Contrasting patterns of woody seedlings diversity, abundance and community composition in Bornean heath and peat swamp forests

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SUMMARY

The diverse lowland forests of Southeast Asia and Borneo are globally recognised biodiversity hotspots containing rare and endangered species and high levels of plant endemism. Heath and peat swamp forests are Bornean lowland forest types with distinctive plant communities that primarily correspond to a soil water gradient from dryland heath to waterlogged peat swamps. Although tree diversity of Bornean heath and peat swamp forests is well described, little is known of their woody seedling communities. This study investigated diversity, abundance and community composition of woody seedlings in mixed peat-swamp (MSF), heath (HF), *kerapah* (KF) and *Shorea albida* peat-swamp (SAP) forests in Brunei Darussalam, Northwest Borneo. Within twenty-two 3 × 3 m plots in these forest types, seedlings of 50 ≤ cm height ≤ 100 were censused and taxonomically identified, and measurements of selected environmental and soil properties were obtained. In total, 84 species of woody seedlings from 71 genera were recorded, with Myrtaceae most abundant in MSF, KF and SAP, while Dipterocarpaceae and Sapotaceae were most abundant in HF. Mean seedling abundance and diversity indices did not differ between forest types, but mean species richness was significantly higher in MSF than SAP. Woody seedling community composition differed between forest types and was influenced by soil properties, with MSF seedling communities influenced by total K concentration and soil pH, while SAP was influenced by soil gravimetric water content and total P concentration. These findings highlight the need for increased research on seedling ecology in tropical heath and peat swamp forest formations to further elucidate mechanisms underlying species diversity in these forests, and to guide programmes for their conservation, sustainable management and reforestation.

KEY WORDS: Brunei Darussalam, peatland, soil water gradient, species diversity, woody seedlings

INTRODUCTION

The lowland forests of Southeast Asia contain diverse plant communities that are threatened by deforestation (Estoque *et al.* 2019). The island of Borneo, in particular, is a biodiversity hotspot containing rare and endangered species and high levels of plant endemism (Neo *et al.* 2020). Heath and peat swamp forests are two of the most important and distinctive lowland forest types in Borneo. These forest formations differ in their plant community composition due to variations in environmental and soil properties (Anderson 1963, Ashton *et al*. 2003), particularly along hydrological and nutrient gradients (Wong *et al.* 2015, Jaafar *et al*. 2016). Heath forests, locally known as *kerangas* forests, occur in Borneo on nutrient-poor, acidic, well-drained sandy soils and contain a thin layer of surface peat (Brunig 1974, Corlett & Primack 2011, MacKinnon *et al.* 2013). In contrast, peat swamp forests exist on peat deposits, comprising partially decomposed organic matter that can reach depths of over 10 m in places, in a highly acidic, waterlogged environment (Page *et al*. 2006, Posa *et al*. 2011, Dommain *et al*. 2016). A sub-type of *kerangas* forest occurs where heath soils experience poor soil drainage due to an impermeable hardpan, resulting in permanently waterlogged *kerapah* forests (Brunig 1990, Proctor 1999).

Floristically, heath and peat swamp forest formations in Borneo have lower tree species diversity than lowland mixed dipterocarp forests, although they contain more endemic species (Davies & Becker 1996, Wong *et al.* 2015). *Kerangas* forests are often characterised by the tropical conifers, *Agathis borneensis* and *Gymnostoma nobile* (Brunig 1974, Wong *et al*. 2015), and Myrtaceae is often the most species-rich family (Davies & Becker 1996, Din *et al*. 2015, Tuah *et al.* 2020). *Kerapah* forests are floristically related to both peat swamp and *kerangas* forests, although are typically less diverse than *kerangas* forests and more diverse than peat swamp forests (Anderson 1963). *Madhuca curtisii* is usually abundant in *kerapah* forests, and Myrtaceae is similarly the most species-rich family (Tuah 2017, Jinnidi 2019). For peat swamp forests in Sarawak and Brunei, six phasic communities have been described (Anderson 1963, Kobayashi 2016), from the mixed peat-swamp forest in the outer first phasic community, to the *Shorea albida*-dominated inner phasic communities (Phasic Communities 2 to 4), the *Tristania-Parastemon-Palaquium* association in Phasic Community 5, and finally the central Phasic Community 6 on the peat swamp dome that is dominated by *Combretocarpus rotundatus* and resembles a stunted heath forest. These phasic communities contrast with peat swamp forests in Kalimantan, Southern Borneo where a different sequence of vegetation types, from riverine forest to mixed-swamp, low-pole and finally (at least in Sebangau) to the tall-interior forest, have been observed (Page *et al*. 1999).

Although the diversity of tropical tree communities in Bornean heath and peat swamp forests has been studied (e.g. Anderson 1963, Davies & Becker 1996, Gunawan *et al*. 2012, Din *et al*. 2015, Maimunah *et al*. 2019), investigations of woody seedling communities and the influence of environmental and soil properties on seedling communities in these unique forests are still lacking. Within Borneo, seedling studies have been focused on lowland mixed dipterocarp forests (Webb & Peart 1999, 2000, Delissio *et al.* 2002, Tito De Morais *et al.* 2020) and secondary forests (Bodegom *et al.* 1999), although Nishimura & Suzuki (2001) compared allometric relationships for seedlings between heath and peat swamp forests in Central Kalimantan, while Din *et al*. (2018) studied seedling abundance and growth performance of two peat swamp dipterocarp species, *Dryobalanops rappa* in Anduki and *Shorea albida* in Badas, Brunei Darussalam. Various abiotic factors, such as water and light availability, litter depth and soil properties, are known to influence seedling communities within tropical forests (Molofsky & Augspurger 1992, Benitez-Malvido & Koassman-Ferraz 1999, Metz 2012, Kupers *et al.* 2018, Xia *et al.* 2019). Seedlings are important in the natural regeneration of a forest community and can determine overall tree diversity (Deb & Sundriyal 2008, Uriarte & Chazdon 2016, Martini *et al*. 2020), thus increased understanding of woody seedling diversity and community compositions in these heath and peat swamp forest formations is crucial.

Heath and peat swamp forest types are of high conservation value but are increasingly facing anthropogenic threats (Becker 2006, Posa *et al.* 2011, Page & Hooijer 2016). Within Brunei Darussalam, Northwest Borneo, heath and peat swamp forests cover approximately 3,000 ha and 90,000 ha, respectively (Wong *et al.* 2015). Brunei's peat swamp forests (PSFs) are the most pristine in Borneo, with 66.7 % of their peatlands still in pristine conditions (Miettinen *et al*. 2016). However, these forests are increasingly experiencing disturbances such as fire, invasive alien species and deforestation (Din *et al*. 2015, Jambul *et al.* 2020, Lupascu *et al.* 2020, Tuah *et al*. 2020) and thus are in urgent need of further study. Here, we investigated patterns of diversity and abundance and community composition of woody seedlings in two heath forest types in Brunei Darussalam: i.e. heath (*kerangas*) forest (HF) and waterlogged heath (*kerapah*) forest (KF); and two peat swamp forest types, i.e. mixed peat-swamp forest (MSF) and *Shorea albida* peat-swamp forest (SAP). Our study aims were to describe differences in woody seedling diversity, abundance and community composition between these contrasting forest types, and to determine whether any of these differences were linked to variation in environmental and soil properties.

METHODS

Study site

The study was conducted in selected sites representing four different forest types: mixed peat-swamp forest (MSF) in Compartment 5 of the Andulau Forest Reserve within the Labi area (04° 38'' N, 114° 30'' E), and heath (HF; 4° 34'' N, 114° 25'' E), *kerapah* (KF; 4° 35'' N, 114° 26'' E), and *Shorea albida* peat-swamp forests (SAP; 04° 36'' N, 114° 26'' E) in the Lumut area, Brunei Darussalam, Northwest Borneo. The Andulau Forest Reserve is mainly comprised of mixed dipterocarp forests (Sukri *et al*. 2012) with pockets of heath and mixed peat-swamp forests (Anderson & Marsden 1984). The MSF site in Labi contained Phasic Community 1 of the PSF dome (Anderson 1963) and is located approximately 13.4 km away from the HF, KF and SAP sites in Lumut (Tuah 2017) (Figure 1). The SAP site contained Phasic Community 4 of the PSF dome (Anderson 1963). Sites were selected based on previous fieldwork experience and advice from Brunei Forestry Department and Wetlands International Brunei.

A total of 22 seedling plots of size 3 × 3 m were set up: six plots each in HF, KF and SAP sites and four plots in MSF (Figure 1). All plots were located within intact forests. Distances between plots within the same forest type were approximately 50 m. Previous seedling studies used transects (e.g. Delissio

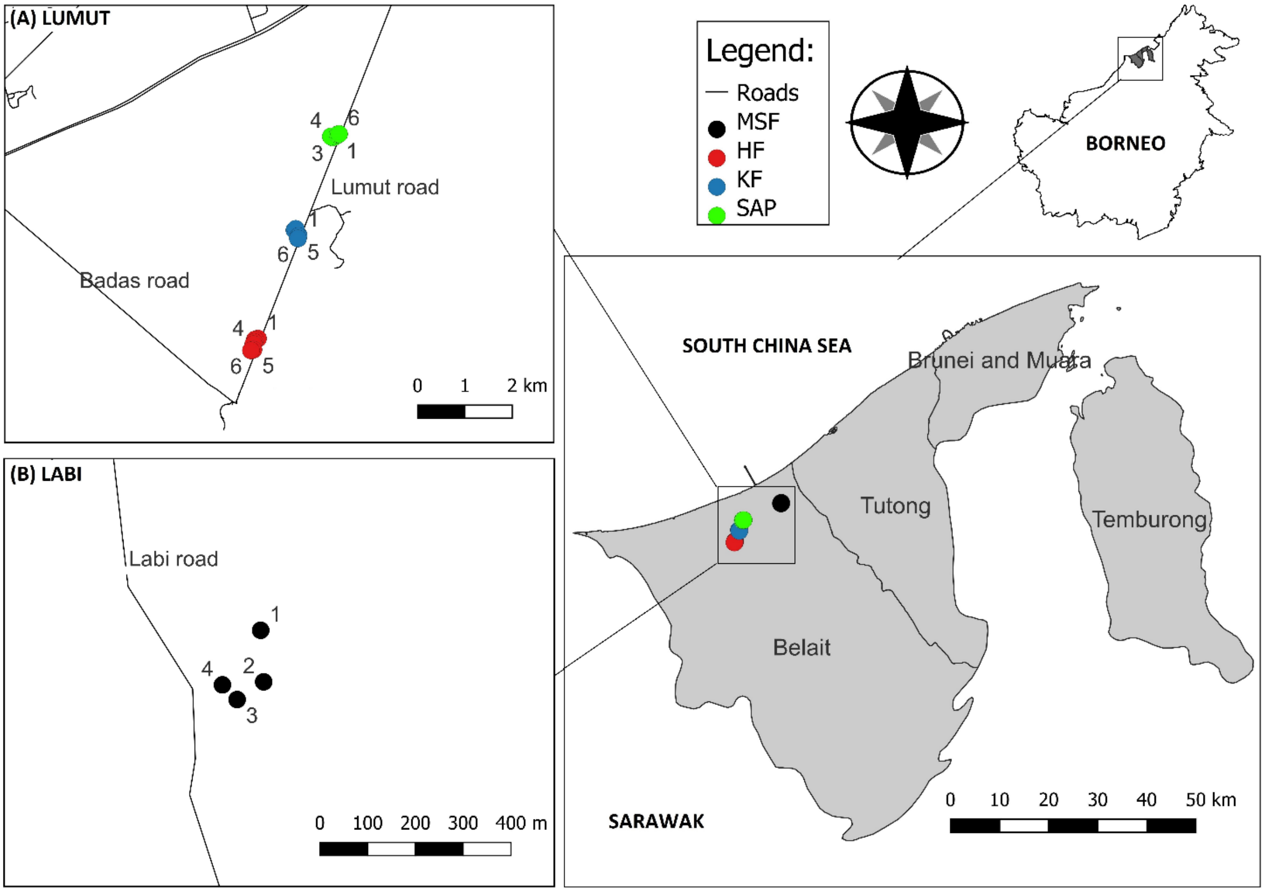

Figure 1. Locations of the study sites consisting of: (a) six 3 m × 3 m plots in heath forest (HF 1-6), *kerapah* forest (KF 1-6) and *Shorea albida* peat-swamp forest (SAP 1-6) in Lumut, and (b) four 3 m × 3 m plots in mixed peat-swamp forest (MSF 1-4) in Labi in the Belait District, Brunei Darussalam, Northwest Borneo. Distances between plots within the same forest type were approximately 50 m. The MSF site in Labi is located approximately 13.4 km away from the HF, KF and SAP sites in Lumut.

et al. 2002) or plots of varying sizes, ranging from smaller plots of 1 × 1 m (Martini *et al*. 2020), 2 × 2 m (Webb & Peart 1999) and 5 × 5 m (Din *et al*. 2018) to larger plots of 1 ha (Nishimura & Suzuki 2001). We therefore chose a smaller plot size of 3 × 3 m to allow adequate replication of plots within forest types. At the Lumut site, HF, KF and SAP plots were set up more than 100 m away from the Lumut road, while at the Labi site, MSF plots were set up at least 50 m away from forest edges, to minimise edge effects. Only four plots were set up in MSF because the MSF habitat in Labi occurred within a small patch (less than 0.5 ha in size; Brunei Forestry Department, personal communication, 2019) that was mainly surrounded by mixed dipterocarp forest. Additionally, MSF plots were set up in Labi as there were no MSFs found in the Lumut area (Tuah 2017) where the HF, KF and SAP plots were set up (Anderson & Marsden 1984). Peat depths at the MSF and SAP plots were not measured but can be classified as shallow peat (< 50 cm depth). MSF plots in Labi were not drained, while SAP plots in Lumut were located approximately 120 m away from a canal of about 1.5 m depth, in which canal blocks were constructed in 2014 by Brunei Liquefied Natural Gas Sdn Bhd to raise the water levels in the area (Wetlands International Brunei, personal communication, 2015).

The climate of Brunei Darussalam is relatively aseasonal, and the average minimum and maximum temperatures during the study period from March 2019 to April 2020 were 35.4˚C and 24.3˚C, respectively. Mean relative humidity was 87 % at the Sungai Liang Agricultural station located approximately 15.4 km and 7.8 km away from Lumut and Labi, respectively (Department of Agriculture and Agrifood, unpublished data). Total annual rainfall for Brunei Darussalam recorded from March 2019 to April 2020 was 3049.2 mm (Brunei Darussalam Meteorological Department, unpublished data), which was higher than the average annual rainfall for Brunei Darussalam from 1984 to 2013 (2976 mm; Pg Ali Hasan *et al.* 2016).

Seedling censuses and measurements of environmental and soil properties

Within the seedling plots, all seedlings 50 ≤ cm height ≤ 100 were tagged. This seedling height range was decided based on previous studies focusing on seedlings of height > 50 cm (Steven 1994, Metz *et al*. 2008) and seedlings of 20 ≤ cm height ≤ 100 (Nicotra 1999). Field identification of the censused seedlings was conducted with assistance from staff of the Brunei National Herbarium (BRUN). Voucher specimens were collected, and taxonomic identification further confirmed by cross-checking against BRUN records.

Air and soil temperatures, and relative humidity were measured using an infrared thermometer (Centre 350 series, Centre Technology Corp, Taiwan) and a whirling hygrometer (Elcometer 116A Whirling Hygrometer, Elcometer Ltd., UK) respectively. To calculate percentage canopy openness, a convex spherical densiometer (Convex Model A, Forestry Suppliers Spherical Crown Densiometer, USA) was used. Litter depth was determined by inserting a metre rule on top of the soil surface up to the top surface of the leaf litter (Dent *et al.* 2006). For consistency across the four forest types, we defined leaf litter as the surface litter (up to 10 cm below the surface) which comprised of visibly undecomposed leaf litter lying on top of the soil or peat surface (Dent *et al*. 2006, Lampela *et al.* 2014). Measurements of surface litter depth were taken at five points in each plot (i.e. at every plot corner and in the plot centre) and were then averaged per plot.

Soil samples were collected using a 10 cm diameter soil auger at a depth of 0–15 cm from each plot per forest type. Within each plot, soil cores were sampled from the same five points as measurements of litter depth, and the five cores were combined together and mixed thoroughly to produce a bulked soil sample for each 3 × 3 m plot (i.e., *n* = 22 bulked soil samples). Fresh soil samples were used to measure soil pH and gravimetric water content (GWC) in the laboratory on the day of sample collection, following Allen *et al*. (1989). The remaining fresh soil samples were left to air-dry at room temperature (approximately 25°C) for 3 to 4 weeks. The air-dried soil samples were then separately ground into fine powder using a ball mill (Mixer Mill MM400, Retch, Germany), before being stored individually in sealed zip-lock bags for soil nutrient analyses. Soil nutrient analysis was conducted to determine the total concentrations of N and P using the Kjeldahl method (Allen *et al*. 1989), while total Ca, Mg and K concentrations were determined using a Flame Atomic Absorption Spectrophotometer (AAS, Thermo Scientific iCE 3300, Sydney, Australia), following Jaafar *et al.* (2016).

Statistical analysis

All statistical analyses were conducted using R version 3.6.3 (R Core Team 2020). Mean seedling abundance and mean species richness were calculated for each of the 22 plots by dividing total abundance of seedlings or total number of species for that plot, respectively, by number of plots per forest type (i.e. *n* = 4 plots for MSF, *n* = 6 plots for HF, KF and SAP). Three diversity indices were determined for each plot: Shannon’s index (H’), Inverse Simpson’s index (Ds) and Evenness (J’) using the R vegan package version 2.5-7 (Oksanen *et al.* 2020). Differences in mean seedling abundance, mean species richness, mean diversity indices and environmental and soil properties between the four forest types were determined using separate one-way analysis of variance (ANOVA) and post-hoc comparisons conducted using Tukey’s HSD tests. Assumptions of normality and homogeneity of variances were tested via the Residuals versus Fitted plot and QQ-plot functions in R version 3.6.3 and were not violated. Non-metric multidimensional scaling (NMDS) ordination was conducted using presence-absence data and Jaccard index (Legendre & Legendre 2012) to explore variations in seedling species communities within the four forest types in relation to environmental and soil properties, using the R vegan package version 2.5-7 (Oksanen *et al.* 2020). To determine floristic similarity between forest types, we conducted PERMANOVA (Anderson 2001) using the *adonis* function in the R vegan package version 2.5-7 for presence-absence data, following Draper *et al.* (2019). The function *pairwise.adonis* was used to conduct pairwise comparisons following PERMANOVA (Martinez Arbizu 2020).

RESULTS

Differences in environmental and soil properties between forest types

Comparisons of the environmental and soil properties between the different forest types are provided in Table 1. Mean relative humidity differed significantly between all forest types, except between KF and SAP plots. Mean percentage canopy openness was significantly lower for MSF plots

Table 1. Differences in mean values of environmental and soil properties in mixed swamp forest (MSF), heath forest (HF), *kerapah* forest (KF) and *Shorea albida* peat-swamp forest (SAP) (n = 6 plots in HF, KF and SAP, and n = 4 plots in MSF). Values are means ± SE, calculated over the total number of plots per forest type. Same letters along a row represent no significant differences between forest types, while different letters represent significant difference at $\alpha = 0.05$ as analyzed using one-way ANOVA and Tukey's HSD test.

	Forest type			
	MSF	HF	KF	SAP
Air temperature (°C)	26.8 ± 0.17^{a}	27.4 ± 0.26^{a}	26.9 ± 0.18^{a}	26.8 ± 0.12^{a}
Humidity (%)	88.73 ± 0.54^{b}	87.48 ± 0.73^{a}	90.97 ± 0.02^{c}	90.53 ± 0.36^{c}
Canopy openness (%)	4.98 ± 0.51^{a}	11.05 ± 0.67^{b}	10.33 ± 0.59^{b}	9.69 ± 0.36^{b}
Litter depth (cm)	5.33 ± 0.2^{c}	2.84 ± 0.13^{a}	4.8 ± 0.18^{b}	4.15 ± 0.22^{b}
Soil temperature (°C)	26.3 ± 0.16^{a}	26.2 ± 0.34^{a}	26.4 ± 0.18^{a}	26.5 ± 0.16^{a}
Soil pH	4.50 ± 0.14^{c}	3.25 ± 0.03^{b}	3.21 ± 0.02^{ab}	3.04 ± 0.02^{a}
Soil GWC (%)	39.51 ± 1.45^{a}	53.7 ± 2.62^{b}	65.88 ± 1.32^{c}	78.24 ± 0.63^{d}
Total N (mg g^{-1})	2.32 ± 0.51^{a}	4.65 ± 0.81^{abc}	6.92 ± 0.78^{c}	5.33 ± 0.16^{b}
Total P (mg g^{-1})	0.13 ± 0.02^{a}	0.21 ± 0.05^{a}	0.22 ± 0.03^{a}	0.24 ± 0.04^{a}
Total Ca (mg g^{-1})	0.03 ± 0.009^{a}	0.36 ± 0.06^{b}	0.41 ± 0.05^{b}	1.91 ± 1.31^{b}
Total Mg (mg g^{-1})	0.13 ± 0.02^{a}	0.54 ± 0.19^{ab}	0.71 ± 0.09^{b}	0.34 ± 0.04^{ab}
Total K (mg g^{-1})	5.17 ± 1.16^{b}	3.04 ± 1.02^{ab}	3.71 ± 0.98^{ab}	1.21 ± 0.38^{a}

compared to plots in the other three forest types, but did not differ significantly between KF, HF and SAP. MSF plots recorded significantly highest mean litter depth while HF recorded significantly lowest mean litter depth, but no significant differences were recorded between KF and SAP plots. Mean air temperature did not significantly differ between forest types.

For soil properties, MSF soils were least acidic but recorded significantly higher total K concentrations and significantly lower soil GWC, total N, Ca and Mg concentrations. SAP plots recorded significantly highest soil GWC but significantly lowest soil pH and total K concentration, while total N and Mg concentrations were significantly highest in KF. No significant differences were detected between forest types for soil temperature and total P concentration.

Differences in abundance, species richness and diversity of woody seedlings between forest types

A total of 461 individual seedlings of 50 ≤ cm height ≤ 100 were censused at the HF, KF and SAP plots in Lumut (n = 378 seedlings), and in MSF plots in Labi (n = 83 seedlings). Mean seedling abundance per area was highest in HF than KF, MSF and SAP, although these differences were not significant (Table 2). Mean species richness per area was significantly higher in MSF than SAP, but no significant differences were detected between other forest types (Table 2). Similarly, there were no significant differences in mean evenness, Shannon's index and Inverse Simpson's index between the four forest types.

A total of 44 families of woody seedlings were recorded across the four forest types, with the most abundant families comprising Myrtaceae (n = 124 seedlings), Dipterocarpaceae (n = 47 seedlings), Rubiaceae (n = 45 seedlings) and Sapotaceae (n = 39 seedlings, Table 3). A total of 84 species of woody seedlings from 71 genera were recorded (Table A1 in the Appendix) and the most species-rich family was Rubiaceae (n = 6 species), followed by Annonaceae, Lauraceae and Dipterocarpaceae (n = 5 species each) and Anacardiaceae, Elaeocarpaceae, Euphorbiaceae and Myrtaceae (n = 4 species each, Table A1). Woody seedlings from three families, Anacardiaceae, Myrtaceae and Rubiaceae, were present in all forest types. Despite comprising only four plots, the MSF plots recorded the highest number of families (22 families), while SAP plots (n = 6 plots) recorded the lowest (15 families, Table 3). Myrtaceae was dominant in MSF, KF and SAP plots (consisting of mainly *Syzygium incarnatum* and

Table 2. Differences in mean seedling abundance and species richness, Shannon's index, evenness, and inverse Simpson's index of woody seedlings (50 ≤ height (cm) ≤ 100) in four different forest types: mixed peat-swamp forest (MSF, n = 4 plots), heath forest (HF, n = 6 plots), *kerapah* forest (KF, n = 6 plots) and *Shorea albida* peat-swamp forest (SAP, n = 6 plots). Values are mean ± SE, calculated over the total number of plots per forest type. Same letters within a column represent no significant differences between forest types and different letters represent significant difference at α = 0.05 as analysed using one-way ANOVA and Tukey's HSD test.

Forest type	Mean abundance	Mean species richness	Shannon's index	Evenness	Inverse Simpson's index
MSF	20.7 ± 1.6^{a}	13.0 ± 2.2^{b}	2.19 ± 0.21^{a}	0.72 ± 0.07^{a}	8.00 ± 1.83^{a}
HF	24.7 ± 3.1^{a}	7.5 ± 1.6^{ab}	1.43 ± 0.33^{a}	0.47 ± 0.11^{a}	4.09 ± 0.96^{a}
KF	22.3 ± 2.4^{a}	9.0 ± 1.0^{ab}	1.70 ± 0.15^{a}	0.56 ± 0.05^{a}	4.58 ± 1.02^{a}
SAP	17.6 ± 1.4^{a}	5.7 ± 0.1^{a}	1.47 ± 0.01^{a}	0.48 ± 0.03^{a}	3.70 ± 0.31^{a}

Syzygium sp.) whereas Dipterocarpaceae and Sapotaceae were abundant in HF (mainly comprised of *Cotylelobium burckii* and *Madhuca curtisii*, respectively). Dipterocarpaceae, Euphorbiaceae and Lauraceae in HF, and Myrtaceae in MSF, KF and SAP, respectively, were recorded as the most species-rich families. Only two species (*Syzygium incarnatum* and *Syzygium* sp.) were observed as seedlings in all four forest types. Two species (*Antidesma coriaceum* and *Stemonurus scorpioides*) were recorded in MSF, HF and SAP; four species (*Diospyros* sp., *Horsfieldia carnosa*, *Timonius* sp. and *Casearia rugulosa*) recorded in MSF, KF and SAP; one species (*Madhuca curtisii*) recorded in SAP, KF and HF; and one species (*Xanthophyllum* sp.) recorded in KF, HF and MSF (Figure A1 in the Appendix). A full checklist of all woody seedlings recorded from the 22 plots in this study is presented in Table A1.

Variations in seedling communities between forest types

Distinct clustering of woody seedling species and plots were observed from the NMDS ordination, based on presence-absence data, for the 22 plots from MSF, HF, KF and SAP (Figure 2). MSF plots were clustered together and significantly influenced by soil pH and total K concentration, while SAP plots were clustered together and significantly influenced by soil GWC and total P concentration (Table A2). All KF plots were clustered together and influenced by soil total N concentration. Additionally, five HF plots were clustered together with all six KF plots, but HF plot 4 was distinct from all other plots in the NMDS. No environmental factors appeared to significantly influence seedling community composition (Table A2).

The results from PERMANOVA showed that woody seedling communities differed significantly between forest types ($F_{3,18}$ = 2.04, R^2 = 0.30, p < 0.001). Significant pairwise differences were detected between MSF and KF plots, MSF and SAP plots, HF and SAP plots, and KF and SAP plots (Table 4). No significant differences were detected between MSF and HF plots, and between HF and KF plots (Table 4).

DISCUSSSION

Variation in environmental and soil properties

With the exception of air and soil temperatures, all environmental and soil properties showed significant differences between MSF, HF, KF and SAP. This is consistent with habitat differences in these contrasting forest types. Heath and *kerapah* forests typically show more open canopies compared to peat swamp forest formations (MacKinnon *et al*. 2013, Wong *et al.* 2015), contributing to the higher percentage canopy openness recorded in HF and KF plots. The waterlogged conditions in KF and SAP plots likely contributed to the higher relative humidity measurements in these forest types. For litter depth, the drier soil conditions and more open canopy in HF plots may facilitate faster litter decomposition rates (Dent *et al.* 2006), resulting in less litter accumulation and shallower litter depth compared to the other forest types.

MSF soils recorded the lowest soil GWC, while KF and SAP soils recorded the highest soil GWC, consistent with the waterlogged conditions in KF and SAP plots. Despite the presence of partly decomposed plant matter, MSF soils were the least acidic among the four forest types, likely due to the

Table 3. Family distribution of censused woody seedlings (50 ≤ height (cm) ≤ 100) across the four forest types: mixed peat-swamp forest (MSF, *n* = 4 plots), heath forest (HF, *n* = 6 plots), *kerapah* (KF, *n* = 6 plots) and *Shorea albida* peat-swamp forest (SAP, *n* = 6 plots). Values for each family are total number of species recorded per forest type (calculated as a total count for all plots per forest type), with the total number of woody seedlings censused per forest type displayed within parenthesis. Families shown in **bold** are present in all four forest types.

No.	Families	Total number of species recorded (Total number of woody seedlings censused)			
		MSF	HF	KF	SAP
1	**Anacardiaceae**	**1 (1)**	**2 (2)**	**1 (4)**	**1 (5)**
2	Annonaceae	2 (4)	3 (8)	2 (6)	
3	Apocynaceae		1 (2)		1 (1)
4	Aquifoliaceae				1 (2)
5	Araucariaceae		1 (1)		
6	Burseraceae			2 (4)	
7	Calophyllaceae	2 (4)			
8	Chrysobalanaceae				1 (3)
9	Clusiaceae	1 (4)			
10	Connaraceae	1 (1)			
11	Convolvulaceae		1 (2)		
12	Dilleniaceae				1 (1)
13	Dipterocarpaceae	1 (3)	4 (42)	1 (2)	
14	Ebenaceae	1 (2)		1 (1)	
15	Elaeocarpaceae		2 (4)	1 (2)	1 (6)
16	Erythroxylaceae		1 (1)		
17	Euphorbiaceae	1 (7)	4 (11)		
18	Fagaceae		1 (1)	1 (5)	
19	Gentianaceae				1 (1)
20	Gnetaceae		1 (10)		
21	Icacinaceae				1 (1)
22	Lamiaceae	1 (2)			
23	Lauraceae	2 (5)	4 (5)	2 (2)	
24	Leguminosae-mimosoideae		1(2)		
25	Leguminosae-papilionoideae	1 (1)	1 (5)		
26	Linaceae	1 (1)			
27	Loganiaceae			1 (4)	
28	Malvaceae	1 (3)			
29	Melastomataceae	2 (3)			
30	Moraceae				1 (4)
31	Myristicaceae	2 (3)		2 (2)	
32	**Myrtaceae**	**3 (18)**	**2 (15)**	**3 (62)**	**2 (29)**
33	Olacaceae	1 (1)			
34	Phyllanthaceae	2 (2)	1 (14)		1 (7)
35	Podocarpaceae			1 (11)	
36	Polygalaceae	1 (1)	1 (2)	2 (5)	
37	Primulaceae			1 (5)	1 (11)
38	**Rubiaceae**	**3 (15)**	**1 (1)**	**3 (12)**	**1 (17)**
39	Rutaceae			1 (2)	
40	Salicaceae	1 (1)		1 (1)	
41	Sapindaceae		1 (2)		
42	Sapotaceae		1 (20)	2 (12)	1 (7)
43	Stemonuraceae		1 (1)		1 (12)
44	Tetrameristaceae	1 (2)			
	Total	**32 (84)**	**35 (151)**	**28 (142)**	**16 (107)**

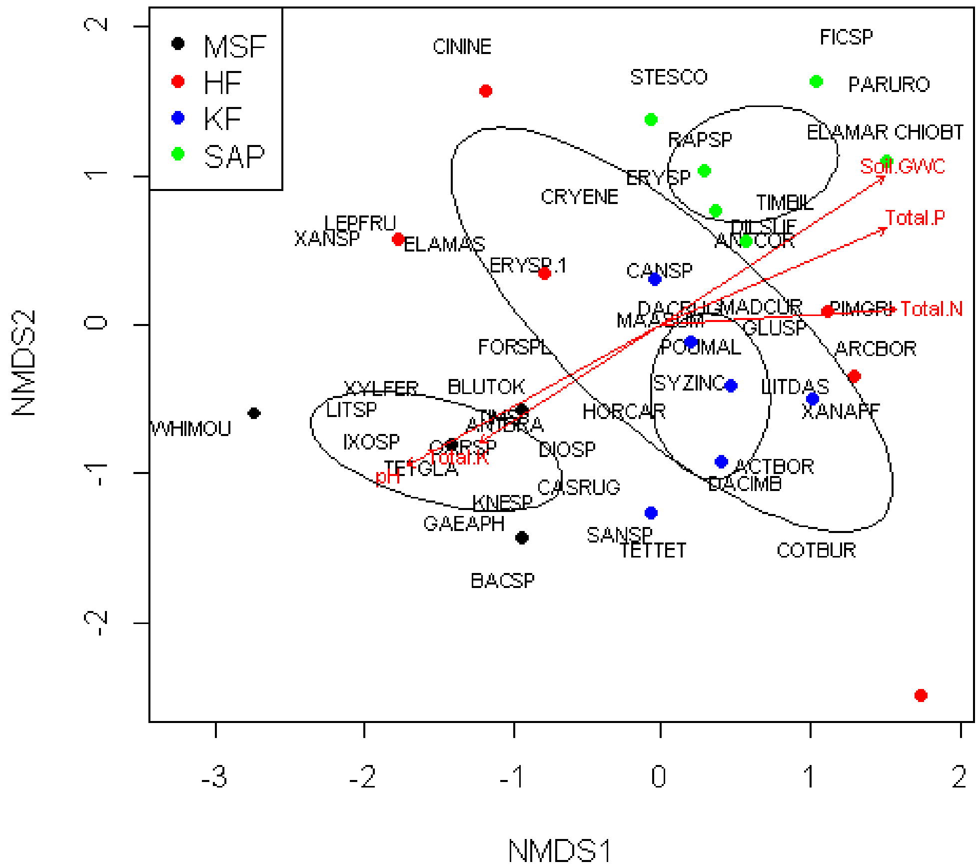

Figure 2. Nonmetric multidimensional scaling (NMDS) ordinations for woody seedlings at the four forest types, using presence-absence data and the Jaccard index, in relation to environmental and soil factors. Different colours denote the four forest types: Mixed peat-swamp forest (MSF, n = 4 plots), heath forest (HF, n = 6 plots), *kerapah* forest (KF, n = 6 plots) and *Shorea albida* peat-swamp forest (SAP, n = 6 plots). The direction of the arrow indicates the most rapid change of that variable while the length of the arrow is proportional to the strength of the correlation.

influence of adjacent mixed dipterocarp forest soils within the Andulau Forest Reserve. Both MSF and HF soils were less acidic than KF and SAP. The highly acidic SAP soils are consistent with low pH for peat swamp forest soils recorded by Jaafar *et al.* (2016) and likely reflect the build-up of humic and fulvic acids released by partly decomposed plant matter in the humus and peat layers (Page *et al.* 1999), and a decrease in soil exchangeable cations concentrations (Grealish & Fitzpatrick 2013). KF and SAP soils were the most nutrient-rich, as KF recorded the highest total N and Mg concentrations while SAP recorded the highest total P and Ca concentrations. The higher soil nutrient concentrations in KF and SAP plots may be due to nutrient accumulation in the thicker humus layers and peat surface (Page *et al.* 2006) as nutrient concentrations decrease down the peat profile (Sulistiyanto 2004, Lampela *et al.* 2014). Although Bornean PSFs are commonly ombrogenous and receive most nutrients from rainfall (Page *et al.* 2006, Dommain *et al.* 2016), our SAP plots were not located at the higher parts of the Badas peat dome which may have allowed more nutrients to accumulate in their surface peat. MSF consistently recorded lower soil nutrient concentrations, except for total K which was the highest as compared to the other forests. The higher litter depth in MSF plots could explain the high total K as this highly mobile cation is normally released during litter decomposition (Krishna & Mohan 2017).

Contrasting patterns in woody seedlings abundance, species richness and diversity

Our study did not detect significant habitat differences in mean seedling abundance and mean species richness, except for the significantly higher mean species richness in MSF than SAP plots. Mean seedling diversity indices represented by Shannon's index, evenness, inverse Simpson's index, were not

Table 4. Pairwise PERMANOVA test results, based on presence-absence data, to show pairwise differences in seedling community composition between forest types: mixed peat-swamp forest (MSF), heath forest (HF), *kerapah* (KF) and *Shorea albida* peat-swamp forest (SAP). The PERMANOVA for presence-absence data was highly significant at $p < 0.001$ with R^2 of 0.30. * indicates significant difference at $p < 0.05$.

Pairwise comparison	F	R^2	p
MSF vs. HF	1.74	0.18	0.096
MSF vs. KF	3.17	0.28	0.042*
MSF vs. SAP	4.72	0.37	0.042*
HF vs. KF	1.57	0.14	0.270
HF vs. SAP	2.43	0.20	0.036*
KF vs. SAP	3.67	0.27	0.030*

significantly different between all forest types. It is possible that this reflects similar seedling abundance, diversity and species richness within these plots, but that larger plot sizes or an increased sample size may reveal different results. The significantly higher mean species richness in MSF (mean 13.0 species per plot) than SAP (5.7 species per plot) is consistent with documented tree diversity differences of the PSF phasic communities (Anderson 1963). With the exception of the tall-interior forest habitat sub-type that appears unique to Sebangau (Page *et al.* 1999), MSFs are the most species-rich of PSF communities (Yamada 1997, Husson *et al.* 2018), while the inner communities of the peat dome where SAPs are found typically show lower tree species richness mainly dominated by *Shorea albida* (Anderson 1963, Kobayashi 2016). Studies comparing seedling diversity between HF, KF and SAP are lacking, although Pg Mazalan (2019) and Jinnidi (2019) recorded significantly higher mean tree species richness in KF than SAP in Brunei, possibly due to higher tree abundance of trees with stem diameter ≥ 5 cm in their KF plots; while significantly higher tree species richness was recorded in HF than PSF in Central Kalimantan (Nishimura *et al*. 2007). Differences in mean species richness in our study compared to tree diversity studies within the same forest types may demonstrate some species loss in the transition from the vulnerable seedling stage to the more established sapling and adult populations (Fenner & Thompson 2005, Kitajima 2007) due to species-specific differences in seedling mortality, though this was not measured in the present study.

Patterns for the most species-rich family of woody seedlings varied between the four forest types studied. Within the HF plots, Lauraceae, Dipterocarpaceae and Euphorbiaceae were the most species-rich, while Myrtaceae and Rubiaceae were the most species-rich in the MSF and KF plots. Interestingly, we did not record any Dipterocarpaceae woody seedlings in our SAP plots. This contradicts known records of Dipterocarpaceae trees within the Lumut SAP itself (Tuah 2017, Jinnidi 2019), as well as the dominance of the family Dipterocarpaceae in most Southeast Asian PSFs (Posa *et al*. 2011). We suggest that the absence of Dipterocarpaceae seedlings in our SAP plots may reflect low seedling recruitment of PSF dipterocarp species which typically have recalcitrant seeds (Corlett 2009) and PSFs can have small-sized seed banks (Graham & Page 2018). Further, mast fruiting of Dipterocarpaceae trees within the Lumut area has not been recorded recently, with only a small masting event observed in nearby Badas in 2014 (RS Sukri, personal observation, 2014, Din et al. 2018), which could have contributed to the absence of Dipterocarpaceae seedlings, particularly *Shorea albida* seedlings, in our SAP plots. High mortality of *Shorea albida* seedling two years after a 1986 masting event in Sarawak and Brunei has been recorded (Kobayashi 1998), and *Shorea albida*-dominated peat swamp forests in Badas, Brunei did not successfully regenerate following natural disturbance (Becek *et al.* 2022), consistent with low seedling recruitment and regeneration potential for this species (Randi *et al.* 2019).

The influence of environmental and soil properties on woody seedlings community composition

The NMDS ordination based on presence-absence data revealed distinct woody seedling community composition between the four forest types, and these differences were highly significant as supported by our PERMANOVA results. MSF plots were the most distinct in terms of their woody seedling community composition and differed significantly from KF and SAP plots. Although distance effects (Ries *et al*. 2004, Bergés *et al*. 2013) may partly determine these differences, as the MSF plots in Labi were approximately 13.4 km away from the other seedling plots located in Lumut, our results indicate that soil properties were influential. MSF plots were strongly influenced by soil pH and total K concentrations in the NMDS, consistent with the highest mean soil pH and total K concentration recorded in MSF. The less acidic MSF soils may promote higher species richness, as high soil acidity (as seen in the KF, HF and SAP plots) leads to nutrient deficiency in soils (Fujii 2014), and species richness decreases with extreme acidity (Currie *et al*. 2004). Total soil K can influence growth, survival and species diversity within forest communities (Tripler *et al.* 2006), and thus could help support the higher woody seedling species richness in MSF plots.

Notably, woody seedling communities in SAP significantly differed from all other forest types (MSF, HF and KF), indicating a unique seedling community in SAP that was strongly influenced by soil gravimetric water content, and consistent with the significantly highest soil GWC recorded in SAP plots. It is notable that during our seedling census in these plots, the SAP plots remained waterlogged, while MSF and HF plots were dry and KF plots were only periodically waterlogged. The SAP seedling community was also significantly influenced by total P concentrations, albeit to a lesser extent. Despite the lack of significant differences in mean total P concentrations between forest types in our study, the significant influence of total P on SAP woody seedling community potentially indicates that P may be an important determinant of species composition in PSFs. The influence of surface peat nutrients on PSF vegetation is still unclear, though the outer PSF communities may benefit from higher nutrient accumulation due to movement of water across the peat dome, which could help support higher vegetation diversity (Page *et al.* 1999). Both soil water availability and soil P can influence tropical plant communities and diversity (Paoli *et al*. 2006, Sukri *et al*. 2012), and the waterlogged conditions and highly acidic soils in PSF can inhibit plant survival and growth (Page *et al.* 1999, Posa *et al.* 2011, Schofield 2014).

Although the KF plots formed a distinct cluster in the NMDS ordination, the PERMANOVA results did not detect significant differences between HF and KF plots. Similarly, the woody seedling communities of MSF and HF plots did not significantly differ, although the NMDS ordination separated them out. Our analysis showed that KF and HF plots shared 15 species of woody seedlings, while MSF and HF plots shared 10 species (see Figure A1). Floristic compositions of tree communities in KF are often described as related to those in HF (Anderson 1963, Wong *et al.* 2015, Tuah 2017, Jinnidi 2019), as the waterlogged *kerapah* forests are a sub-type of the dry *kerangas* forests (Brunig 1990, Proctor 1999) and the two forest types share similarities in their soil type (Jaafar *et al.* 2016). An interesting result from the NMDS was the separation of one HF plot (i.e. plot no. 4) from all other plots due to the dominance of *Cotylelobium burckii* (n = 38 seedlings) in this plot. Seedlings of *Cotylelobium burckii* were present only in HF plot 4 and appeared to be absent from all other forest plots except for KF plot 1 (n = 1 seedling) and KF plot 4 (n = 1 seedling). This species is restricted to HF and endemic to Borneo (Ashton 2004) and was the most abundant species of woody seedlings recorded in our study.

Conservation implications

This study has demonstrated that the four forest types (MSF, HF, KF and SAP) investigated have high conservation value due to the presence of several species listed as near threatened, vulnerable and endangered in the IUCN Red List (IUCN 2020; Appendix 1). Five species were listed in the IUCN Red List across the four forest types: one species documented in MSF (*Horsfieldia carnosa*^{NT}), four species recorded in HF (*Agathis borneensis*^{EN}, *Cotylelobium burckii* ^{EN}, *Dryobalanops rappa* ^{EN} and *Madhuca curtisi*^{VU}), three species found in KF (*Agathis borneensis* ^{EN}, *Cotylelobium burckii* ^{EN} and *Madhuca curtisii*^{VU}) and one species observed in SAP (*Madhuca curtisii*^{VU}). The presence of seedlings of these high conservation value species within the study sites indicate the viability of these forests, and therefore highlights the need to prioritise their conservation.

The diversity of woody seedlings recorded in these four forest types as well as the presence of high conservation value species indicates an urgent need to conserve these forests. While the MSF plots in the Lumut area are located within the protected Andulau Forest Reserve, the HF, KF and SAP habitats in Lumut are not currently legally protected as forest reserves. The Lumut area has experienced forest fires during drier periods (Tuah 2017) but is not under threat from logging and deforestation. Logging in all peat swamp forests is currently prohibited in Brunei Darussalam and the whole of the Belait peat-swamp complex, which contains the Badas peat dome, is included in Brunei Darussalam's designated Heart of Borneo area and is in the process of being legally gazetted (Brunei Forestry Department, personal communication, 2019). This presents an excellent opportunity for conservation of these intact forests and for further studies on their ecology.

As our study focused on two specific locations within Brunei and had a limited number of plots per forest type, it is crucial to replicate our work in similar heath and peat swamp forest formations in Brunei and elsewhere in Borneo. Additionally, the distance of 50 m away from forest edges may not be sufficient to avoid the influence of edge effects upon our MSF seedling plots, as seed rain and soil effects from different forest types adjacent to our plot locations are likely, though these were not measured in our study. Regardless, our study present the first known comparison of woody seedling diversity in these four forest types, demonstrating a significant influence of soil properties upon the composition of these contrasting seedling communities. Future studies focusing on seedling establishment, recruitment and survival over the long term, coupled with parallel tree diversity and forest dynamics studies, within these contrasting forest types would facilitate increased understanding of the role of seedling communities in influencing the eventual composition of tree communities. Concerted efforts to quantify the viability of woody seedling populations in these forests are especially important in guiding conservation, forest management and reforestation programmes of these threatened forests in Brunei Darussalam and in Borneo.

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AUTHOR CONTRIBUTIONS

RSS conceived the study, and RSS, NSN and FM designed the study. NSN performed all field and laboratory measurements and conducted all statistical analysis. MYSMY conducted field measurements for heath and *kerapah* forests. SMJ conducted additional statistical analysis, prepared additional tables and figures, and assisted with laboratory measurements. NSN and RSS wrote the manuscript. All authors provided feedback to the manuscript and approved the final version of the manuscript.

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Appendix

Table A1. Full checklist of censused woody seedlings (50 ≤ height (cm) ≤ 100) across the four forest types: mixed peat-swamp forest (MSF, n = 4 plots), heath forest (HF, n = 6 plots), *kerapah* (KF, n = 6 plots) and *Shorea albida* peat-swamp forest (SAP, n = 6 plots). Values are total seedling abundance for each species recorded per forest type. Superscript labels indicate the conservation status of the species according to the IUCN Red List (LC - Least Concern, NT - Near Threatened, VU - Vulnerable, EN – Endangered) (IUCN 2020).

No.	Family	Species	Species Code	MSF	HF	KF	SAP
1	Anacardiaceae	*Gluta laxiflora* Ridl.	GLULAX	1			5
		Gluta usitata (Wall.) Ding Hou	GLUUSI			4	
		Gluta sp.	GLUSP		1		
		Parishia maingayi Hook.f.	PARMAI		1		
2	Annonaceae	*Alphonsea johorensis* J. Sinclair	ALPJOH			2	
		Maasia sumatrana (Miq.) Mols, Kessler & Rogstad. [LC]	MASSSUM		6	4	
		Stelechocarpus sp.	STESP		1		
		Uvaria excelsa (Hook.f. & Thomson) King	UVAEXC	1			
		Xylopia ferruginea (Hook.f. & Thomson) Baill.	XYLFER	3	1		
3	Apocynaceae	*Chilocarpus obtusifolius* Merr.	CHIOBT				1
		Willughbeia angustifolia (Miq.) Markgr.	WILANG		2		
4	Aquifoliaceae	*Ilex* sp.	ILESP				2
5	Araucariaceae	*Agathis borneensis* Warb. [EN]	AGABOR		1		
6	Burseraceae	*Dacryodes rugosa* (Blume) H.J.Lam [LC]	DACRUG			3	
		Santiria sp.	SANSP			1	
7	Callophyllaceae	*Calophyllum* sp.	CALSP	3			
		Kayea sp.	KAYSP	1			
8	Chrysobalanaceae	*Parastemon urophyllus* (Wall. Ex AD.C) AD.C	PARURO				3
9	Clusiaceae	*Garcinia* sp.	GARSP	4			
10	Connaraceae	*Connarus* sp.	CONSP	1			
11	Convolvulaceae	*Erycibe* sp.	ERYSP		2		
12	Dilleniaceae	*Dillenia suffruticosa* (Griff.) Martelli	DILSUF				1
13	Dipterocarpaceae	*Cotylelobium burckii* (Heim) Heim [EN]	COTBUR		38	2	
		Dryobalanops rappa Becc. [EN]	DRYRAP		1		
		Hopea sp.	HOPSP		1		
		Vatica micrantha Slooten [LC]	VATMIC	3			
		Vatica sp.	VATSP		2		

14	Ebenaceae	*Diospyros* sp.	DIOSP	2		1	
15	Elaeocarpaceae	*Elaeocarpus clementis* Merr. [LC]	ELACLE		1		
		Elaeocarpus marginatus Stapf ex Weibel	ELAMAR				6
		Elaeocarpus mastersii King	ELAMAS		3		
		Elaeocarpus sp.	ELASP			2	
16	Erythroxylaceae	*Erythroxylum* sp.	ERYSP		1		
17	Euphorbiaceae	*Agrostistachys longifolia* (Müll.Arg.) Kurz	AGRLON		6		
		Blumeodendron tokbrai Blume (Kurz).	BLUTOK	7	1		
		Neoscortechinia kingii (Hook.f.) Pax & K.Hoffm.	NEOKIN		3		
		Pimelodendron griffithianum (J. Mueller-Arg. in Alph. de Candolle) Benth.	PIMGRI		1		
18	Fagaceae	*Lithocarpus dasystachyus* (Miq.) Rehder	LITDAS		1	5	
19	Gentianaceae	*Utania teysmannii* (Cammerl.)	UTATEY				1
20	Gnetaceae	*Gnetum* sp.	GNESP		10		
21	Icacinaceae	*Platea* sp.	PLASP				1
22	Lamiaceae	*Teijsmanniodendron subspicatum* (Hallier f.) Kosterm. [LC]	TEISUB	2			
23	Lauraceae	*Actinodaphne borneensis* Meissn.	ACTBOR		1	1	
		Cinnamomum iners Wight [LC]	CININE		1		
		Cryptocarya enervis Hook. f. [LC]	CRYENE		2	1	
		Cryptocarya griffithiana Wight	CRYGRI	1			
		Litsea sp.	LITSP	4	1		
24	Leguminosae-mimosoideae	*Archidendron borneense* (Benth.) I.C.Nielsen	ARCBOR		2		
25	Leguminosae-papilionoideae	*Fordia splendidissima* (Miq.) Buijsen [LC]	FORSPL	1	5		
26	Linaceae	*Indorouchera griffithiana* (Planch.) Hallier f.	INDGRI	1			
27	Loganiaceae	*Strychnos axillaris* Colebr.	STRAXI			4	
28	Malvaceae	*Microcos cinnamomifolia* Burret	MICCIN	3			
29	Melastomataceae	*Memecylon* sp.	MEMSP	1			
		Pternandra sp.	PTESP	2			
30	Moraceae	*Ficus* sp.	FICSP				4
31	Myristicaceae	*Horsfieldia carnosa* Warb. [NT]	HORCAR	1		1	
		Horsfieldia pallidicaula W.J.de Wilde	HORPAL			1	
		Knema sp.	KNESP	2			
32	Myrtaceae	*Syzygium incarnatum* (Elmer) Merr. & L.M.Perry	SYZINC	9	8	25	1
		Syzygium sp.	SYZSP	1	7	36	28
		Tristaniopsis pentandra (Merr.) Peter G.Wilson & J.T.Waterh.	TRIPEN			1	
		Whiteodendron moultonianum (W.W.Sm.) Steenis	WHIMOU	8			
33	Olacaceae	*Strombosia javanica* Thwaites	STRJAV	1			

34	Phyllanthaceae	*Antidesma coriaceum* Tul.	ANTCOR		14		7
		Antidesma brachybotrys Airy Shaw	ANTBRA	1			
		Baccaurea sp.	BACSP	1			
35	Podocarpaceae	*Dacrycarpus imbricatus* Blume [LC]	DACIMB			11	
36	Polygalaceae	*Xanthophyllum affine* Korth. ex Miq.	XANAFF			1	
		Xanthophyllum sp.	XANSP	1	2	4	
37	Primulaceae	*Ardisia hosei* Merr.	ARDHOS			5	
		Rapanea sp.	RAPSP				11
38	Rubiaceae	*Canthium* sp.	CANSP			1	
		Gaertnera aphanodioica Malcomber	GAEAPH	6			
		Gaertnera junghuhniana Miq. [LC]	GAEJUN		1		
		Ixora sp.	IXOSP	8			
		Timonius billitonensis Valeton	TIMBIL			5	17
		Timonius sp.	TIMSP	1		6	
39	Rutaceae	*Tetractomia* sp.	TET			2	
40	Salicaceae	*Casearia rugulosa* Blume	CASRUG	1		1	
41	Sapindaceae	*Lepisanthes fruticosa* (Roxb.) Leenh. [LC]	LEPFRU		2		
42	Sapotaceae	*Madhuca curtisii* (King & Gamble) Ridl. [VU]	MADCUR		20	10	7
		Pouteria malaccensis (C.B.Clarke) Baehni	POUMAL			2	
43	Stemonuraceae	*Stemonurus scorpioides* Becc.	STESCO		1		12
44	Tetrameristaceae	*Tetramerista glabra* Miq.	TETGLA	2			
		Total number of species recorded	**84**				
		Total number of seedlings recorded per forest type		84	151	142	107
		Total number of species recorded per forest type		32	35	28	16

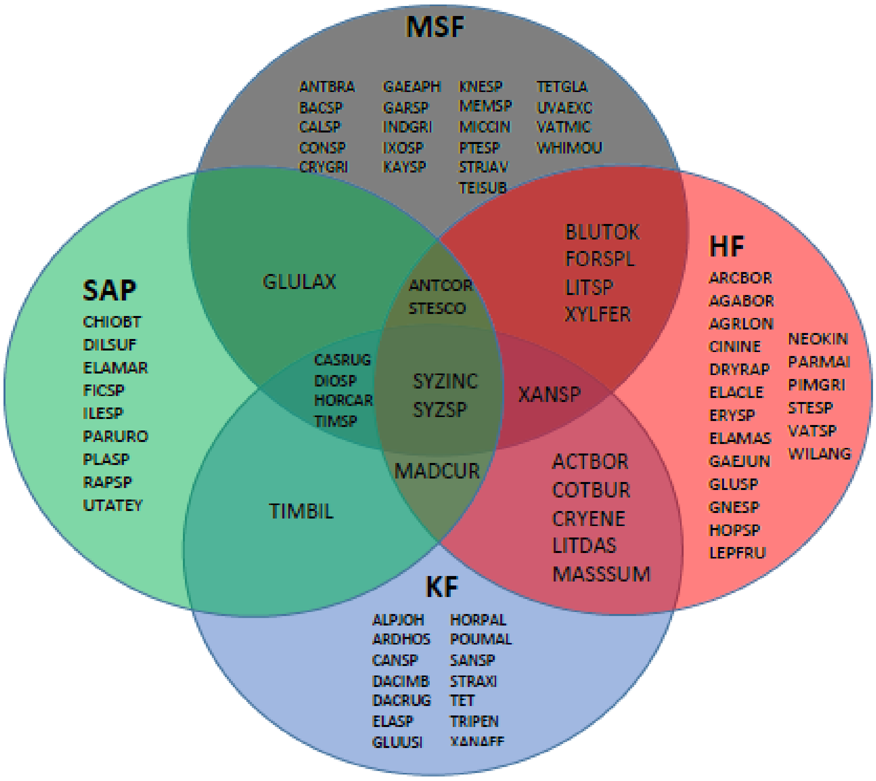

Figure A1. Venn-diagram to illustrate the distribution of woody seedling species recorded across the four forest types: mixed peat-swamp forest (MSF, n = 4 plots), heath forest (HF, n = 6 plots), *kerapah* (KF, n = 6 plots) and *Shorea albida* peat-swamp forest (SAP, n = 6 plots). Species codes and their definitions are listed in Table A1.

Table A2. Fits of environmental and soil properties onto NMDS ordination, based on presence-absence data using the Jaccard index, of woody seedlings across 22 plots from mixed peat-swamp forest (MSF, n = 4 plots) heath forest (HF, n = 6 plots), *kerapah* forest (KF, n = 6 plots), and *Shorea albida* peat-swamp forest (SAP, n = 6 plots). r^2 values indicate the correlation coefficient denoting the strength of the correlation with p-values assessed using 1000 permutations. Significant p-values (α = 0.05 level; * p < 0.05; ** p < 0.01; *** p < 0.001) are highlighted in bold.

	Property	Code in NMDS	r^2	p-value
Environmental properties	Air temperature	Air.temp	0.009	0.92
	Relative humidity	Humidity	0.06	0.55
	Canopy openness	Canopy	0.07	0.52
	Litter depth	Litter.depth	0.03	0.76
Soil properties	Soil temperature	Soil.temp	0.04	0.67
	Soil pH	pH	0.52	**< 0.01****
	Soil GWC	Soil.GWC	0.44	**< 0.01 ****
	Total N	Total.N	0.34	**< 0.05 ***
	Total P	Total.P	0.37	**< 0.05 ***
	Total Ca	Total.Ca	0.23	0.08
	Total Mg	Total.Mg	0.27	0.06
	Total K	Total.K	0.29	**< 0.05***