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Post-fire impacts on tree diversity in coastal heath forests of Brunei Darussalam

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Abstract

The adverse impacts of fires on the diversity of native plants in forest ecosystems are well documented. Tree diversity was studied in coastal heath (*Kerangas*) forests of Brunei Darussalam, Northwest Borneo after fire events. Eight 20 x 20 m plots were set up in once-burnt (3 plots), twice-burnt (3 plots) and unburnt heath forests (2 plots). All trees (live and dead) with stem diameter of 1 cm and above were censused, and percentage canopy openness and soil variables (pH, gravimetric water and organic matter content, and concentrations of total nitrogen and phosphorus) were measured. Soil pH, gravimetric water content and total nitrogen and phosphorus concentrations, and canopy openness were significantly higher in the burnt plots. Stem diameters were significantly higher in the unburnt heath forests than in the burnt plots. Tree species richness and diversity were significantly lower in the once-burnt plots than in unburnt, intact heath forest plots, indicating a substantial loss of native tree diversity in fire-affected habitats. Tree community compositions of the once-burnt plots were dominated by invasive *Acacia mangium*, which were abundant in these plots as smaller stems (<10 cm dbh). This study highlights the negative impact of fire on the native tree diversity, soil properties and canopy openness of these coastal *Kerangas* forests, and further provides preliminary evidence that fire events have facilitated the successful establishment of invasive *Acacia* species.

Index Terms: Borneo, forest fire, disturbance, *Kerangas* forest, tree diversity, invasive species, *Acacia mangium*

1. Introduction

Fire is a well-known agent of disturbance that affects the composition of plant communities in various ecosystems.^{1,2} Following fire, immediate ecosystem changes occur, including nutrient upsurge from nutrient-rich ash formation,³ an increase in light availability as pre-existing plants in the area are removed or reduced, and the shifting of hydrological, chemical and microbial properties of the soil from their initial states because of increased soil porosity and water retention.⁴⁻⁷ Consequently, the plant community

changes by favouring the growth of one species (usually fire-adaptive) but suppressing the growth of others.^{4,8} Native plant species often exhibit low tolerance towards fire events.^{8,9} Furthermore, fire reduces the ability of native plant species to recover as they fail to adapt to habitat changes.¹⁰⁻¹² The subsequent post-fire reduction in the plant canopy increases light penetration and alters the soil characteristics, often resulting in unfavourable conditions which can exacerbate the increased mortality of the native species.¹³⁻¹⁵

Deforestation, logging and agricultural land use changes have resulted in increasing incidences of forest fires in Borneo, which are further aggravated by droughts during El Niño years.^{16,17} For example, intense droughts during the 1997-1998 El Niño period resulted in extensive forest fires,¹⁸ particularly in Indonesian Borneo.¹⁹ Forest fires directly cause tree mortality,^{20,21} as well as modifying the forest structure and significantly decreasing the plant species composition.²² Repeated forest fires have been shown to limit regeneration of native plant species,²⁰ eventually resulting in the conversion of forest ecosystems into low-diversity grasslands,²³ often supporting invasive alien species.^{9,24,25}

Although intact Bornean tropical forests are typically protected from fires due to their high humidity and rainfall levels,¹ high fuel loads during droughts and dry periods are known to increase their susceptibility to fires.²⁶ Bornean heath (*Kerangas*) forests are especially vulnerable to fires during droughts and dry periods due to their drier soils, more open canopy and the higher concentrations of plant roots near the soil surface.²⁷ Within the coastal *Kerangas* forests in Brunei Darussalam, anthropogenic fires occur almost yearly^{28,29} and these fire events intensify during El Niño years.³⁰ Following these fire events, invasive *Acacia* species successfully spread into, and establish in, these disturbed, fire-degraded heath areas, often forming almost monospecific stands.²⁸ *Kerangas* forests are high conservation value habitats with high plant endemism, and harbour unique plants such as carnivorous plants and myrmecophytes.²⁹⁻³¹ These heath forests account for less than 1% of Brunei's forests, and occur on nutrient-poor, acidic sandy soils,³¹ but are increasingly becoming lost to intensive urbanisation.²⁹

We studied the effects of fire on the abundance and diversity of tree flora in coastal *Kerangas* forests in Brunei Darussalam. We hypothesized that forest fires would lower native *Kerangas* tree diversity and affect forest structure in our study sites, through a decrease in tree abundance, stem diameter and canopy openness. We also

hypothesized that forest fires would affect the soil pH, gravimetric water content and nutrient concentrations within our study sites.

2. Experimental approach

2.1 Study site

Our study was conducted in coastal heath forests near the Muara-Tutong Highway and surrounding Universiti Brunei Darussalam (4°58'21.89°N 114°53'38.43°E). In the study area, remnant *Kerangas* forests and degraded *Kerangas* forests co-occur as patches within urban and settlement areas, as well as *Acacia*-invaded habitats.

Using chronosequences in Google Earth,³² we identified locations within the study area in which fire events have occurred within a 12-year period (2003-2014). In particular, we identified sites that were burnt only once (in 2009; henceforth referred to as "Once-burnt"), burnt twice (in 2009 and 2013; henceforth referred to as "Twice-burnt"), and sites that did not experience fires from 2003 to 2014 (henceforth referred to as "Control"). Within these three sites, we randomly set up eight 20 x 20 m plots (Plots 1 to 3 in Once-burnt, Plots 4 to 6 in Twice-burnt, and Plots 7 and 8 in Control; see **Figure 1**).

2.2 Environmental parameters and soil analysis

At each plot, we measured the percentage (%) canopy openness at the plot centre using a spherical densiometer (Model A, Pioneer Ave Rapid City, SD, USA). Soil samples in replicates of four were randomly collected from each plot using a soil auger at depths of 0-15 cm, and bulked for each plot. Fresh samples were used to determine the soil gravimetric water content and pH,³³ and the remaining fresh samples were air-dried and ground, and sieved through a 0.25 mm sieve.

Air-dried and sieved soil samples were used to determine the total nitrogen (N) and total phosphorous (P) concentrations, and organic matter content. The samples were digested using 95-97% H₂SO₄ and Kjeldahl tablets in a block digester (BD-46, LACHAT Instruments,

Colorado, USA) and the total N and P concentrations were measured using Flow Injection Analyzer (FIA; Model FIAstar 5000, Hoganas, Sweden). The organic matter content was determined using the loss-on-ignition technique,³³ with the samples kept in a 550°C Gallenkamp furnace size 2 (Apeldoorn, Netherland) for two hours.

2.3 Measurements of tree diversity

All study plots were surveyed in October 2013 to February 2014 to assess tree diversity after fire incidences. Within each plot, all trees with a diameter at breast height (dbh) ≥ 1 cm were tagged and their stem diameters were measured. We censused both live and dead trees to assess the effects of fire on the tree abundance and diversity in these plots. Voucher specimens of all live tree species were collected, and identified at the Brunei National Herbarium (BRUN).

2.4 Data analysis

The software package R version 3.0.3³⁴ was used for all data analyses. One-way ANOVA was used to determine between-habitat differences in the environmental and soil parameters, the stem diameters and the abundances of live and dead trees. Species richness (defined as the number of species recorded per plot) and diversity indices (Shannon Index, evenness and Simpson's Index) were calculated using the vegan package in R (Version 2.0-10)³⁵. Species richness and diversity indices were also subjected to one-way ANOVA to determine between-plot differences in tree species richness and diversity. Assumptions of normality and equal variances were checked, and \log_{10} transformations were used when these were violated. Significant ANOVA results were further subjected to a Tukey HSD's test. The non-parametric Kruskal-Wallis test was used for data that could not be successfully transformed.

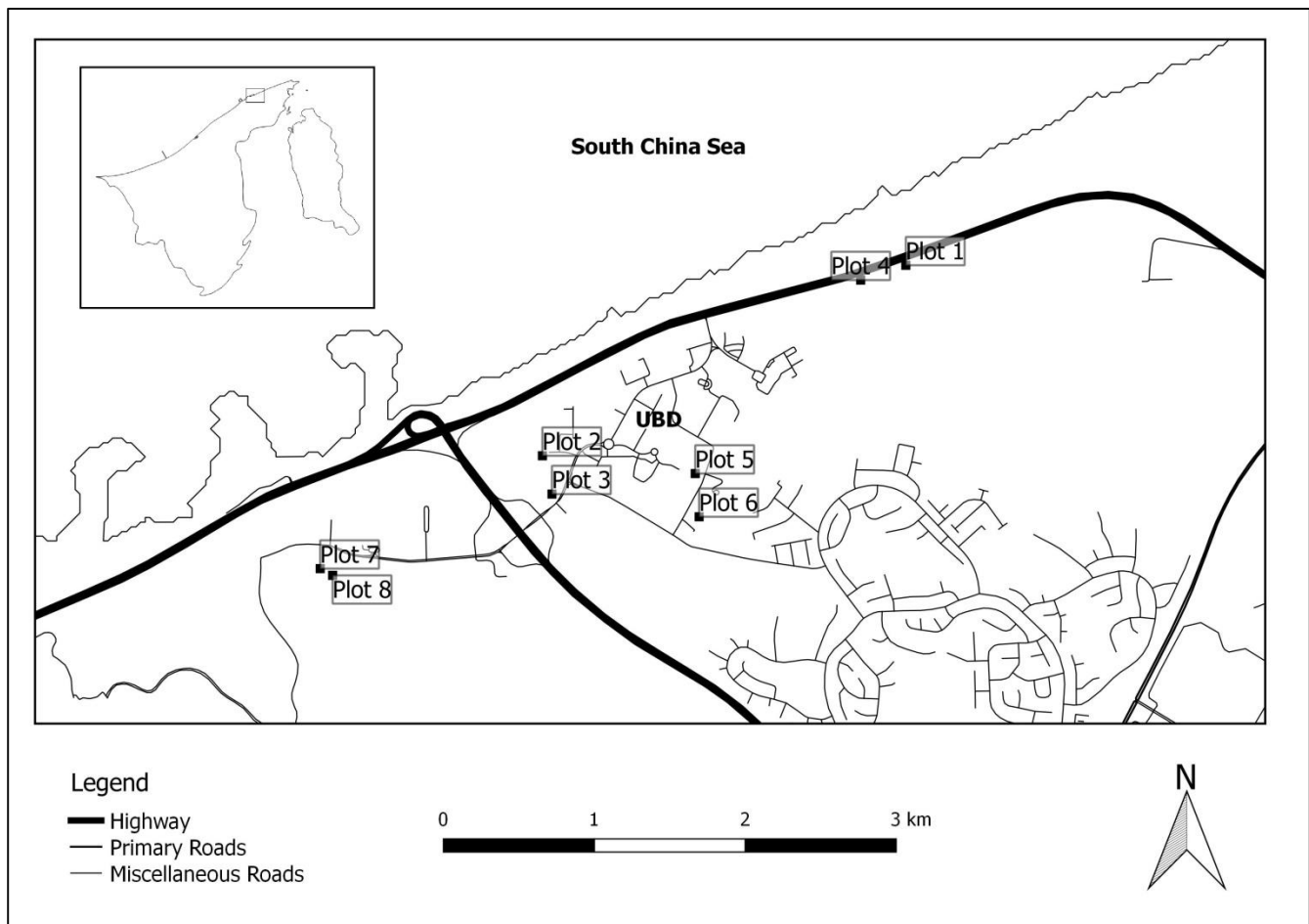


Figure 1. Locations of the study sites consisting six plots in burnt sites (Plot 1-3 in once-burnt sites; Plots 4-6 in twice-burnt sites) and two controls (Plot 7 and 8) within the coastal heath (*Kerangas*) forests of Brunei Darussalam.

3. Results

3.1 Variation in soil parameters and canopy openness

The soil pH was highest in the Twice-burnt plots and lowest in the Control plots ($p < 0.001$; see **Table 1**). The gravimetric water content was significantly higher in the Once-burnt than in the Control plots ($p < 0.01$), while the total N concentration was higher in the Twice-burnt than in the Control plots ($p < 0.05$). No significant differences were detected in the Total P concentrations or organic matter content. We recorded the highest percentage canopy openness in the Twice-burnt plots and the lowest in the Control plots ($89.1 \pm 3.7\%$ vs. $1.2 \pm 0.5\%$; $p < 0.001$).

3.2 Differences in stem diameters and abundance of live and dead trees

Live trees in the Control plots recorded the highest mean diameter (7.04 ± 0.47 cm) and the mean diameter values were significantly different between the Once-burnt and Twice-burnt plots ($p < 0.01$) and between the Once-burnt and Control plots ($p < 0.001$; see **Figure 2**). However, the mean diameters of trees in the Twice-burnt and Control plots were not significantly different. For dead trees, there was a significant difference in the mean stem diameters between plots ($p < 0.01$). The highest stem diameter of dead trees was recorded in the Once-burnt plots (mean dbh = 5.44 cm \pm 0.90).

Table 1. Variation in mean (\pm SE) of canopy openness and soil variables (pH, Gravimetric Water Content (GWC), Total N concentration, Total P concentration and percentage of organic matter) for once burnt, twice burnt and control plots. Different letters within a column indicate significant differences at $P < 0.05$ as obtained from Tukey's HSD after one-way analysis of variance (ANOVA).

Plot type	Canopy openness (%)	pH	GWC (%)	OM (%)	Total N (mg/g)	Total P (mg/g)
Once	39.1 ± 9.6^a	3.92 ± 0.09^a	18.4 ± 1.5^a	4.4 ± 0.9^a	0.631 ± 0.157^{ab}	0.070 ± 0.008^a
Twice	89.1 ± 3.7^b	4.16 ± 0.14^b	13.6 ± 2.1^{ab}	5.3 ± 0.4^a	0.648 ± 0.154^a	0.094 ± 0.008^a
Control	1.2 ± 0.5^c	3.79 ± 0.10^c	12.2 ± 1.7^b	3.5 ± 0.2^a	0.260 ± 0.105^b	0.093 ± 0.009^a

A total of 1962 individual trees were recorded in all eight plots ($n = 1131$ live trees vs. $n = 831$ dead trees). The Once-burnt plots recorded a significantly higher mean abundance of live trees ($n = 253 \pm 41$), while the Twice-burnt plots showed the lowest ($n = 20 \pm 6$; see **Figure 3**). The highest mean abundance of dead trees was found in the Twice-burnt plots ($n = 261 \pm 104$) and no dead trees were recorded in the Control plots.

3.3 Variations in species richness and diversity

A total of 23 families were recorded within the three Once-burnt plots and 26 families were recorded in the two Control plots (see **Figure 4**). Myrtaceae was the most species-rich family

recorded ($n = 5$ species), followed by Euphorbiaceae, Rubiaceae, Lauraceae Leguminosae-Mimosoideae ($n = 3$ species each) and Moraceae ($n = 2$). The families Bonnetiaceae, Leguminosae-Caesalpinioideae, Anacardiaceae and Anisophyllaceae were each represented by a single species. Diversity measurements for the Twice-burnt plots were not determined, as individual trees in the Twice-burnt plots were too charred to be positively identified.

A total of 36 species were recorded in the Once-burnt plots, but the most abundant species varied among the different plots: *Acacia mangium* in Plot 1 ($n = 56$), *Timonius flavescens* ($n = 89$) and

A. mangium (n = 48) in Plot 2, and *Dillenia suffruticosa* (n = 40) and *A. mangium* (n = 34) in Plot 3. Of the 44 species recorded in the two

Control plots, the most abundant species was *Gaertnera vaginans* (n = 65).

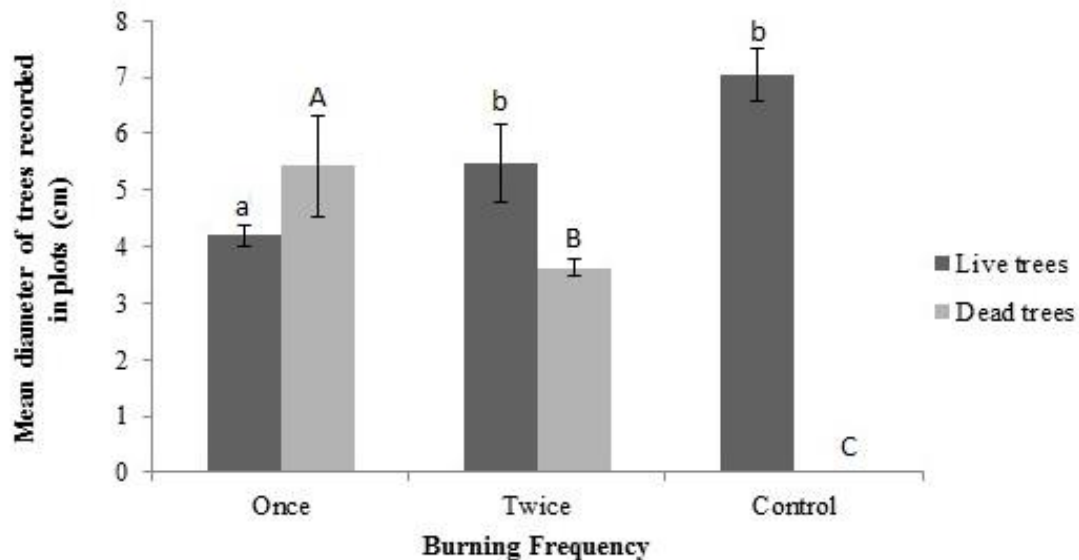


Figure 2. Variation in diameter of live and dead trees (mean \pm SE) for plots that have experienced different burning frequencies (Once, Twice and Control). Different letters within a panel indicate significant differences at $P < 0.05$ as obtained from Tukey's HSD after one-way analysis of variance (ANOVA).

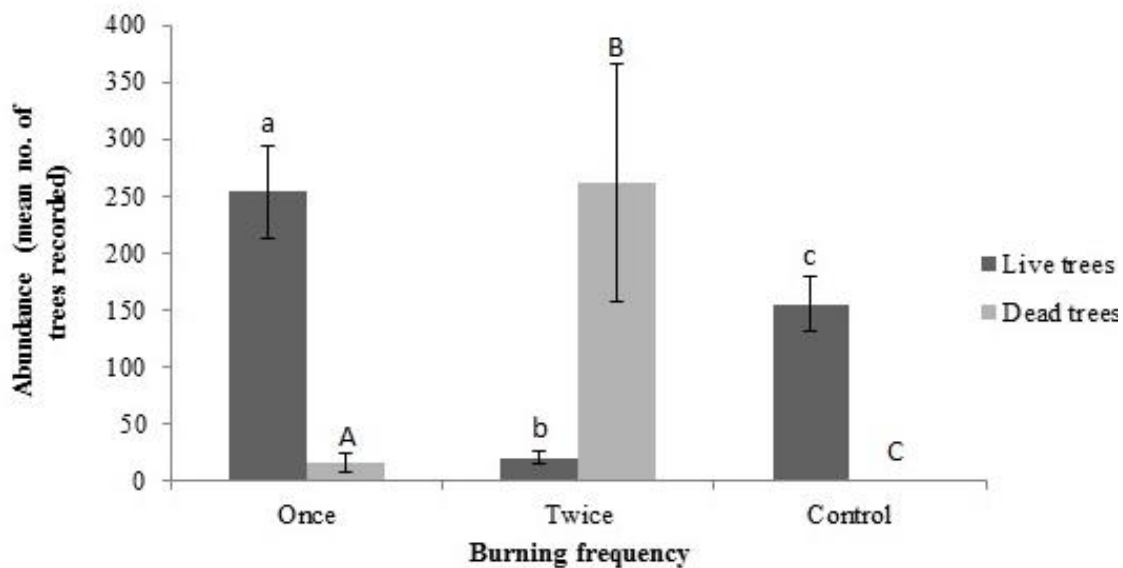


Figure 3. Variation in abundance of live and dead trees (mean \pm SE) for plots that have experienced different burning frequencies (Once, Twice and Control). Different letters within a panel indicate significant differences at $P < 0.05$ as obtained from Tukey's HSD after one-way analysis of variance (ANOVA).

Species richness differed significantly between the Once-burnt and Control plots ($p < 0.001$; see **Table 2**). Both Control plots were more species-rich (n = 31 and n = 29 species) than the Once-

burnt plots, with the exception of Once-burnt Plot 3 (n = 26 species). The lowest species richness was recorded in Once-burnt Plot 1 (n = 5 species), which was heavily dominated by *A.*

mangium. Diversity indices (Shannon Index, Evenness and Inverse Simpson's Index) were similarly significantly higher ($p < 0.05$) in the

Control plots than the Once-burnt plots (see **Table 2**). The full list of species recorded is listed in **Table 3**.

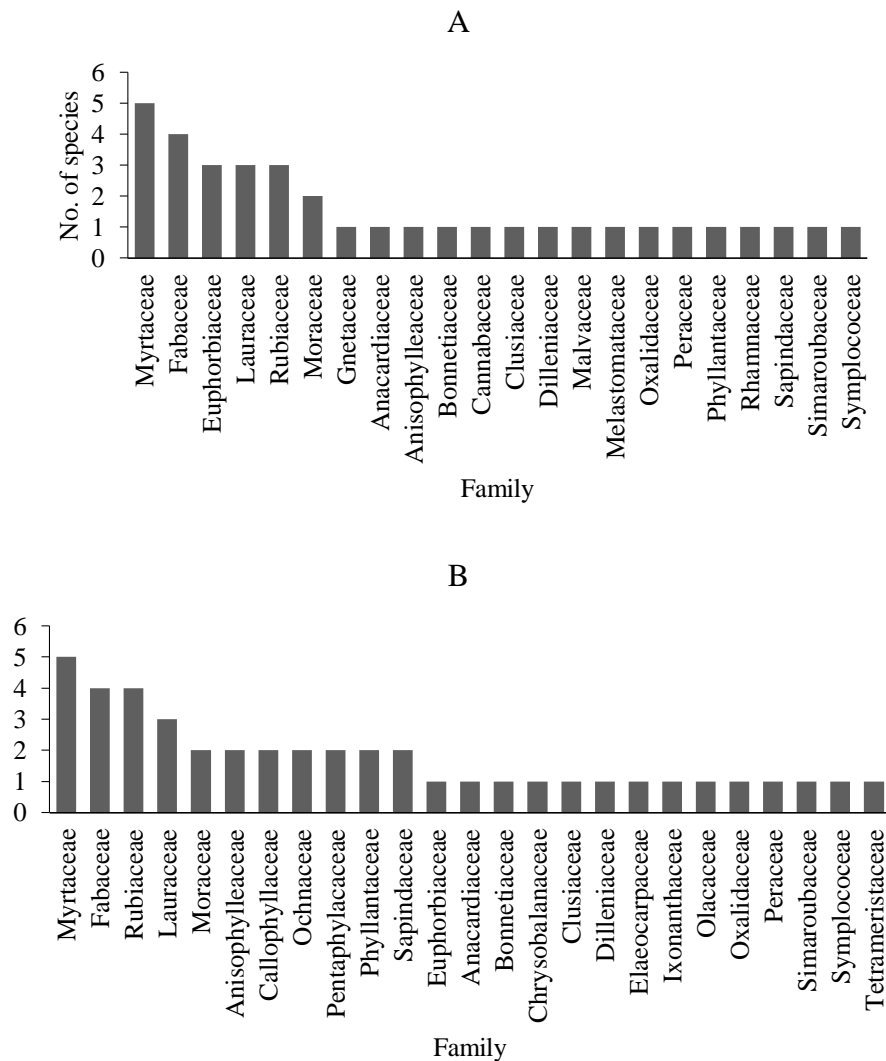


Figure 4. Abundance of species for each family in (A) once-burnt plots and (B) control plots, arranged from most to least abundant

4. Discussion

4.1 Effects of forest fires on soil parameters and canopy structure

Soils in the Once-burnt and Twice-burnt plots were less acidic, with higher GWC and total N concentrations, compared to the unburnt Control plots. The fire intensity, duration and frequency of fire regimes can alter many soil attributes such as the pH, N availability, and organic matter due to an increase in plant-available nutrients, the removal of organic matter or microbial death,^{15,36}

which may not be favourable to post-fire recolonisation by native species. The significantly higher total N concentrations recorded in the Twice-burnt plots may also be due to the high density of seedlings of invasive *Acacia* species seen in these plots (Tuah, *personal observation*), which can increase the soil N concentration due to the ability of these leguminous plants to fix nitrogen directly from the atmosphere.³⁷⁻³⁹

Repeated fire events have also resulted in a significant increase in canopy openness in the

Twice-burnt plots. Burning eliminates canopy cover, resulting in increased light exposure and empty space that allows pioneer species, as well as invasive species such as *A. mangium*, to colonize and grow.^{8,40,41} Our findings here are

consistent with studies that have shown significant post-fire increases in canopy openness as well as other measures of canopy structure, such as the leaf area index.^{22,42}

Table 2. Variation in species richness and diversity indices (Shannon Index (H'), Evenness (J) and Inverse Simpson's Index (1/D)) of once burnt plots and control plots, expressed as mean values (\pm SE). Plots 4, 5 and 6 (twice burnt plots) were excluded from analyses due to lack of species identification data. Different letters within a column indicate significant differences at $P < 0.05$ as obtained from Tukey's HSD after one-way analysis of variance (ANOVA).

Plot No.	Burning frequency	Species richness	Shannon Index (H')	Evenness (J)	Inverse Simpson's Index (1/D)
1	Once	5.00 \pm 0.03 ^a	0.07 \pm 0.04 ^a	0.22 \pm 0.09	0.33 \pm 0.02 ^a
2	Once	13.00 \pm 0.05 ^b	0.33 \pm 0.01 ^b	0.62 \pm 0.05	0.53 \pm 0.01 ^b
3	Once	26.00 \pm 0.05 ^c	0.47 \pm 0.02 ^c	0.78 \pm 0.02	0.74 \pm 0.04 ^c
7	Control	31.00 \pm 0.06 ^c	0.50 \pm 0.02 ^c	0.85 \pm 0.03	0.87 \pm 0.05 ^{cd}
8	Control	29.00 \pm 0.02 ^c	0.51 \pm 0.01 ^c	0.90 \pm 0.02	0.93 \pm 0.03 ^d

Table 3. The checklist of tree species recorded in three Once-burnt plots and two Control plots.
(* Bornean endemic, ● native Kerangas species).

Plants	Family	Species
GYMNOSPERM	GNETACEAE	<i>Gnetum latifolium</i> Blume s.l.
ANGIOSPERMS	ANACARDIACEAE	<i>Buchanania arborescens</i> (Blume) Blume●
	ANISOPHYLLEACEAE	<i>Anisophyllea disticha</i> (Jack) Baill.● <i>Combretocarpus rotundatus</i> (Miq.) Danser
	BONNETIACEAE	<i>Ploiarium alternifolium</i> (Vahl) Melchior●
	CALLOPHYLLACEAE	<i>Calophyllum obliquenervium</i> Merr.● <i>Calophyllum</i> sp. 1
	CANNABACEAE	<i>Trema cannabina</i> Lour.
	CHRYSOBALANACEAE	<i>Parastemon urophyllus</i> (A.DC.) A.DC.●
	CLUSIACEAE	<i>Garcinia miquelli</i> Pierre <i>Garcinia</i> sp. 1
	DILLENACEAE	<i>Dillenia suffruticosa</i> (Griff.) Martelli●
	ELAEOCARPACEAE	<i>Elaeocarpus mastersii</i> King●
	EUPHORBIACEAE	<i>Endospermum diadenum</i> (Miq.) Airy Shaw <i>Macaranga conifera</i> (Zoll.) Muell.Arg <i>Macaranga gigantea</i> (Rchb.f. & Zoll.) Muell.Arg. <i>Pimelodendron griffithianum</i> (Muell.Arg.) Benth
	FABACEAE	<i>Dialium indum</i> L. <i>Acacia mangium</i> Willd. <i>Archidendron kunstleri</i> (Prain) Kosterm <i>Albizia</i> sp. 1 <i>Derris trifoliata</i> (Lour.) Taub. <i>Ormosia bancana</i> (Miq.) Merr.●

IXONANTHACEAE	<i>Ixonanthes reticulata</i> Jack●
LAURACEAE	<i>Actinodaphne borneensis</i> Meisn.* <i>Cinnamomum politum</i> Miq.*● <i>Dehaasia</i> sp. 1 <i>Litsea elliptica</i> Blume <i>Litsea rubicunda</i> Kosterm
MALVACEAE	<i>Commersonia bartramia</i> (L.) Merr. – (Malesia)
MELASTOMATACEAE	<i>Melastoma beccarianum</i> Cogn. *●
MORACEAE	<i>Artocarpus kemando</i> Miq. <i>Artocarpus nitidus</i> Trecul <i>Ficus spathulifolia</i> Corner● <i>Ficus sundaica</i> Blume●
MYRTACEAE	<i>Rhodomyrtus tomentosa</i> (Aiton) Hassk.● <i>Syzygium acuminatissimum</i> (Blume) DC. <i>Syzygium alcinae</i> (Merr.) Merr. & L.M. Perry <i>Syzygium areaghii</i> <i>Syzygium incarnatum</i> (Elmer) Merr. & L.M. Perry● <i>Syzygium jambos</i> (L.) Alston <i>Syzygium megalophyllum</i> Merr. & L.M. Perry <i>Syzygium</i> sp. <i>indet</i>
OCHNACEAE	<i>Brackenridgea palustris</i> Bartell <i>Brackenridgea palustris</i> Bartell subsp. <i>palustris</i>
OLACACEAE	<i>Strombosia ceylanica</i> Gardner
OXALIDACEAE	<i>Sarcotheca glauca</i> Hallier f.
PENTAPHYLACACEAE	<i>Adinandra dumosa</i> Jack● <i>Ternstroemia aneura</i> Miq.*●
PERACEAE	<i>Chaetocarpus castanocarpus</i> (Roxb.) Thwaites
PHYLLANTACEAE	<i>Glochidion kerangae</i> Airy Shaw*● <i>Glochidion rubrum</i> Blume
RHAMNACEAE	<i>Alphitonia philippinensis</i> Braid
RUBIACEAE	<i>Canthium</i> sp. 1 <i>Gaertnera vaginans</i> (DC.) (DC.) Merr. <i>Nauclea subdita</i> (Korth.) Steud. <i>Timonius flavescens</i> (Jack) Baker● <i>Timonius mutabilis</i> (Korth.) Walp <i>Psydrax</i> sp. 1
SAPINDACEAE	<i>Guioa bijuga</i> (Hiern) Radlk.● <i>Nephelium maingayi</i> Hiern
SIMAROUBACEAE	<i>Eurycoma longifolia</i> Jack
SYMPLOCOCEAE	<i>Symplocos polyandra</i> Brand●
TETRAMERISTACEAE	<i>Tetramerista glabra</i> Miq.

4.2 Effects of fires on forest structure

Live trees in our Control plots were less abundant but had larger stem sizes than those in the Once-burnt plots. The absence of fires in the Control plots have likely enabled live trees to allocate

resources for stem growth over population growth to increase their resilience to disturbance.^{43,44} It is highly unusual to find no dead trees within a plot, with for example Velazquez *et al.*⁴⁵ reporting sapling mortalities

between ~1 and ~7% per annum in BCI for shade-tolerant and light-demanding species. However, our observation of no dead trees in the Control plots only captured a snapshot in time during the five-month study period in October 2013 to February 2014, and it is likely that mortality would be recorded in the Control plots if they were re-censused. Tree mortality rates in *Kerangas* forests have not been studied, although sapling mortality at another *Kerangas* forest site in Brunei was observed to increase during a severe drought in 1992.⁶⁵

In the Once-burnt plots, live tree diameters were smaller but more abundant, possibly a sign of the mortality of bigger trees in these plots from the previous 2009 fire event. These smaller, younger trees now found in the Once-burnt plots are also indicative of natural regeneration from the 2009 fire event, either from seed banks or via seed dispersal from neighbouring communities, that in time may repopulate the burnt areas.^{28,46} At our study sites, twice-burning incidents eradicated smaller trees, while trees with larger diameters survived. In these Twice-burnt plots, we suggest that regeneration likely occurred after the initial fire occurrence in 2009, but the second fire event in 2013 then eliminated a majority of the newly regenerating trees that had not reached the optimal maturity level to withstand fires. A similar reduction of small-mean-diameter trees was documented in repeated burnt areas in lowland dipterocarp rain forests in East Kalimantan, Indonesia.⁴⁷

4.3 The effects of fires on native tree diversity

Our study presents preliminary evidence that different fire frequencies significantly modify the native tree species richness and diversity of coastal *Kerangas* forests in Brunei Darussalam. Our findings showed lower species richness in the Once-burnt plots ($n = 36$ species) compared to the Control plots ($n = 44$ species). Furthermore, in the Once-burnt plots, native *Kerangas* tree species have been replaced mainly by pioneers, such as *Rhodymyrtus tomentosa*, *Timonius flavescens*, *Dillenia suffruticosa*, *Commersonia bartramia* and *Alphitonia philippensis* that are commonly found in degraded *Kerangas* and secondary forests.⁴⁸ For example,

Rhodymyrtus tomentosa grows on degraded acidic soils^{49,50} and *Dillenia suffruticosa* is a shrub commonly existing in disturbed, open areas.⁵¹

Several native species (*Actinodaphne borneensis*, *Anisophyllea disticha*, *Buchanania aborescens*, *Chaetocarpus castanocarpus*, *D. suffruticosa*, *Eurycoma longifolia*, *Glochidion kerangae*, *Memphelium maingayi*, *Ploiarium alternifolium*, *Sarcotheca glauca*, *Symplocos polyandra*, *Syzygium areaghii* and *Timonius flavescens*) were recorded in both the Once-burnt and Control plots, indicating that these species may be habitat generalists⁴⁸ and are potentially able to inhabit and utilise the resources of various habitats, regardless of fire occurrences. However, several species such as *Ormosia bancana*, *Derris trifoliata* and *Brackenridgea palustris* were exclusively found in the Control plots. These species are known to be habitat specialists in intact *Kerangas*, mangrove swamps, lowland forest and white sand areas,^{48,52} and may be unable to survive fire events or cannot co-exist with invasive *Acacia* species.

Interestingly, the species richness and diversity in Once-burnt Plot 3 was as high as in the Control plots. The most dominant native species in Plot 3 was *D. suffruticosa* ($n = 40$), a known pioneer species that is abundantly found in open habitats and secondary forests in Brunei. It is possible that the 2009 fire event did not affect this plot as intensely as Plots 1 and 2, thus allowing for the regeneration of native *Kerangas* species from seed banks.^{28,53} The presence of native *Kerangas* species such as *Anisophyllea disticha*, *Buchanania arborescens*, *Glochidion kerangae*, *Ploiarium alternifolium* and *Symplocos polyandra* in Plot 3 supports this. Woods⁵⁴ also found that certain native species can tolerate low-intensity fires in tropical forests in Sabah, Malaysia, and were able to re-establish after low-intensity fire events.

4.4 Acacia invasion into coastal Kerangas forests

A crucial finding of our study was that the tree community composition of the Once-burnt plots was primarily dominated by *A. mangium*, based

on the relatively high proportion of stems (54.5%) recorded in these plots. In an earlier study of *Acacia* invasion along the Tutong-Muara Highway in Brunei Darussalam, Kahar⁵⁵ also recorded a high abundance of *A. mangium* in once-burnt plots. The seed germination of *Acacia* is known to be enhanced by fires,^{46,56} and these fire regimes appear to have facilitated the invasion of *Acacia* into our burnt plots. It is possible that *A. mangium* may have invaded these burnt sites via seeds from the original plantations, located in the nearby Berakas Forest Reserve (BFR; 4°59'4.83"N 114°55'19.28"E) and the coastal highway,²⁸ both of which are close to our study areas. We recorded the highest abundance of *A. mangium* in Once-burnt Plot 1, which is located closest to BFR and the coastal highway (approximately 2 km away from the BFR entrance). In contrast, Once-burnt Plots 2 and 3 are located within the UBD campus area approximately 4 km away from the BFR entrance. The greater distance from the original seed source may lower the invasion pressure for the more inland plots, as is seen by the dominance of native species over *A. mangium* in these sites (Plot 2 = *Timonius flavescens*, Plot 3 = *Dillenia suffruticosa*).

A plant species is considered to be invasive if it has spread and naturalized more than 100 m from the original planting site in a period of less than 50 years.⁵⁷ The spread of *A. mangium* documented in our study into sites more than 2 km away from the original planting site is consistent with designating this exotic species as an invader of the coastal *Kerangas* forests in Brunei Darussalam. We suggest that fire events in these coastal *Kerangas* areas have facilitated the spread of *Acacia*, in particular *A. mangium*, by decreasing the competition by native species²⁸ and inducing favorable microhabitat conditions such as an increased light availability and suitable soil conditions. Roadsides provide more nutrient-rich, humid and much-illuminated habitats than interior forests.⁵⁸ The seed germination of *Acacia* species is also known to be stimulated by fires.^{59,60} Thus, a combination of favorable microhabitat conditions, fire occurrence and close proximity to seed sources

likely resulted in the high invasion pressure of *A. mangium* seeds in our study sites.

Despite the Control plots being mostly dominated by native *Kerangas* species, three *A. mangium* individuals were recorded in these plots. This may indicate that *A. mangium* invasion, albeit at a lower intensity, is still possible, despite the absence of fires in these intact *Kerangas* forests over the decade from 2003 to 2013. We suggest that some *A. mangium* seeds dispersed to these Control plots were able to germinate despite the absence of fire cues to break their seed dormancy. The fast germination of *A. mangium* seeds in the absence of fires has also been recorded when their seeds were treated with temperatures as low as only 20°C.⁵⁹⁻⁶¹

4.5 Implications for the conservation of Brunei's coastal *Kerangas* forests

Our results demonstrate the negative impacts of fire on native tree flora diversity, soil properties and canopy openness in coastal *Kerangas* forests, and furthermore provide evidence that fire events have facilitated the establishment of invasive *A. mangium*. The latter finding is particularly crucial, as increasing frequencies of fire events in Brunei³⁰ could further facilitate the spread of this invasive species. Although intact tropical forests are thought to be resistant to invasion by exotic species,^{62,63} *Acacia* appears to have a competitive advantage over native *Kerangas* species when trying to establish in fragmented forests that are surrounded by high and ever-present *Acacia* seed sources. There is intense propagule pressure from established *Acacia* species currently thriving in the matrix of invaded and disturbed *Kerangas* forests in the coastal areas of Brunei Darussalam,⁶⁴ resulting in seed dispersal into intact forests. Fuentes-Ramirez *et al.*⁴¹ have similarly recorded the invasion of *Acacia dealbata* into intact Mediterranean deciduous forest areas in South-Central Chile, and conclude that its high competitive ability and allelopathy mechanisms enable *A. dealbata* to displace native species.

Although our study sites were urbanised with a large extent of forest fragmentation, several

native *Kerangas* species of conservation importance (e.g. *Combretocarpus rotundatus*) and Bornean endemics (*Actinodaphne borneensis*, *Cinnamomum politum*, *Glochidion kerangae* and *Ternstroemia aneura*) were found in the Control plots. This finding underlines the conservation value of these increasingly rare tropical coastal *Kerangas* forests, and the urgent need to protect these forests from further fire events and the subsequent post-fire spread of invasive *Acacia* species.

5. Conclusions

Our study recorded significantly smaller stem diameters in burnt heath forests, while tree species richness and diversity were significantly lower in the once-burnt plots than in the unburnt plots. The tree community compositions of the once-burnt plots were dominated by invasive *Acacia mangium*. The soil pH, gravimetric water content and total nitrogen and phosphorus concentrations, and canopy openness were significantly higher in the burnt plots, which further highlights the negative impacts of fire on the native tree diversity, soil properties and canopy openness in these coastal *Kerangas* forests. If left unmanaged, increasing fire events arising from more frequent droughts and dry periods will further lower the native tree species richness and diversity of the coastal *Kerangas* forests in Brunei Darussalam.

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