measurement pole when walking these transects. Tree cover (dimensionless fraction) was estimated as the number of points with overhead canopy divided by 204.

We used satellite data to quantify fire frequency across the sites, as no ground data is available for Chatthin Wildlife Sanctuary. We made a fire frequency map using the MODIS (Moderate Resolution Imaging Spectroradiometer) burned area products (https://modis.gsfc.nasa.gov/data). We downloaded archived active fire data from January 2001 to December 2017 (the maximum available sequence prior to sampling) using MODIS Collection 6, a remote-sensing product produced by USA's NASA, and hosted in https://firms.modaps.eosdis.nasa.gov/download/ (Giglio et al., 2016, 2018). MODIS Collection 6 uses a fire detection algorithm that classifies all pixels (~1km^2) in its swath as "missing data", "cloud", "fire", "non-fire" or "unknown". The location of all the "fire" pixels are then recorded and made available for download at a daily temporal resolution. For this analysis, since MODIS Collection 6 only allows "fire" pixels to be downloaded, each "fire" pixel was then centered and aligned to a 30-arc second (~1km) grid over the study extent. Each grid pixel was then scored '1' if it was a "fire" pixel for at least once for a particular year, or '0' if otherwise, thus each can get a maximum score of 17 used as fire frequency values. The fire frequency score for each sampling site was then extracted using the 'extract' function in the R package *raster* (Hijmans, 2019).

3.4 Statistical analysis

All analyses were processed using R software (v.3.0.2; R Foundation for Statistical Computing, Vienna, Austria). Prior to analyses, we constructed species accumulation curves of the tree and herb data for each of the 15 plots to check whether our sampling was sufficient or not. We concluded that our sampling was sufficient for the herb layer but possibly under-sampled for the trees (Figure S1 and S2, Supporting Information).

To address our first question, whether herb layer composition matched overstory tree composition and was partitioned into the same community groups, we sought to (1) verify that our initial plot classification was supported by the composition data, and (2) test whether the tree data only, herb data only, and combined tree and herb data, clustered similarly. Using this analysis we also sought to determine whether the data clustered into two groups (mixed deciduous and dry Dipterocarp communities) or three clusters (mixed deciduous and two types of dry Dipterocarp communities, High Indaing and Low Indaing). We classified the plots in our study using hierarchical clustering with principal components (HCPC) using the R package *FactoMineR* (Husson et al., 2018) using species presence-absence data (Pasion et al., 2018). The HCPC method first generates the data in a hierarchical tree using Ward's criterion and then the identified clusters are mapped onto the PCA axes generated by the same data and K-means clustering reassigns individual plots to different clusters based on the nearest cluster means to each plot. For our analyses we use

only the clustering based on Ward's criterion, as we have previously demonstrated this to be effective for clustering tropical forest communities in Southeast Asia (Pasion et al., 2018). We removed all species that had fewer than four individuals from each data matrix prior to clustering. For the combined species clusters we also calculated species relative importance value (RIV) using the function "importancevalue" in the R package *BiodiversityR* (Kindt, 2018) to identify the ten most important species of different life forms at each forest type. The RIV is a combination of three parameters: relative frequency, relative abundance and relative dominance (Kent, 2011).

Second, we used the derived clusters based on the combined tree and herb data to compare environmental and structural differences between the communities. Environmental comparisons included fire frequency, tree cover, and soil properties. Structural comparisons included species richness of trees, herbs, and C_4 grasses, abundance of tree stems and abundance and cover of C_4 grasses. Most data was normally distributed, so group comparisons were conducted with ANOVA and posthoc Tukey's HSD tests (Table 2). However, species richness was modelled with poisson errors, so group comparisons were conducted with Chi-square tests.

Third, we tested whether vegetation patterns (richness, abundance, basal area for trees / cover for the herb layer) were associated with the environmental predictors, separately for each predictor. Plot-level tree species richness and abundance were taken as the total number of species and individuals recorded in the plot, and basal area was the summed stem cross-sectional area of all trees measured at DBH across the plot. Plot-level herb-layer richness was taken as the total number of species recorded in all 48 1 m x 1 m squares across the 50 m x 50 m plot. Abundance was recorded as the number of times each species was encountered across the 50 m x 50 m plot. Species cover was the total combined cover across the 12 sampled 1 m x 1 m squares in each 50 m x 50 m plot. We did not attempt multi-predictor analyses due to the low amount of replication (15 plots). Species cover, abundance, and species richness were tested using lm and glm modelling, respectively.

4. Result

4.1 Composition and Community Classification

Across the 15 sampled plots, we identified 159 morphospecies, of which 67 were trees (mean per plot ± standard deviation: 21.8 ± 10.5, ranging from 8 to 47) and the remaining 91 (29.9 ± 6.3, ranging from 17 to 39) were species of the herb layer community (excluding tree seedlings), including 22 C_4 species (6.6 ± 1.9, ranging from 3 to 10, including 1 Cyperaceae and 21 Poaceae species). Two Poaceae and three Cyperaceae species are still unidentified, so potentially there are more C_4 species in the sample. The abundance of trees was 197.5 ± 82.7, the abundance of herb layer plants was 272.5 ± 67.4, of which the abundance of C_4 plants was 71.2 ± 25.9.

Ward's clustering with the tree data identified three clusters, one containing four MD plots, one containing four HI plots, and the remaining cluster containing all LI plots plus MD1

and HI4 (Figure 3). Ward's clustering with the herb-layer data generated three clusters, one with four MD sites, one with all the LI sites, and one with all HI sites and MD1. The combined tree and herb data generated the identical three clusters to those generated by the herb-layer data. The overall pattern suggests that MD2 - MD5, LI1 - LI5, and HI1 - HI3, HI5 were stable across tree, herb-layer and combined tree and herb-layer clustering. For the remaining analyses we used the clusters generated by combined tree and herb layer data (MD1 included with HI sites). The top 10 species of trees and herb-layers with highest importance value in each of three communities are given in Table 1.

Table 1. Ten dominant species of different life-forms at each community type represented with their importance values (IV). The IV of the trees was calculated as the sum of frequency, count and basal area (cm^2) of the trees, while frequency, count and cover were used to calculate the IV of herbaceous layer species. Juvenile trees were excluded from the herbaceous layer data prior to IV calculation.

Trees		**Mixed deciduous**				**Low Indaing**				**High Indaing**			
Species	**Family**	**F**	**C**	**BA**	**IV F**	**C**	**BA**	**IV**	**F**	**C**	**BA**	**IV**
Buchanania cochinchinensis	Anacardiaceae					1	91	8435	13.1	0.6	93	11992	10
Gluta usitata	Anacardiaceae									0.6	153	14317	12.9
Lannea coromandelica	Anacardiaceae	1	36	15100	9.9	1	82	3929	10.5				
Holarrhena antidysenterica	Apocynaceae	0.7	106	10199	12.3								
Celtis timorensis	Cannabaceae	1	60	14297	11.3	1	80	7593	12.1	0.9	176	6441	12.9
Lophopetalum wallichii	Celastraceae	1	39	13905	9.8					0.9	103	21211	14.6
Terminalia tomentosa	Combretaceae	1	32	17172	10.4	1	111	12934	16.3	0.9	62	6292	8.6
Dillenia parviflora	Dilleniaceae					1	131	7643	14.8	0.9	136	11416	12.9
Shorea oblongifolia	Dipterocarpaceae					1	269	59348	46.6				
Shorea siamensis	Dipterocarpaceae	1	40	10958	8.8	1	76	6334	11.3	0.6	368	41701	29
Shorea obtusa	Dipterocarpaceae	0.5	67	27276	14.8								
Dipterocarpus tuberculatus	Dipterocarpaceae	0.5	152	45365	26.4	1	203	54609	40.9	1	597	166625	76.9
Bombax insigne	Malvaceae					1	121	3703	12.4	0.7	74	4004	7.6
Chukrasia tabularis	Meliaceae	1	53	7760	8.7								
Aldina cordifolia	Rubiaceae	1	47	27160	14.7								
Dioecrescis erythroclada	Rubiaceae					1	294	14339	26.4				
Tamilnadia uliginosa	Rubiaceae									0.6	190	1163	10.4

Table 1 (cont.)

Herbaceous layer		**Mixed Deciduous**				**Low Indaing**				**High Indaing**			
Species	**Family**	**F**	**A**	**C**	**IV**	**F**	**A**	**C**	**IV**	**F**	**A**	**C**	**IV**
Syngonium sp	Araceae	0.8	35	4.2	11.1								
Commelina benghalensis	Commelinaceae									0.7	76	14.4	14
Costus speciosus	Costaceae	1.0	36	7.8	15.4								

Cyperaceae 3	Cyperaceae									0.1	46	72.1	29.8
Dioscorea persimilis	Dioscoreaceae	0.8	57	9.2	18								
Premna herbacea	Lamiaceae					0.8	29	6.1	10.6				
Premna sp	Lamiaceae					1.0	45	15.5	19.9	0.7	55	8.3	10.4
Hibiscus furcatus	Malvaceae					1.0	35	4.3	11.1				
Hibiscus fragrans	Malvaceae	1.0	40	4.8	13.3					0.9	76	7	12.1
Andropogon ascinodis	Poaceae C_4					1.0	34	6.2	12.3				
Andropogon fastigiatus	Poaceae C_4	0.8	39	8	14.8					0.9	84	20.6	17.5
Aristida funiculate	Poaceae C_4					0.8	69	18.2	23.3				
Dendrocalamus strictus	Poaceae	0.8	26	5.8	11.4								
Eragrostis nigra	Poaceae C_4									0.9	98	19.3	17.9
Grass 2	Poaceae					0.8	75	3.2	13.7				
Saccharum ravennae	Poaceae C_4	0.5	37	15.1	19.3					0.7	93	27.5	19.8
Setaria lutescens	Poaceae					1.0	57	10.8	18	0.7	65	8.1	11
Hedyotis diffusa	Rubiaceae					1.0	34	3.5	10.4				
Smilax macrophylla	Smilacaceae	0.8	47	8	15.8								
Cissus 1	Vitaceae									0.9	51	5.2	9.8
Curcuma petiolata	Zingiberaceae	1.0	51	3.9	14	1.0	53	7.3	15.1				
Kaempferia candida	Zingiberaceae	1.0	28	4.7	11.7	0.8	36	5.5	11	0.7	76	12	13.1

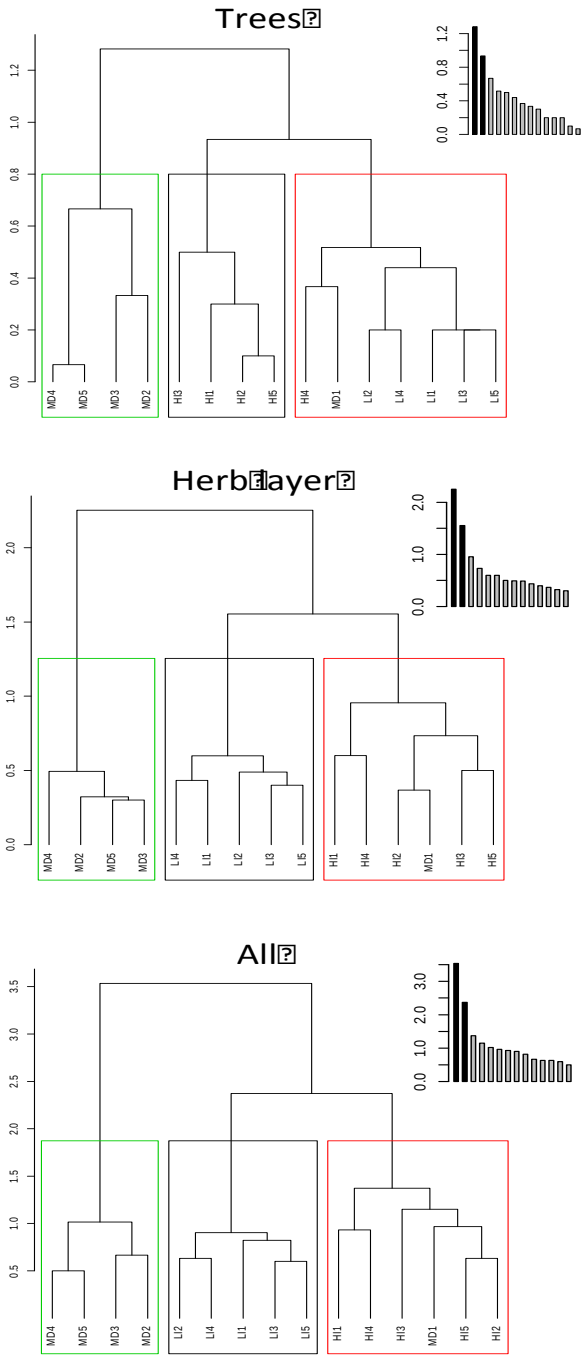

Figure 3.Cluster generated by hierarchical clustering on principal components (HCPC) on the presence-absence plot data for the study area (a) Tree DBH ≥ 5cm only (b) herb-layer only, and (c) combined tree DBH ≥5cm and herb-layer data. Clusters were constructed after removing all singletons, doubletons and tripletons, from the three data matrices.

4.2 Environmental and vegetation structure variations among the community types

Several environmental variables and vegetation parameters differed significantly amongst the community types based on ANOVAs and posthoc tests (Table 2, Figures 4 and 5). Several other environmental variables and vegetation parameters show visually apparent differences among community types that are not significantly different. We describe these

as well because the lack of statistical difference is potentially due to the small sample size (n = 15).

Table 2. Variance analysis results on the environmental and vegetation structure variables for the three community types. Pseudo-R^2 estimates for poisson-type models are calculated according to the Cragg-Uhler method. Variance analyses conducted with ANOVA for normally-disitrbuted variables and with Chi-square tests for Poisson-distributed variables. Bold values indicate models with significantly explained variance ($P < 0.1$).

Predictors	**Transformation**	**Multiple R^2 value**	**P-value**
Environmental variables			
Fire-frequency		0.20	0.269
Tree-cover		**0.49**	**0.017**
Soil total N		0.26	0.169
Soil total P	$\log_e$	0.30	0.111
Soil total K	$()^{1/2}$	0.40	**0.048**
pH	$()^{1/2}$	0.35	**0.078**
Vegetation structure			
Tree: basal area		**0.35**	**0.078**
Tree: abundance		**0.48**	**0.020**
Tree: richness	Poisson model	0.94	**<0.001**
Herb layer: cover		0.06	0.686
Herb layer: abundance		0.14	0.408
Herb layer: richness	Poisson model	0.31	**0.06**
C4: cover		0.08	0.590
C4: abundance		0.49	**0.018**
C4: richness	Poisson model	0.24	0.13

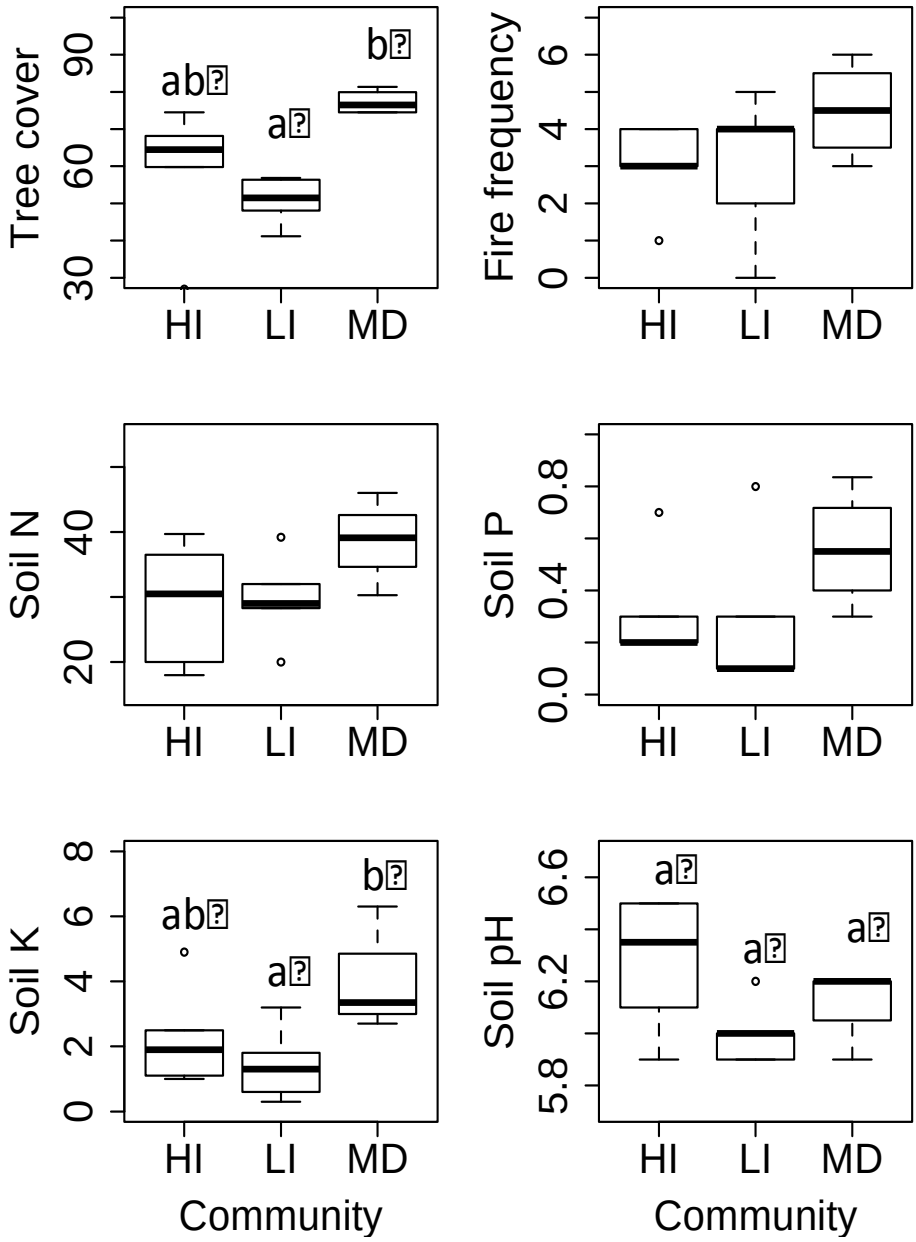

Figure 4.Environmental variation across different identified community types (HI = High Indaing, LI = Low Indaing, MD = Mixed Deciduous). Significant differences between groups based on Tukey HSD pairwise tests are indicatedwithdifferent letters.

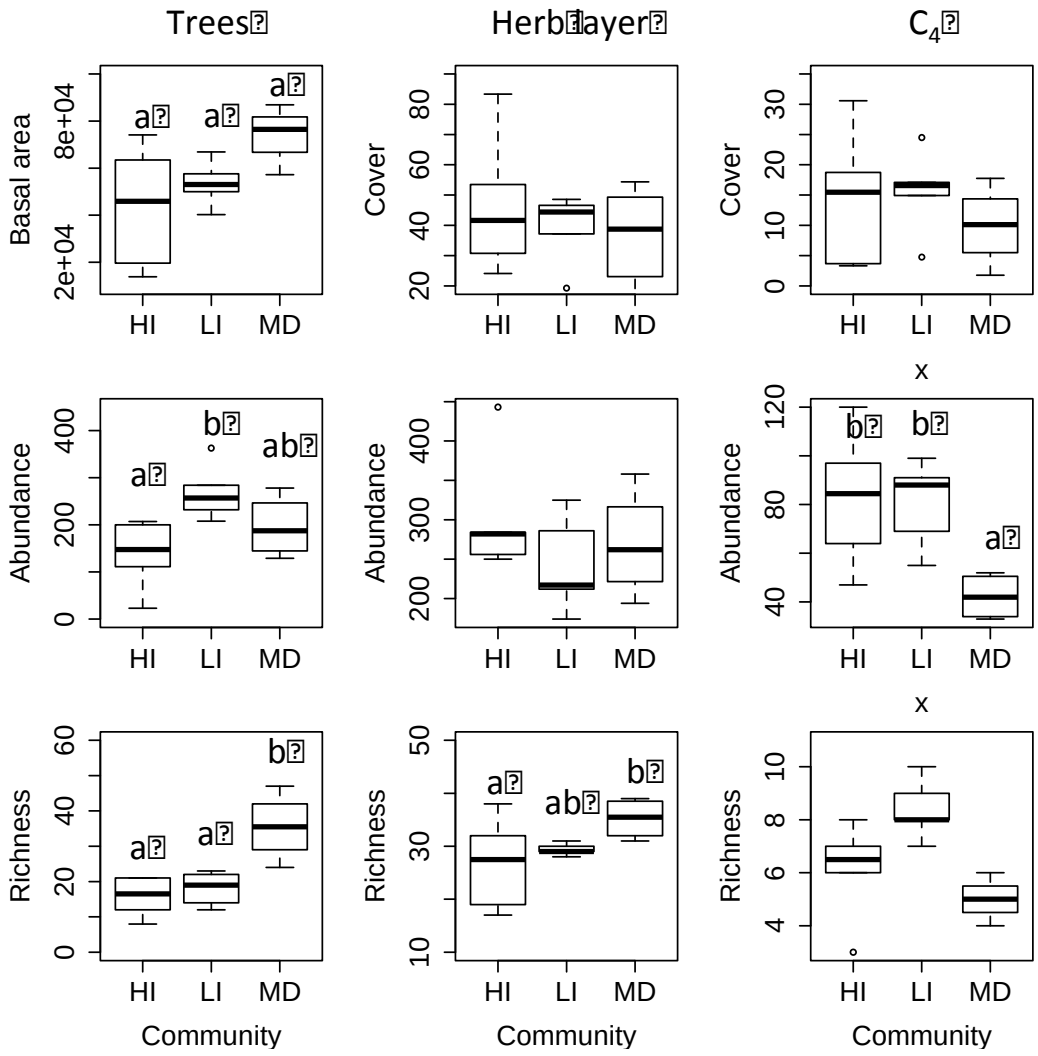

Figure 5. Vegetation structure across different identified community types (HI = High Indaing, LI = Low Indaing, MD = Mixed Deciduous). Significant differences between groups based on Tukey HSD pairwise tests are indicated with letters.

Among environmental parameters, tree cover, soil potassium (K) were significantly greater for MD plots than LI plots (with HI plots having intermediate values). Soil nitrogen (N) and soil phosphorus (P) were not statistically different, but the boxplot of data suggests that MD plots had higher ranges of N and P than HI or LI (Figure 4). The ANOVA for soil pH was significant at 0.1 level and the boxplots suggest pH may be greater for HI than LI plots, with MD having intermediate values. Fire frequency did not differ significantly across community types, with the average number of fires ranging from 3 to 5 fires over 17 years across the 3 community types.

Among plant structure parameters, tree basal area and tree species richness were greater for MD communities than LI or HI plots, whereas tree abudance was greatest for LI and least for HI. For herb-layer, richness was higher in MD than HI communities (LI was intermediate). For C_4 plants, abundance was significantly greater for HI and LI communities than MD communities, and richness ranged at higher values for LI and HI communities than MD communities (not significant due to outlier in HI).

4.3 Vegetation associations with environmental variables

When the vegetation data was treated as continuous rather than grouped by community type, several parameters showed significant associations to environmental variables (Table 3). Tree basal area was positively related to tree cover, soil N and soil P, tree abundance was negatively related to soil K, and tree richness was positively related to fire frequency, tree cover, soil N, soil phosphorus and soil potassium. Herb-layer richness was only negatively related to soil pH. C_4 abundance was negatively related to tree cover, soil N and soil P, and C4 richness was negatively related to tree cover.

4.4 Community types identified using the combination of tree data and herbs data

Community classifications of the plots based on the tree data only, herb-layer data only, and the combined tree and herb-layer data identified the three community types with few changes. The major differences among the clustering results were that one plot of MD and HI each moved positions and were assigned to LI or HI community types. This suggests that the tree and herb-layer communities of MD, LI and HI are each distinctive. Notably the herb data and the total data generated consistent classifications, but the tree data classified two plots (MD1 and HI4), with LI. MD1 had much lower species richness than the other MD plots (Figure S1, Supplementary Materials), and both MD1 and HI4 had 3 species commonly associated with LI, *Buchanania cochinchinensis Dillenia parviflora,* and *Shorea oblongifolia*. Chatthin Wildlife Sanctuary is heavily utilized by local communities for timber and other resources (Songer et al., 2011), so it is possible that the few disagreements in the plot data between herb-layer and tree clustering are due to timber harvesting. Using both tree and herb-layer data to identify communities may go some way to overcoming the effects of human interference, because of increased pools of species available to identify each group using presence-absence data as applied here (Pasion et al., 2018). It is also possible that increased plot sampling could stabilize the community types as the distinctive species of each community are more strongly detected by the clustering algorithm.

4.5 Fire frequency does not differ among community types

We found no evidence that fire frequency explains differences between the communities and only tree richness increased with fire frequency recorded during the prior 17 fire seasons (see Methods). There are several possible interpretations of this finding.

First, the fire frequency data may not be of sufficiently high quality to distinguish fine-scaled variability because they are based on low-resolution (1 km^2) satellite data. Further, there is some debate about how well MODIS detects ground-burning fires under dense canopies (Kobsak Wanthongchai, pers. comm. 2014). This corroborates with the local knowledge of the field guides who assisted with the sampling, as they claimed that the fire frequency maps we used for locating plots are inaccurate. This suggests that our fire data likely underestimates the true number of fires happening in each of our sampling plots in Chatthin Wildlife Sanctuary. This leads to the second interpretation, that fire is a common disturbance experienced by all community types at Chatthin Wildlife Sanctuary, and by extension, in all the Deciduous Dipterocarp and Mixed Deciduous communities in Southeast Asia (Rundel and Boonpragob, 1995; Wanthongchai et al., 2011; Baker and Bunyavejchewin, 2017). Certainly there is an accumulating body of evidence that tree species in the communities possess functional adaptations for coping with fire, including thick bark that protects cambium from fire, subcutaneous lateral meristems protected from fire, strong resprouting ability post fire, and substantial reserve storage in roots to support resprouting post-fire (Stott, 1988; Whelan, 1997; Marod et al., 2002; Ratnam et al., 2016). Recent experimental work in Deciduous Dipterocarp communities in Vietnam has demonstrated that fire has a strong selective effect on juvenile classes, causing severe mortality of dominant tree species (Nguyen et al., 2019). Given that long-term suppression of fire creates suitable conditions for destructive crown fires (Stott, 1988), it would be useful to extend fire manipulation to mixed deciduous communities and to develop longer-term fire experiments with multiple fire intervals to understand structural development and to develop benchmark fire management regimes. Presently these are lacking in Asia.

4.6 Tree canopy differs between community types and affects C_4 abundance and richness.

Tree canopy cover and tree richness were greater for MD plots than HI or LI (Figure 4). Tree canopy cover was positively associated with tree basal area and tree richness, but had negative effects on C_4 abundance and richness (Table 3), consistent with observations across savanna-forest transitions in Africa (Charles-Dominique et al., 2018) and South America (Hoffmann et al., 2012). LI, HI and MD communities had mean tree cover of 50.8% (95% CI: 42.7 to 58.8), 59.7% (95% CI: 42.1 to 77.4) and 77.2% (95%: 71.9 to 82.5) respectively. Thus LI has a high C_4 abundance and low tree canopy cover (<60%), consistent with physiognomic descriptions of the savanna biome, HI has high C_4 abundance but a range of tree cover values that overlaps values thought to be typical for savannas and forests (Hirota et al., 2011; Staver et al., 2011), whereas MD has low C_4 abundance and high tree canopy cover (> 70%) previously identified as forest biome (Hirota et al., 2011; Staver et al., 2011). The combined evidence of frequent fires, open tree canopies and high C_4 abundance suggest that the Dipterocarp-dominated LI can be classified as savanna. The higher tree cover but abundant C_4 understory suggest that the Dipterocarp-dominated HI cannot yet be unequivocally located to savanna or fores . The understory structure of MD is less grassy

than the other two communities, suggesting that MD does not match savanna for at least two criteria - low C_4 diversity and high tree canopy cover, but the community still appears to be fire-adapted. Fire in these communities is sustained by substantial leaf litter from the deciduous trees each year (Stott 1988; Wanthongchai et al., 2011; personal observations by the authors in Chatthin Wildlife Sanctuary). The deciduous nature of these communities may be the key reason that they sustain fire in spite of low grass biomass, in contrast to well-studied savanna-forest boundaries in the Cerrado, South Africa and West Africa where fire is restricted to savanna and does not move into the forest except in unusually dry years (Hoffmann et al., 2012; Oliveras and Malhi, 2016; Charles-Dominique et al., 2018). In those systems the forest canopy is dominated by evergreen or semi-deciduous species, meaning that the understory vegetation may not dry out as severely nor do they generate as much leaf litter as in the deciduous communities of South and Southeast Asia (Stott, 2000; Franco et al., 2006; Hennenberg et al., 2006; Wanthongchai et al., 2011). Thus MD is a community that appears to be well-adapted to fire, but is physiognomically closer to forest.

Table 3. Plant functional group responses to environmental variables. Coefficients of determination (R^2) and model variance tests (F tests for normal data and Chi-square tests for Poisson data) are given for all models. Signs of regression slope coefficients are given only for models with significant ($P < 0.1$) variance explained. Pseudo-R^2 estimates for Poisson-type models are calculated according to the Cragg-Uhler method.

Response	**Fire frequency**			**Tree cover**			**N**			**P**			**K**			**pH**		
	R^2	**P(F)**	**Coef.**	**R^2**	**P(F)**	**Coef.**	**R^2**	**P(F)**	**Coef.**	**R^2**	**P(F)**	**Coef.**	**R^2**	**P(F)**	**Coef.**	**R^2**	**P(F)**	**Coef.**
Tree basal area	0.04	0.493		**0.33**	**0.026**	**+**	**0.43**	**0.008**	**+**	**0.32**	**0.029**	**+**	0.02	0.587		0.01	0.667	
Herb-layer cover	0.00	0.847		0.02	0.662		0.03	0.538		0.03	0.525		0.05	0.424		0.04	0.485	
C4 cover	0.03	0.556		0.12	0.199		0.00	0.763		0.06	0.369		0.04	0.484		0.10	0.240	
Tree abundance	0.00	0.831		0.05	0.416		0.00	0.946		0.00	0.920		**0.21**	**0.088**	-	0.35	0.298	
Herb-layer abundance	0.01	0.669		0.00	0.861		0.02	0.635		0.00	0.764		0.07	0.343		0.00	0.946	
C4 abundance	0.08	0.294		**0.39**	**0.012**	**-**	**0.36**	**0.018**	**-**	**0.22**	**0.074**	-	0.04	0.459		0.02	0.600	
Tree richness	**0.36**	**0.01**	**+**	**0.82**	**<0.001**	**+**	**0.91**	**<.001**	**+**	**0.60**	**<.001**	**+**	**0.42**	**0.004**	**+**	0.02	0.595	
Herb-layer richness	0.15	0.12		0.13	0.15		0.08	0.27		0.06	0.36		0.09	0.24		**0.29**	**0.02**	**-**
C4 richness	0.01	0.76		0.18	**0.09**	**-**	0.08	0.27		0.16	0.10		0.05	0.39		0.07	0.30	

4.7 Soil fertility differs between savanna and forest types

The three community types could be distinguished on the basis of soil properties. MD had significantly greater soil K and also appeared to occur at higher ranges of soil P and N (Figure 4). This all suggests that soil fertility is greater in MD than the two deciduous Dipterocarp-dominated communities (Troup, 1921; Champion and Seth, 1968). Across plots, tree basal area increased with increasing soil N and soil P (Table 3). Given that fire is found in all three communities, this suggests that the environmental driver controlling tree density and tree cover, and by extension, switches between Dipterocarp communities (LI and HI) and Mixed Deciduous forest (MD), is soil fertility (Lloyd et al., 2008) or soil water availability (Rodriguez-Iturbe et al., 2019). Potassium has previously been identified as a probable key nutrient constraining plant growth in savannas (Bond, 2010). Presently we lack any data to test whether soil water is constraining, although its probable role has been highlighted before (Bunyavejchewin et al., 2011) so this needs proper examination in the future. Transitions between community types appeared to be quite abrupt (personal observation), and the community types are interspersed (see Figure 1), probably reflecting soil heterogeneity created by the alluvial history of the soils (Aung et al., 2004). With respect to nutrients, given that fire is part of all communities involved, it seems probable that positive feedbacks between fire and grass do not maintain the vegetation transitions between Dipterocarp Savanna and Mixed Deciduous Forest; rather the boundaries are maintained by soil constraints on tree growth (Lloyd et al., 2008; Bond, 2010). Long-term planned fire frequency manipulation experiments could disentangle how soil and fire processes interact to drive the community differences

5. Discussion

5.1 Community types identified using the combination of tree data and herbs data

Community classifications of the plots based on the tree data only, herb-layer data only, and the combined tree and herb-layer data identified the three community types with few changes. The major differences among the clustering results were that one plot of MD and HI each moved positions and were assigned to LI or HI community types. This suggests that the tree and herb-layer communities of MD, LI and HI are each distinctive. Notably the herb data and the total data generated consistent classifications, but the tree data classified two plots (MD1 and HI4), with LI. MD1 had much lower species richness than the other MD plots (Figure S1, Supplementary Materials), and both MD1 and HI4 had 3 species commonly associated with LI, *Buchanania cochinchinensis Dillenia parviflora,* and *Shorea oblongifolia*. Chatthin Wildlife Sanctuary is heavily utilized by local communities for timber and other resources (Songer et al., 2011), so it is possible that the few disagreements in the plot data between herb-layer and tree clustering are due to timber harvesting. Using both tree and herb-layer data to identify communities may go some way to overcoming the effects of human interference, because of increased pools of species available to identify each group using presence-absence data as applied here (Pasion et al., 2018). It is also possible that

increased plot sampling could stabilize the community types as the distinctive species of each community are more strongly detected by the clustering algorithm.

5.2 Fire frequency does not differ among community types

We found no evidence that fire frequency explains differences between the communities and only tree richness increased with fire frequency recorded during the prior 17 fire seasons (see Methods). There are several possible interpretations of this finding. First, the fire frequency data may not be of sufficiently high quality to distinguish fine-scaled variability because they are based on low-resolution (1 km^2) satellite data. Further, there is some debate about how well MODIS detects ground-burning fires under dense canopies (Kobsak Wanthongchai, pers. comm. 2014). This corroborates with the local knowledge of the field guides who assisted with the sampling, as they claimed that the fire frequency maps we used for locating plots are inaccurate. This suggests that our fire data likely underestimates the true number of fires happening in each of our sampling plots in Chatthin Wildlife Sanctuary. This leads to the second interpretation, that fire is a common disturbance experienced by all community types at Chatthin Wildlife Sanctuary, and by extension, in all the Deciduous Dipterocarp and Mixed Deciduous communities in Southeast Asia (Rundel and Boonpragob, 1995; Wanthongchai et al., 2011; Baker and Bunyavejchewin, 2017). Certainly there is an accumulating body of evidence that tree species in the communities possess functional adaptations for coping with fire, including thick bark that protects cambium from fire, subcutaneous lateral meristems protected from fire, strong resprouting ability post fire, and substantial reserve storage in roots to support resprouting post-fire (Stott, 1988; Whelan, 1997; Marod et al., 2002; Ratnam et al., 2016). Recent experimental work in Deciduous Dipterocarp communities in Vietnam has demonstrated that fire has a strong selective effect on juvenile classes, causing severe mortality of dominant tree species (Nguyen et al., 2019). Given that long-term suppression of fire creates suitable conditions for destructive crown fires (Stott, 1988), it would be useful to extend fire manipulation to mixed deciduous communities and to develop longer-term fire experiments with multiple fire intervals to understand structural development and to develop benchmark fire management regimes. Presently these are lacking in Asia.

5.3 Tree canopy differs between community types and affects C_4 abundance and richness

Tree canopy cover and tree richness were greater for MD plots than HI or LI (Figure 4). Tree canopy cover was positively associated with tree basal area and tree richness, but had negative effects on C_4 abundance and richness (Table 3), consistent with observations across savanna-forest transitions in Africa (Charles-Dominique et al., 2018) and South America (Hoffmann et al., 2012). LI, HI and MD communities had mean tree cover of 50.8% (95% CI: 42.7 to 58.8), 59.7% (95% CI: 42.1 to 77.4) and 77.2% (95%: 71.9 to 82.5) respectively. Thus LI has a high C_4 abundance and low tree canopy cover (<60%), consistent with physiognomic descriptions of the savanna biome, HI has high C_4 abundance but a range

of tree cover values that overlaps values thought to be typical for savannas and forests (Hirota et al., 2011; Staver et al., 2011), whereas MD has low C_4 abundance and high tree canopy cover (> 70%) previously identified as forest biome (Hirota et al., 2011; Staver et al., 2011). The combined evidence of frequent fires, open tree canopies and high C_4 abundance suggest that the Dipterocarp-dominated LI can be classified as savanna. The higher tree cover but abundant C_4 understory suggest that the Dipterocarp-dominated HI cannot yet be unequivocally located to savanna or fores . The understory structure of MD is less grassy than the other two communities, suggesting that MD does not match savanna for at least two criteria - low C_4 diversity and high tree canopy cover, but the community still appears to be fire-adapted. Fire in these communities is sustained by substantial leaf litter from the deciduous trees each year (Stott 1988; Wanthongchai et al., 2011; personal observations by the authors in Chatthin Wildlife Sanctuary). The deciduous nature of these communities may be the key reason that they sustain fire in spite of low grass biomass, in contrast to well-studied savanna-forest boundaries in the Cerrado, South Africa and West Africa where fire is restricted to savanna and does not move into the forest except in unusually dry years (Hoffmann et al., 2012; Oliveras and Malhi, 2016; Charles-Dominique et al., 2018). In those systems the forest canopy is dominated by evergreen or semi-deciduous species, meaning that the understory vegetation may not dry out as severely nor do they generate as much leaf litter as in the deciduous communities of South and Southeast Asia (Stott, 2000; Franco et al., 2006; Hennenberg et al., 2006; Wanthongchai et al., 2011). Thus MD is a community that appears to be well-adapted to fire, but is physiognomically closer to forest.

5.4 Soil fertility differs between savanna and forest types

The three community types could be distinguished on the basis of soil properties. MD had significantly greater soil K and also appeared to occur at higher ranges of soil P and N (Figure 4). This all suggests that soil fertility is greater in MD than the two deciduous Dipterocarp-dominated communities (Troup, 1921; Champion and Seth, 1968). Across plots, tree basal area increased with increasing soil N and soil P (Table 3). Given that fire is found in all three communities, this suggests that the environmental driver controlling tree density and tree cover, and by extension, switches between Dipterocarp communities (LI and HI) and Mixed Deciduous forest (MD), is soil fertility (Lloyd et al., 2008) or soil water availability (Rodriguez-Iturbe et al., 2019). Potassium has previously been identified as a probable key nutrient constraining plant growth in savannas (Bond, 2010). Presently we lack any data to test whether soil water is constraining, although its probable role has been highlighted before (Bunyavejchewin et al., 2011) so this needs proper examination in the future. Transitions between community types appeared to be quite abrupt (personal observation), and the community types are interspersed (see Figure 1), probably reflecting soil heterogeneity created by the alluvial history of the soils (Aung et al., 2004). With respect to nutrients, given that fire is part of all communities involved, it seems probable that positive feedbacks between fire and grass do not maintain the vegetation transitions between Dipterocarp Savanna and Mixed Deciduous Forest; rather the boundaries are maintained by

soil constraints on tree growth (Lloyd et al., 2008; Bond, 2010). Long-term planned fire frequency manipulation experiments could disentangle how soil and fire processes interact to drive the community differences.

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References

Allen, K., Dupuy, J.M., Gei, M.G., Hulshof, C., Medvigy, D., Pizano, C., Salgado-Negret, B., Smith, C.M., Trierweiler, A., Bloem, S.J. Van, Waring, B.G., Xu, X., Jennifer S Powers, 2017. Will seasonally dry tropical forests be sensitive or resistant to future changes in rainfall regimes ? Environ. Res. Lett. 12, 1–16. https://doi.org/10.1088/1748-9326/aa5968.

Ashton, P., 2014. On the Forest of Tropical Asia. KEW, UK.

Aung, M., Khaing, K., Oo, T., Kyaw, K., Leimgruber, P., Allendorf, T., Duncan, C., Wemmer, C., 2004. The environmental history of Chatthin Wildlife Sanctuary , a protected area in Myanmar (Burma). J. Environ. Manage. 72, 205–216. https://doi.org/10.1016/j.jenvman.2004.04.013.

Baker, P.J., Bunyavejchewin, S., 2017. Complex historical disturbance regimes shape forest dynamics across a seasonal tropical landscape in western Thailand, in: Amoroso, M.M., Daniels, L.D., Baker, P.J., Camarero, J.J. (Eds.), Dendroecology: Tree-ring analyses applied to ecological studies. Ecological Studies 231. Springer Nature, Switzerland, pp. 75-96.

Bond, W.J., 2010. Do nutrient-poor soils inhibit development of forests? A nutrient stock analysis. Plant Soil 334, 47–60. https://doi.org/10.1007/s11104-010-0440-0.

Bruhl, J.J., Wilson, K.L. 2007. Towards a comprehensive survey of C_3 and C_4 photosynthetic pathways in Cyperaceae. Aliso 23, 99-148. http://scholarship.claremont.edu/aliso/vol23/iss1/11.

Bunyavejchewin, S., Baker, P.J., Davies, S.J., 2011. Seasonally Dry Tropical Forests in continental Southeast Asia: structure, composition, and dynamics, in: McShea, M.J., Davies, S.J., Bhumpakphan, N. (Eds.), The Ecology and Conservation of Seasonally Dry Forests in Asia. Smithsonian Institution Scholarly Press, Washington D.C., pp. 9–35.

Champion, H.G., Seth, S.K., 1968. A Revised Survey of the Forest Types of India. Government of India Press, Delhi.

Charles-Dominique, T., Midgley, G.F., Tomlinson, K.W., Bond, W.J., 2018. Steal the light: shade vs fire adapted vegetation in forest–savanna mosaics. New Phytol. 218, 1419–1429. https://doi.org/10.1111/nph.15117.

Craine, J.M., Froehle, J., Tilman, D.G., Wedin, D.A., Chapin, F.S.III., 2001. The relationships among root and leaf traits of 76 grassland species and relative abundance along fertility and disturbance gradients. Oikos 93, 274-285.

Dexter, K.G., Smart, B., Baldauf, C., Baker, T.R., Balinga, M.P.B., Brienen, R.J.W., Fauset, S., Feldpausch, T.R., Silva, L.F.-D., Muledi, J.I., Lewis, S.L., Lopez-Gonzalez, G., Marimon-Junior, B.H., Marimon, B.S., Meerts, P., Page, N., Parthasarathy, N., Phillips, O.L., Sunderland, T.C.H., Theilade, I., Weintritt, J., Affum-Baffoe, K., Araujo, A., Arroyo, L., Begne, S.K., Neves, E.C.-D., Collins, M., Cuni-Sanchez, A., Djuikouo, M.N.K., Elias, F., Foli, E.G., Jeffery, K.J., Killeen, T.J., Malhi, Y., Maracahipes, L., Mendoza, C., Monteagudo-Mendoza, A., Morandi, P., Santos, C.O.-D., Parada, A.G., Pardo, G., Peh, K.S.-H., Salomão, R.P., Silveira, M., Sinatora–Miranda, H., Slik, J.W.F., Sonke, B., Taedoumg, H.E.,

Toledo, M., Umetsu, R.K., Villaroel, R.G., Vos, V.A., White, L.J.T., Pennington, R.T., 2015. Floristics and biogeography of vegetation in seasonally dry tropical regions. Int. For. Rev. 17, 10–32. https://doi.org/10.1505/146554815815834859.

Franco, A.C., Haridasan, M., Hoffmann, W.A., Silva, L.C.R., Rossatto, D.R., Horwath, W.R., 2006. Can savannas become forests? A coupled analysis of nutrient stocks and fire thresholds in central Brazil. Plant Soil 373, 829–842. https://doi.org/10.1007/s11104-013-1822-x.

Fynn, R.W.S., Morris, C.D., Kirkman, K.P., 2005. Plant strategies and trait trade-offs influence trends in competitive ability along gradients of soil fertility and disturbance. J. Ecol. 93, 384-394.

Giglio, L., Schroeder, W., Hall, J. V, Justice, C.O., 2018. MODIS Collection 6 Active Fire Product User's Guide Revision B. http://modis-fire.umd.edu/files/MODIS_C6_Fire_User_Guide_B.pdf

Giglio, L., Schroeder, W., Justice, C.O., 2016. The collection 6 MODIS active fire detection algorithm and fire products. Remote Sens. Environ. 178, 31–41. https://doi.org/10.1016/j.rse.2016.02.054.

Hennenberg, K.J., Fischer, F., Kouadio, K., Goetze, D., Orthmann, B., Linsenmair, K.E., Jeltsch, F., Porembski, S., 2006. Phytomass and Fire Occurrence along Forest-Savanna Transects in the Comoé National Park, Ivory Coast. J. Trop. Ecol. 22, 303–311.

Higgins, S.I., Bond, W.J., S.W., W.T., 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. J. Ecol. 88, 213–229. https://doi.org/10.1046/j.1365-2745.2000.00435.x.

Hijmans, R.J., 2019. Package "raster" Type Package Title Geographic Data Analysis and Modeling.

Hirota, M., Holmgren, M., Van Nes, E.H., Scheffer, M., 2011. Global Resilience of Tropical Forest and Savanna to Critical Transitions. Science 334, 232-235. https://doi.org/10.1126/science.1210657.

Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C.R., Lau, O.L., Haridasan, M., Franco, A.C., 2012. Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. Ecol. Lett. 15, 759–768. https://doi.org/10.1111/j.1461-0248.2012.01789.x.

Husson, A.F., Josse, J., Le, S., Mazet, J., Husson, M.F., 2018. Package ' FactoMineR .' https://doi.org/10.1201/b10345-2.

Kent, M., 2011. Vegetation Description and Data Analysis: A Practical Approach. Second edition. Wiley-Blackwell, London, United Kingdom. p. 428.

Khaing, N., 2013. Structure and Site Conditions of Dry Deciduous Forests in Central Myanmar. PhD thesis, Georg-August-Universität, Göttingen, Germany.

Khant, H.E., 2017. Changes in habitat structures of dry deciduous dipterocarp forest and abundance of Eld's deer (*Panolia eldii*- thamin) in Chatthin Wildlife Sanctuary, Myanmar. MSc Thesis, Kasetsart University, Bangkok, Thailand.

Kidd, P.S., Proctor, J., 2001. Why plants grow poorly on very acid soils : are ecologists missing the obvious ? J. Exp. Bot. 52, 791–799. https://doi.org/https://doi.org/10.1093/jexbot/52.357.791.

Kindt, R., 2018. BiodiversityR: package for community ecology and suitability analysis. https://rdrr.io/cran/BiodiversityR/#vignettes

Lloyd, J.O.N., Bird, M.I., Vellen, L., Miranda, A.C., Veenendaal, E.M., Djagbletey, G., Miranda, H.S., Farquhar, G.D., 2008. Contributions of woody and herbaceous vegetation to tropical savanna ecosystem productivity : a quasi-global estimate. Tree Physiol. 28, 451–468.

Marod, D., Kutintara, U., Tanaka, H., Nakashizuka, T., 2002. The effects of drought and fire on seed and seedling dynamics in a tropical seasonal forest in Thailand. Plant Ecol. 161, 41–57. https://doi.org/https://doi.org/10.1023/A:1020372401313.

Miles, L., Newton, A.C., DeFries, R.S., Ravilious, C., May, I., Blyth, S., Kapos, V., Gordon, J.E., 2006. A global overview of the conservation status of tropical dry forests. J. Biogeogr. 33, 491–505. https://doi.org/10.1111/j.1365-2699.2005.01424.x.

Nepolo, E., Mapaure, I., 2012. Short-Term Influence of Fire on Herbaceous Composition, Diversity and Grass Biomass Production in Semi-Arid Savanna Woodland in Windhoek, Namibia. Int. J. Ecosyst. 2, 154–160. https://doi.org/10.5923/j.ije.20120206.02.

Nguyen, T.T., Murphy, B.P., Baker, P.J., 2019. The existence of a fire-mediated tree-recruitment bottleneck in an Asian savanna. J. Biogeogr. 46, 745–756. https://doi.org/10.1111/jbi.13518.

Oksanen, J., 2018. Vegan: ecological diversity. https://cran.r-project.org/web/packages/vegan/vignettes/diversity-vegan.p.

Oliveras, I., Malhi, Y., 2016. Many shades of green: the dynamic tropical forest–savannah transition zones. Philos. Trans. R. Soc. B Biol. Sci. 371, 20150308. https://doi.org/10.1098/rstb.2015.0308.

Osborne. C.P., Salomaa, A., Kluyver, T.A., Visser, V., Kellogg, K.A., Morrone, O., Vorontsova, M.S., Clayton, W.D., Simpson, D.A., 2014. A global database of C_4 photosynthesis in grasses. New Phytol. 204, 441-446. https://doi.org/10.1111/nph.12942.

Pasion, B.O., Roeder, M., Liu, J., Yasuda, M., Corlett, R.T., Slik, J.W.F., Tomlinson, K.W., 2018. Trees represent community composition of other plant life-forms, but not their diversity, abundance or responses to fragmentation. Sci. Rep. 8, 2–14. https://doi.org/10.1038/s41598-018-29635-9.

Pennington, R.T., Lavin, M., Oliveira-Filho, A., 2009. Woody plant diversity, evolution and ecology in the Tropics: perspectives from Seasonally Dry Tropical Forests. Annu. Rev. Ecol. Evol. Syst. 2009. 40:437–57. https://doi.org/10.1146/annurev.ecolsys.110308.120327.

Ratnam, J., Bond, W.J., Fensham, R.J., Hoffmann, W.A., Archibald, S., Lehmann, C.E.R., Anderson, M.T., Higgins, S.I., Sankaran, M., 2011. When is a “forest” a savanna, and why does it matter? Glob. Ecol. Biogeogr. 20, 653–660. https://doi.org/10.1111/j.1466-8238.2010.00634.x.

Ratnam, J., Chengappa, S.K., Machado, S.J., Nataraj, N., Osuri, A.M., Sankaran, M., 2019. Functional Traits of Trees From Dry Deciduous "Forests" of Southern India Suggest Seasonal Drought and Fire Are Important Drivers. Front. Ecol. Evol. 7, 1–6. https://doi.org/10.3389/fevo.2019.00008.

Ratnam, J., Tomlinson, K.W., Rasquinha, D.N., Sankaran, M., 2016. Savannahs of Asia : antiquity , biogeography , and an uncertain future. Philos. Trans. R. Soc. 371: http://dx.doi.org/10.1098/rstb.2015.0305.

Rodriguez-Iturbe, I., Chen, Z., Stave, A.C., Levin, S.A., 2019. Tree clusters in savannas result from islands of soil moisture. Proc. Natl. Acad. Sci. 116, 6679-6683. https://doi.org/10.1073/pnas.1819389116.

Rundel, P., Boonpragob, K., 1995. Dry forest ecosystems of Thailand, in: Bullock, S.H., Mooney, H.A. (Eds.), Seasonally Dry Tropical Forests. Cambridge University Press, pp. 93–123. https://doi.org/doi.org/10.1017/CBO9780511753398.005.

Singh, J.S., Chaturvedi, R.K., 2018. Tropical Dry Deciduous Forest : Research Trends and Emerging. Springer. https://doi.org/10.1007/978-981-10-7260-4.

Slik, J.W.F., Franklin, J., Arroyo-, V., Field, R., Aguilar, S., Aguirre, N., Aiba, S., Alves, L.F., Anitha, K., Mora, F., C, G.A.A., Báez, S., Balvanera, P., Bastian, M.L., Bastin, J., Bellingham, P.J., Berg, E. Van Den, Con-, P., Boeckx, P., Boehning-gaese, K., Boyle, B., Brambach, F., Brearley, F.Q., Brown, S., Chai, S., Chazdon, R.L., Chhang, P., Chuyong, G., Ewango, C., Coronado, I.M., Cristóbal-azkarate, J., Culmsee, H., Damas, K., Dattaraja, H.S., Davidar, P., Dewalt, S.J., Din, H., Drake, D.R., Duque, A., Eichhorn, K., Eler, E.S., Enoki, T., Ensslin, A., Fandohan, A.B., Farwig, N., Feeley, K.J., Fischer, M., Forshed, O., Souza, Q., Garkoti, S.C., Gillespie, T.W., Gillet, F., Gonmadje, C., Granzow-de, I., Griffith, D.M., Grogan, J., Rehman, K., Harris, D.J., Harrison, R.D., Hector, A., Hemp, A., Homeier, J., Hussain, M.S., Hanum, I.F., Imai, N., Patrick, A., Joly, C.A., Joseph, S., Kartawinata, K., Kearsley, E., Kelly, D.L., Kessler, M., Timothy, J., Kooyman, R.M., Laumonier, Y., Susan, G., Laurance, W.F., Lawes, M.J., Susan, G., Lindsell, J., Lovett, J., Lozada, J., Lu, X., Lykke, A.M., Mahmud, K. Bin, Diana, N.P., Mansor, A., Marshall, A.R., Emanuel, H., Calderado, D., Matos, L., Meave, J.A., Felipe, P.L., Huberto, Z., Mendoza, A., Metali, F., Medjibe, V.P., Metzger, J.P., Metzker, T., Mohandass, D., Munguía-rosas, M.A., Muñoz, R., Oliveira, E.L. De, Parolin, P., Parthasarathy, N., Paudel, E., Perez, R., Pérez-garcía, E.A., Pommer, U., Poorter, L., Qi, L., Piedade, M.T.F., Roberto, J., Pinto, R., Poulsen, D., Poulsen, J.R., Powers, J.S., Prasad, C., Puyravaud, J., Rangel, O., Rocha, D.S.B., Rolim, S., Rovero, F., Santos, B., Roberto, J., Sarker, S.K., Schmitt, C.B., Schoengart, J., Schulze, M., Sist, P., Souza, A.F., Spironello, W.R., Sposito, T., Steinmetz, R., Stevart, T., Seiji, M., Suresh, H.S., Suzuki, E., Tabarelli, M., Tang, J., Tanner, E.V.J., Targhetta, N., Theilade, I., Thomas, D., Timberlake, J., Morisson, M. De, Valkenburg, J. Van, Do, T. Van, Sam, H. Van, Vandermeer, J.H., Verbeeck, H., Vetaas, O.R., Vieira, S.A., Webb, C.O., Webb, E.L., Whitfeld, T., Wich, S., Williams, J., Wiser, S., Wittmann, F., Yang, X., Yao, C.Y.A., Yap, S.L., Zahawi, R.A., Zakaria, R., Zang, R., 2018. Phylogenetic classification of the world ' s tropical forests. PNAS 115, 1837–1842. https://doi.org/10.1073/pnas.1803346115.

Songer, M., Aung. M., Swe, K.K., Oo, T., Wemmer, C., DeFries, R., Leimgruber, P., 2011. The impact of local communities on a Dry Tropical Forest sanctuary: a case study from Upper Myanmar (Burma), in: in: McShea, M.J., Davies, S.J., Bhumpakphan, N. (Eds.), The Ecology and Conservation of Seasonally Dry Forests in Asia. Smithsonian Institution Scholarly Press, Washington D.C., pp. 305–320.

Staver, A.C., Archibald, S., Levin, S.A., 2011. The Global Extent and Determinants of Savanna and Forest as Alternative Biome States. Science 334, 230 LP-232. https://doi.org/10.1126/science.1210465.

Stott, P., 2000. Combustion in tropical biomass fires: a critical review. Prog. Phys. Geogr. Earth Environ. 24, 355–377. https://doi.org/10.1177/030913330002400303.

Stott, P., 1988. The Forest as Phoenix: Towards a Biogeography of Fire in Mainland South East Asia. Geogr. J. 154, 337–350. https://doi.org/10.2307/634607.

Troup, R.S., 1921. The Silviculture of Indian Trees. Oxford University Press.

Van Langevelde, F., Van De Vijver, C.A.D.M., Kumar, L., Van De Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J., Prins, H.H.T., Rietkerk, M., 2003. Effects of fire and herbivory on the stability of savanna ecosystems. Ecology84,337–350.https://doi.org/10.1890/0012-9658(2003)084[0337:EOFAHO]2.0.CO;2.

Wanthongchai, K., Goldammer, J.G., Bauhus, J., 2011. Effects of fire frequency on prescribed fire behaviour and soil temperatures in dry dipterocarp forests. Int. J. Wildl. Fire 20, 35–45. https://doi.org/10.1071/WF08098.

Whelan, R.J., 1997. The Ecology of Fire. J. Wildl. Manage. 61, 26–27.