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Differential Impacts of *Acacia* Invasion on Nutrient Fluxes in Two Distinct Bornean Lowland Tropical Rain Forests

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Abstract: Invasive *Acacia* species can alter nutrient cycling processes in forest ecosystems, particularly affecting total litterfall production and litter decomposition patterns. This study examined the effects of exotic *Acacia mangium* Willd. on total litterfall production, nutrient concentrations in leaf litterfall fractions, leaf litter decomposition, and nutrient release in lowland heath (HF) and mixed dipterocarp forests (MDF) in Brunei Darussalam, Borneo. Above-ground litterfall traps were installed in HF and MDF with and without invasive *Acacia* present, representing four habitat types in total, and monthly collections were conducted for 12 months. Litter decomposition bags were deployed to determine the rates of decomposition and nutrient release. Habitats invaded by *Acacia* exhibited higher total litterfall production, increased leaf litter concentrations of nitrogen, potassium, and calcium, and increased addition of all nutrients measured in litter (nitrogen, phosphorus, potassium, calcium, and magnesium, especially in the *Acacia*-invaded mixed dipterocarp forest (AMDF) and nitrogen and potassium in *Acacia*-invaded heath forest (AHF)), reduced nitrogen and potassium use efficiencies in AHF, and reduced stand-level nitrogen and calcium use efficiencies in AMDF. Litter decomposition rates and nutrient release were lower in AMDF than in the three other habitats. The significantly higher total litterfall production coupled with higher nutrient addition in the two *Acacia*-invaded habitats is expected to progressively increase the abilities of these habitats to produce large quantities of nutrient-rich litter and will likely eventually lead to an enrichment of nutrients in the soil, thus facilitating further invasion by *Acacia*, particularly in the MDF.

Keywords: Brunei; heath forests; invasive species; Kerangas forests; litterfall production; litter decomposition; nutrient additions; nutrient use efficiency; mixed dipterocarp forests; Fabaceae



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1. Introduction

The impacts of plant invasion on nutrient cycling are widely recognized [1–4]. Invasive species can alter nutrient pools through their effects on soil properties, plant biomass, and nutrient cycling process. Plant invasions generally increase nutrient content and nutrient availability in invaded ecosystems [1,5], though contrasting patterns have also been observed [6]. Fast-growing invasive species increase above-ground plant biomass, which elevates total litterfall production [7] and produce a nutrient-rich litter that typically decomposes faster [8]. This triggers higher rates of litter nutrient release, increases mineralization rates [9], and facilitates nutrient transfer to the soil [10,11]. Nitrogen-fixing abilities of invasive plants through their symbiotic bacterial associations [12–14] also elevate soil N [2]. Invasive plants also show higher nutrient use efficiency as a strategy to enhance plant nutrient uptake [15] and thus maximize their growth in low-nutrient soils [16].

Invasive plant species are recognized as a major contributor to biodiversity loss but remain little studied in tropical Asia [17] and in Southeast Asia [18]. Southeast Asia is a major biodiversity hotspot [19] and faces an urgent biodiversity crisis driven by anthropogenic disturbance, particularly from deforestation and habitat loss [20]. As one of the most invasive genera of plant species [21], *Acacia* from the family Fabaceae have spread and established in tropical countries in East Asia [22] and Southeast Asia [17,18]. *Acacia* species are widely utilized in agroforestry as their N-fixing ability allows them to thrive in low-fertility soils [23]. However, most *Acacia* species have the capacity to become invasive when introduced beyond their native ranges [21]. Invasive *Acacia* species alter nutrient cycling in invaded areas [24,25] and typically produce high total litterfall and nutrient-rich litter, with especially high N concentrations. This nutrient-rich litter increases the concentrations of organic and available nutrients in the soil [24–26]. Increased nutrient cycling rates eventually directly impact native plants that are adapted to a low-nutrient environment [24].

Within tropical Brunei Darussalam, located in Northwest Borneo, the introduction of three exotic *Acacia* species (*Acacia mangium* Willd., *Acacia auriculiformis* A. Cunn ex Benth., and *Acacia cincinnata* F. Muell.) started in the early 1990s for soil erosion mitigation and plantation forestry [27]. These species, particularly *A. mangium*, now dominate disturbed and secondary forests as well as roadsides in Brunei Darussalam [28,29]. Studies have shown that invasive *Acacia* species can modify soil and leaf litter properties, impact ion deposition and decrease native tree diversity [28–32]. *Acacia* species have been recorded to invade two lowland forest types in Brunei: heath forest (HF) and mixed dipterocarp forests (MDF) [32]. These forests differ naturally in their soil chemical and physical properties [33–35], stand structure, and floristic composition [36–38]. HF overlies sandy, well-drained nutrient-poor soils and is characterized by smaller, pole-sized trees and plants with specialized adaptations to the nutrient-poor environment [39]. In contrast, as the main forest type in Brunei and across the rest of Borneo, MDF overlies clayey, poorly drained nutrient-rich soils and contain highly diverse tree communities that are dominated by the family Dipterocarpaceae [40].

The impact of invasive *Acacia* species on nutrient cycling in Bornean lowland tropical forests remains less understood. Studies of nutrient fluxes in Brunei's HF have shown that *Acacia* trees can potentially alter leaf litter and soil physicochemical properties, affecting nutrient availability and nutrient cycling [30,41]. However, the response of nutrient fluxes within MDF to *Acacia* invasion requires investigation. Our study examined the effects of invasive *Acacia* species on variation in total litterfall production and leaf litter decomposition in two contrasting forest types (HF vs. MDF) in Brunei Darussalam. Because N-fixing *Acacia* species typically exhibit an invasion advantage in nutrient-poor soils [42], we hypothesized that *Acacia* would differentially impact measures of nutrient fluxes in the nutrient-poor HF to a greater extent than in the nutrient-rich MDF. We focused on three main research questions:

1. Do rates of litterfall production differ between the intact and *Acacia*-invaded heath and mixed dipterocarp forests?
2. Do leaf litterfall nutrient concentrations, nutrient addition via litterfall, and stand-level nutrient use efficiency (NUE) differ between the intact and *Acacia*-invaded heath and mixed dipterocarp forests?
3. Are there any differences in nutrient release between *A. mangium* litter and mixed-species litter in *Acacia*-invaded habitats?

2. Materials and Methods

2.1. Study Site

The study was conducted in the Andulau Forest Reserve, in Brunei Darussalam, north-west Borneo (4°37'60.00" N, 114°31'60.00" E) within two forest types, HF and MDF. Within these forest types, four distinct habitat types were defined based on the absence (referred to as "intact") or presence (referred to as "invaded") of invasive *Acacia* trees, as follows: intact heath forest, HF (4°35'59.70" N, 114°30'58.30" E), *Acacia*-invaded heath forest, AHF

($4^{\circ}35'34.50''$ N, $114^{\circ}31'30.80''$ E), intact mixed dipterocarp forest, MDF ($4^{\circ}39'23.69''$ N, $114^{\circ}31'17.83''$ E) and *Acacia*-invaded mixed dipterocarp forest, AMDF ($4^{\circ}39'48.53''$ N, $114^{\circ}30'18.36''$ E; Figure 1). Andulau Forest Reserve is dominated by MDF [43], but it contains small areas of HF embedded within it [38,44]. Six 20×20 m plots were randomly established within accessible locations in each of the four habitat types, resulting in 24 plots in total. Plots within the same habitat type were located ca. 50–500 m apart. Each 20×20 m plot was further subdivided into four 10×10 m subplots. Intact forest plots (HF and MDF plots) were located within areas of primary forest where *Acacia* species were absent and with no previous history of logging, while *Acacia*-invaded plots (AHF and AMDF) were set up in areas where *Acacia* trees were found.

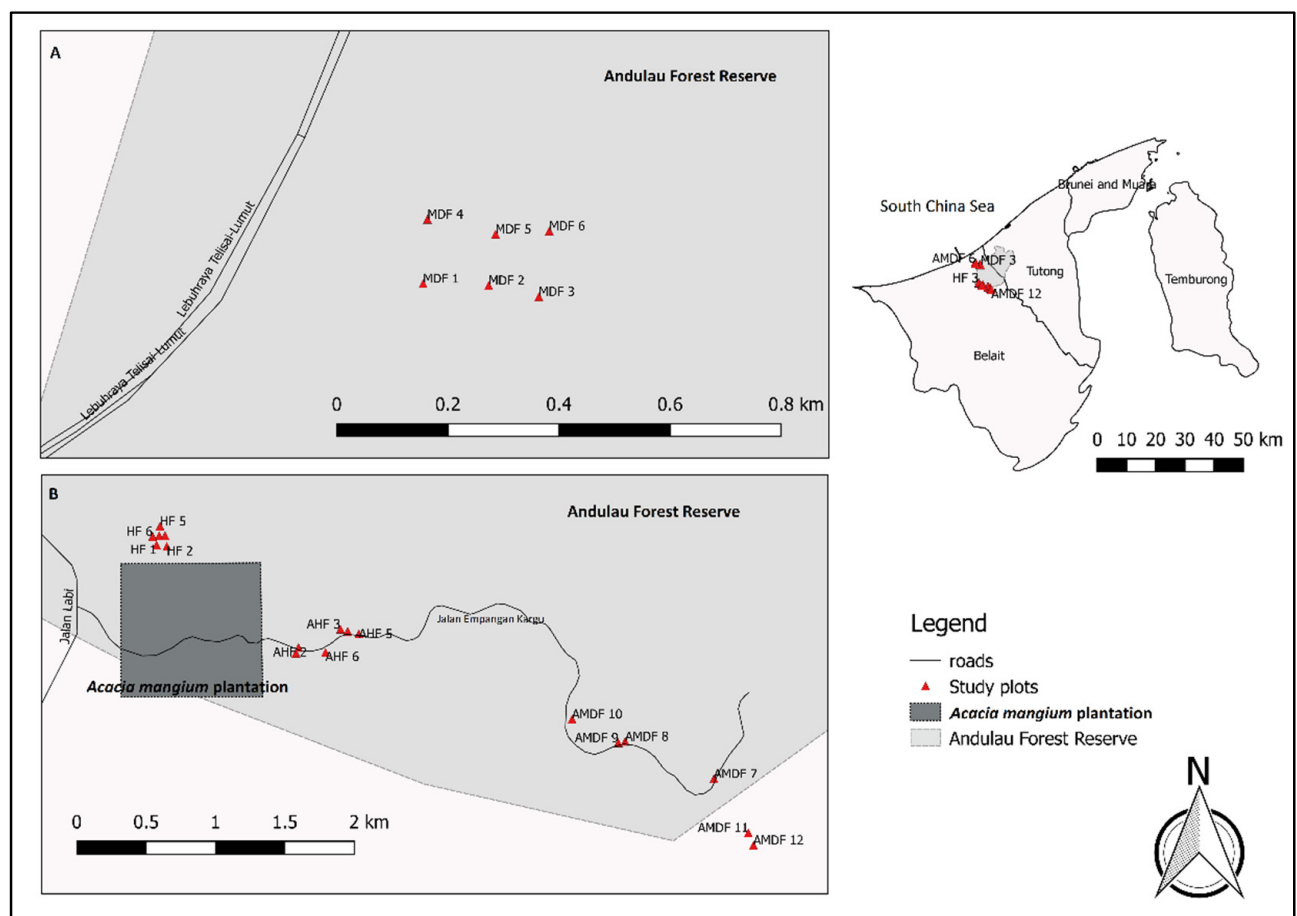


Figure 1. Locations of the study sites containing six plots ($20 \text{ m} \times 20 \text{ m}$) in each of the intact heath forest (HF 1–6), *Acacia*-invaded heath forest (AHF 1–6), intact mixed-dipterocarp forest (MDF 1–6) and *Acacia*-invaded mixed dipterocarp forest (AMDF 7–12) within Compartments 7 and 8 of the Andulau Forest Reserve in the Belait District, Brunei Darussalam. AHF and AMDF plots along the Jalan Empangan Kargu roadsides were set up in areas invaded by *Acacia* trees. Distances between plots within the same habitat type ranged from ca. 50–500 m. (A) represents the inset of plots MDF 1–6, and (B) represents the inset of plots HF 1–6, AHF 1–6, and AMDF 7–12.

To ensure that the abundance of trees within all plots did not influence litter and soil properties, all trees with diameter breast height (dbh) ≥ 1 cm in all plots were counted, and no significant differences were recorded in mean (\pm SEM) tree abundance (HF = 411 ± 12.3 , AHF = 348 ± 7.40 , MDF = 327 ± 8.72 , AMDF = 277 ± 15.7 ; $F = 1.87$, $p > 0.05$). All *Acacia* trees within the AHF and AMDF plots were identified as *Acacia mangium*, while trees within AHF and AMDF plots consisted of a mix of native species and *A. mangium* trees, respectively. The AHF and AMDF plots recorded a similar abundance of *A. mangium* trees

($n =$ four to seven trees per $20\text{ m} \times 20\text{ m}$ plot) of the same estimated age (≤ 20 years) and a high abundance of *A. mangium* seedlings and saplings [45]. The origin of the invading *A. mangium* is a 1 km^2 *A. mangium* plantation located close to the study sites ($4^\circ 35' 44.9''$ N, $114^\circ 30' 51.7''$ E, Figure 1). The plantation was established by the Brunei Forestry Department in 1998, selectively harvested in 2010, and left without maintenance in the subsequent years after harvest (Mr. Haji Ryni Hj Sofian, Plantation Unit Officer, personal communication), resulting in resprouting of the stumps of harvested *A. mangium* trees and its spread into the neighboring forests [46].

The climate of Brunei Darussalam is aseasonal with a mean annual rainfall of 1950.8 mm and 3164.1 mm and mean annual temperature of 27.1°C and 26.9°C recorded at the Sungai Liang Agricultural station (ca. 2 km away from Andulau Forest Reserve) in 2016 and 2017, respectively (Department of Agriculture and Agrifood, Ministry of Primary Resources and Tourism, unpublished work). During the study, periods of high rainfall (defined as exceeding 200 mm total monthly rainfall) in Sungai Liang were recorded from September to January 2016–2017 and from May to July 2018.

2.2. Determination of Litterfall Production

Above-ground litterfall traps were constructed following Muller-Landau and Wright [47]. Each trap was made by suspending a $1.2 \times 1.2\text{ m}$ piece of nylon window screen with a mesh size of $2 \times 2\text{ mm}$ inside a $1 \times 1\text{ m}$ square frame of polyvinyl chloride (PVC) tubing positioned 80 cm above the ground. One litterfall trap was installed in each of the $10\text{ m} \times 10\text{ m}$ subplots in August 2016, resulting in a total of 96 above-ground litterfall traps installed across four habitats. The location of traps was based on a stratified random design to maintain a minimum distance of 10 m between traps and to avoid positioning traps below canopy gaps. Although infrequent, some traps were damaged by tree falls or disturbed by wild animals. Damaged and missing traps were repaired and replaced within three days, and litter data collected from damaged traps were excluded from subsequent analysis for the affected months only.

Litterfall collection was conducted once a month from October 2016 until September 2017, covering a 12-month sampling period. Litter samples collected were oven-dried at 60°C for 48 h and then sorted into four fractions [48]: leaf litterfall, small wood (from approximately 2 mm to 50 cm fragments), reproductive parts (fruit and flower parts), and trash (any parts that passed through a 1 cm mesh sieve, including dead invertebrates and fecal matter). Each fraction was weighed to the nearest 0.1 g for every trap and collection time, and monthly total litterfall production was calculated by summing the four fractions.

2.3. Determination of Leaf Litter Decomposition Rates

The litter bag technique was used to quantify leaf litter decomposition rates [49,50]. Litter bags ($20 \times 20\text{ cm}$) made from 2 mm nylon mesh to exclude soil macrofauna [51,52] were filled with ca. 20 g of air-dried leaf litter that had been mixed thoroughly. Two leaf litter types were used: (1) *Acacia mangium* phyllodes litter (hereafter, *Acacia* litter) as the standard litter samples, and (2) a mixture comprising leaf litter from native (and invasive) tree species found within the study plots (hereafter, mixed-species litter). *Acacia* litter was collected from the 1 km^2 *A. mangium* plantation only. The mixed-species litter consisted of a mixture of leaf litter collected at three random locations per plot and bulked into one sample per plot for all twenty-four $20 \times 20\text{ m}$ plots. Litter collection was conducted by hand from the forest floor, and only freshly fallen leaf litter with no signs of damage was collected over two months (July–August 2016). All litter collected was then air-dried at room temperature (24°C) for a week and brushed clean of any soil particles, dust, and roots. To determine the initial nutrient concentration of the leaf litter, 10 sub-samples (ca. 20 g each) of air-dried leaf litter from the bulk sample collected in each plot were analyzed at the start of the experiment, and the measurements were then used for the calculation of percentage nutrient release.

A total of 864 litter bags were prepared for the leaf litter decomposition experiment. In each $20\text{ m} \times 20\text{ m}$ plot, two parallel transect lines located 10 m apart and approximately 5 m

long were set up at random within the plot and marked with colored pipes to indicate the positions of *Acacia* litter bags and mixed-species litter bags. Bags were allocated at random along the 48 transect lines. Along each transect, 18 litter bags were buried underneath the forest floor litter (approximately 3 cm depth) at distances of 0.5 m to maximize contact with decomposer organisms. Litter bags were deployed in October 2016, and the first and last collection of litter bags were conducted in October 2016 and September 2017, respectively.

Acacia litter was used to quantify the decomposition rates of *Acacia* litter across the different habitat types. For this *Acacia* litter decomposition experiment, all bags containing *Acacia* litter were deployed in all 24 plots. Mixed-species litter was used to determine the background decomposition rate within each habitat type corresponding to the plot-level mixed-species collection. For this mixed-species litter decomposition experiment, litter bags containing leaf litter collected from its original plot were deployed back into the same plot. Three litter bags per litter type or transect line were collected randomly from each of the 24 plots across four habitats after 14, 21, 42, 84, 168, and 336 days. Retrieved litter samples from each litter bag were cleaned of debris, such as soil, roots, and small insects. Cleaned samples were oven-dried at 60 °C for 72 h, and the dry mass of remaining litter samples in each litter bag was determined.

2.4. Chemical Analyses

Only the leaf fraction from the litterfall production survey was analyzed for nutrient concentrations. For each monthly collection, leaf fractions (ca. 20 g) from one litterfall trap per plot (20 m × 20 m) were chosen at random for analysis. For the leaf litter decomposition experiment, the three litter bags per litter type collected on one sampling day were bulked and treated as one sample. Samples from both studies were analyzed separately for pH and Nitrogen (N), Phosphorus (P), Potassium (K), Calcium (Ca), and Magnesium (Mg) concentrations. Prior to all analyses, oven-dried samples were crushed by hand and ground using a ball mill (Retch GmbH Mixer Mill MM400, Germany).

Measurement of pH followed Perez-Harguindeguy et al. [53] using a calibrated benchtop pH meter (Thermo Scientific Orion Star A211 pH Benchtop Meter, USA). N and P concentrations were determined using the Kjeldahl method by digesting ground samples in concentrated H₂SO₄ and analyzed using a Flow Injector Analyser (FI Astar 5000, Hoganas, Sweden). For analysis of K, Ca, and Mg concentrations, ground samples were acid-digested using a block digester with 70% H₂SO₄ and H₂O₂ and measured using a Flame Atomic Absorption Spectrophotometer (AAS; Thermo Scientific iCE 3300, Sydney, Australia), following a modified procedure described by Allen et al. [54].

2.5. Data Analysis

2.5.1. Litterfall Production

To calculate the monthly total litterfall production in a 1 ha area, dry masses of mean total litterfall and its fractions per habitat type were converted to kg ha⁻¹. Based on the dry masses recorded for the monthly leaf fractions and the nutrient concentrations obtained from sub-sampling the leaf litterfall fractions, the estimated nutrient addition from leaf litterfall and nutrient use efficiency (NUE) index were calculated. The estimated nutrient addition from leaf production in each study site for one year (October 2016–September 2017) was calculated from nutrients (N, P, K, Ca, and Mg) determined in leaf fractions and expressed in mg kg⁻¹ multiplied by dry masses of mean monthly leaf litterfall fractions expressed in kg ha⁻¹, following Dent et al. [52]. Estimated stand-level NUE was obtained by dividing the total annual leaf litterfall fractions dry mass (kg ha⁻¹ yr⁻¹) by the estimated total annual leaf fraction nutrient concentrations (kg ha⁻¹ yr⁻¹), following Vitousek [55,56] and Moran et al. [33]. Nutrient use efficiency (NUE) is used as an index of the nutrient status of tropical rainforest ecosystems [33,55–57]. The NUE of leaf litter production tends to be lower when nutrient concentrations in leaf litterfall increase [55], and values of NUE are negatively related to nutrient availability in soil [55,56].

2.5.2. Leaf Litter Decomposition Rates

For the leaf litter decomposition experiment, the values of percentage litter mass remaining, decay coefficients ($K \text{ day}^{-1}$ and $K \text{ yr}^{-1}$), half-lives ($t_{0.5}$ in days), and percentages of nutrients released and remaining were determined following the formulae described in Dent et al. [52], Sukri [58], and Suhaili [41]. All parameters were calculated separately for *Acacia* and mixed-species litter for all 24 plots at 14, 21, 42, 84, 168, and 336 days of the leaf litter decomposition experiment.

The percentage of litter mass remaining from the litter bags at time t was calculated as follows:

$$\% \text{ of litter mass remaining} = \frac{(\text{mass of dry litter at the start of experiment} - \text{mass of dry litter at time } t)}{\text{mass of dry litter at the start of the experiment}} \times 100\%$$

Decay coefficient ($K \text{ day}^{-1}$) was calculated following Olson [59]:

$$X_t/X_0 = e^{-Kt},$$

where X_0 is the original dry mass of leaf litter in the bags in g, X_t is the dry mass of leaf litter remaining at time t in g, t is the time interval of sampling in days, and K is the decay coefficient (day^{-1}). The value of $K \text{ yr}^{-1}$ is obtained by simply multiplying $K \text{ day}^{-1}$ by 365 days (1 year).

The half-lives ($t_{0.5}$) or the time periods to 50% litter mass loss were calculated following Bockheim et al. [60]:

$$t_{0.5} = \ln(0.5)/-K = 0.693/-K,$$

where K is the decay coefficient on day^{-1} .

Percentages (%) nutrient release and nutrient remaining were calculated following Bragazza et al. [61]:

$$\begin{aligned} \% \text{ nutrient release} &= \frac{(X_0W_0 - X_1W_1)}{X_0W_0} \times 100\% \\ \% \text{ nutrient remaining} &= 100\% - \% \text{ nutrient release}, \end{aligned}$$

where X_0 is the mean nutrient concentration (N, P, K, Ca or Mg) in the leaf litter at the start of the experiment, X_1 is the mean nutrient concentration in the leaf litter at time t , and W_0 and W_1 are litter mass at the start and at time t respectively. Positive values indicate net mineralization rates, and negative values indicate net immobilization rates.

2.6. Statistical Analyses

The effects of forest type (HF vs. MDF), *Acacia* invasion (Intact vs. Invaded), and rainfall (expressed as sliding thirty days total rainfall; STDT) and their interactions on litterfall production (total litterfall, leaf litterfall, small wood, reproductive and trash), were explored through linear mixed-effects (LME) models using the nlme version 3.1-137 package in R [62]. To estimate the total rainfall for every collection month, sliding thirty days total rainfall (STDT) was calculated by summing the rainfall recorded for a particular sampling day and the preceding 29 days [33,58,63]. Forest type, *Acacia* invasion, and rainfall were modeled as fixed effects, and collection months were fitted as random effects. Rainfall was included as a fixed effect in LME models on litterfall production because it has been shown to significantly affect litterfall production in a previous study at the Andulau Forest Reserve [41] and is known to significantly influence litterfall production in aseasonaltropical forests [64,65].

The effects of forest type and *Acacia* invasion and their interactions were separately analyzed using LME on the following variables: (1) pH and concentrations of nutrients (N, P, K, Ca, and Mg) of leaf litterfall fractions, (2) estimated amounts of nutrients (N, P, K, Ca, and Mg) added from leaf litterfall fractions, and (3) estimated indices of stand-level nutrient use efficiency (NUE) of different nutrient (N, P, K, Ca, and Mg) concentrations

from leaf litterfall fractions. Forest type and *Acacia* invasion were modeled as fixed effects, and collection months were fitted as random effects.

The effects of forest type, *Acacia* invasion, and litter type (i.e., *Acacia* litter vs. mixed-species litter) on the following variables: (1) percentage of litter mass remaining and decay coefficients ($K \text{ day}^{-1}$) and (2) pH values and percentage of litter nutrients remaining (N, P, Mg, Ca and K) in the litter bags from day 0 to 336, were also explored using separate LME models. Forest type, *Acacia* invasion, and litter type were modeled as fixed effects, and collection day was fitted as a random effect.

Model selection was based on the protocols by Pinheiro and Bates [66] and Zuur et al. [67]. Models with different variance-covariates and correlation structures were initially fitted via restricted maximum likelihood (REML) and compared using log-likelihood tests and the Akaike Information Criterion (AIC). Models were then fitted using maximum likelihood (ML), and non-significant fixed effects were sequentially deleted from the model to obtain the optimum fixed effects structure [66]. Variance inflation factors [67] of all retained covariates were less than 3, indicating that no collinearity was detected between any of the covariates in the LME model.

For each LME model, pairwise comparisons were conducted within forest types for intact and *Acacia*-invaded habitat types (HF vs. AHF and MDF vs. AMDF) by obtaining the least-square means using the lsmeans version 2.3 package [68]. When necessary, response variables were either arcsine square root (for proportion data only) or \log_{10} -transformed before analysis. All statistical analyses were conducted in R 3.5.1 software [69].

3. Results

3.1. Litterfall Production

3.1.1. Variation in Litterfall Production

For all forest types and habitat types, the relative overall contribution of each litterfall fraction to dry mass of total litterfall production was as follows: leaf litterfall > small wood > reproductive > trash (Table 1). In AHF, leaf litterfall comprised about 71%, small wood comprised 18%, trash 6%, and reproductive 5%, whereas, in AMDF, leaf litterfall comprised about 69%, small wood 17%, reproductive 11% and trash 3% of total litterfall production. The estimated dry mass of mean total litterfall production of the AMDF was significantly higher by 31% compared to MDF ($p < 0.001$; Table 1), but total litterfall production did not differ significantly between HF and AHF ($p > 0.05$; Table 1).

Table 1. Estimated dry masses of mean litterfall production (total litterfall, leaf litterfall, small wood, reproductive and trash) expressed in $\text{t ha}^{-1} \text{ yr}^{-1}$ from 24 litterfall traps in four habitat types (intact and *Acacia*-invaded heath forest, and intact and *Acacia*-invaded mixed dipterocarp forest) over a 12-month period (October 2016–September 2017).

Litterfall Production	Heath Forest		Mixed Dipterocarp Forest	
	Intact	Invaded	Intact	Invaded
Total litterfall	9.51 ± 0.76	9.97 ± 0.64	9.05 ± 0.82	11.9 ± 0.91 ***
Leaf litterfall	6.84 ± 0.60	7.05 ± 0.56	6.45 ± 0.69	8.19 ± 0.63 ***
Small wood	1.97 ± 0.21	1.77 ± 0.20	1.92 ± 0.25	2.07 ± 0.25
Reproductive	0.33 ± 0.05	0.54 ± 0.06 ***	0.40 ± 0.10	1.35 ± 0.28 ***
Trash	0.36 ± 0.07	0.62 ± 0.28	0.29 ± 0.05	0.33 ± 0.08

Values are means ± standard error, SE. Significant differences between intact and invaded habitats within each forest type were detected after a linear mixed effects (LME) analysis followed by an lsmeans pairwise comparisons test at $\alpha = 0.05$ level (***) $p < 0.001$. Values in bold indicate a significant difference in response to *Acacia* invasion within a forest type.

Rainfall (expressed as STDT) significantly influenced leaf litterfall and reproductive parts production ($p < 0.05$; Table S1). High leaf litterfall and reproductive output generally coincided with low rainfall periods in both forest types and regardless of habitat (Figure S1). The highest STDT was recorded in October 2016 (489.9 mm), and the lowest STDT was recorded in April 2017 (123.2 mm).

3.1.2. Variation in Nutrient Concentrations in Leaf Litterfall Production

Leaf fractions in the AHF recorded significantly greater concentrations of mean N and K by 45% and 97%, respectively ($p < 0.001$) but significantly lower concentrations of mean Ca and Mg by 21% ($p < 0.01$) and 17% ($p < 0.001$), respectively, than HF (Table 2). In contrast, leaf fractions in the AMDF recorded significantly higher values of mean pH and N, K, and Ca concentrations (by 4.8%, 55%, 52%, and 88%, respectively; $p < 0.001$; Table 2) but a 5% lower estimated Mg concentration than MDF ($p < 0.01$).

Table 2. Mean pH and nutrient concentrations from leaf litterfall production (N, P, K, Ca, and Mg) expressed in mg g^{-1} from 24 litterfall traps in four habitat types (intact and *Acacia*-invaded heath forest; and intact and *Acacia*-invaded mixed dipterocarp forest) over a 12-month period (October 2016–September 2017).

Leaf Litterfall Chemical Trait	Heath Forest		Mixed Dipterocarp Forest	
	Intact	Invaded	Intact	Invaded
pH	4.70 ± 0.03	4.70 ± 0.03	4.62 ± 0.03	4.84 ± 0.03 ***
N	34.5 ± 0.64	49.9 ± 1.43 ***	45.0 ± 1.63	69.8 ± 0.83 ***
P	1.82 ± 0.05	1.78 ± 0.08	1.77 ± 0.06	2.27 ± 0.31
K	8.18 ± 0.42	16.1 ± 0.67 ***	13.4 ± 0.62	20.4 ± 0.53 ***
Ca	29.1 ± 1.13	24.1 ± 1.00 **	8.89 ± 0.37	16.7 ± 0.65 ***
Mg	10.3 ± 0.22	8.81 ± 0.26 ***	10.2 ± 0.46	9.68 ± 0.18 **

Values are means ± standard error, SE. Significant differences between intact and invaded habitats within each forest type were detected after a linear mixed effects (LME) analysis followed by an lsmeans pairwise comparisons test at $\alpha = 0.05$ level (** $p < 0.01$; *** $p < 0.001$). Values in bold indicate a significant difference in response to *Acacia* invasion within a forest type.

3.1.3. Nutrient Addition from Leaf Litterfall Production

AHF generated a significantly greater annual flux of N (by 47%; $p < 0.001$) and K (by 107%; $p < 0.001$) but less Ca (by 20%; $p < 0.05$) in leaf litter than HF (Table 3). In contrast, the AMDF generated significantly greater fluxes of N, P, K, Ca, and Mg (by approximately 92%; $p < 0.001$, 51%; $p < 0.001$, 94%; $p < 0.001$, 138%; $p < 0.001$ and 19%; $p < 0.01$, respectively) in leaf litter (Table 3).

Table 3. Estimated nutrient addition ($\text{kg ha}^{-1} \text{yr}^{-1}$) from leaf litterfall production from 24 litterfall traps in four habitat types (intact and *Acacia*-invaded heath forest and intact and *Acacia*-invaded mixed dipterocarp forest) over a 12-month period (October 2016–September 2017).

Nutrient Addition	Heath Forest		Mixed Dipterocarp Forest	
	Intact	Invaded	Intact	Invaded
N	238 ± 23.1	352 ± 31.4 ***	298 ± 38.7	571 ± 43.4 ***
P	12.5 ± 1.22	12.7 ± 1.32	11.7 ± 1.47	17.70 ± 1.62 ***
K	55.1 ± 4.70	114 ± 10.5 ***	86.1 ± 9.87	167 ± 13.5 ***
Ca	201 ± 21.3	168 ± 11.7 *	58.0 ± 6.97	138 ± 14.5 ***
Mg	71.7 ± 8.05	62.7 ± 6.09	66.9 ± 8.62	79.5 ± 6.71 **

Values are calculated as mean monthly nutrient concentrations (N, P, K, Ca, and Mg) from leaf litterfall production expressed in mg kg^{-1} multiplied by dry masses of mean monthly leaf litterfall expressed in kg ha^{-1} . Calculations follow Dent et al. [41]. Values are mean ± standard error, SE. Significant differences between intact and invaded habitats within each forest type were detected after a linear mixed effects (LME) analysis followed by an lsmeans pairwise comparisons test at $\alpha = 0.05$ level (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Values in bold indicate a significant difference in response to *Acacia* invasion within a forest type.

3.1.4. Variation in Stand-Level Nutrient Use Efficiency (NUE) of Leaf Litter Production

The stand-level Ca and Mg use efficiencies were significantly greater by 27% and 22%, respectively, in the AHF than in HF ($p < 0.01$; Figure 2). AMDF recorded significantly lower estimated stand-level N and Ca use efficiencies, by 17% and 32%, respectively, but significantly higher stand-level Mg use efficiency by 33% than the MDF ($p < 0.01$; Figure 2). Stand-level P use efficiency did not vary between habitat types ($p > 0.05$; Figure 2).

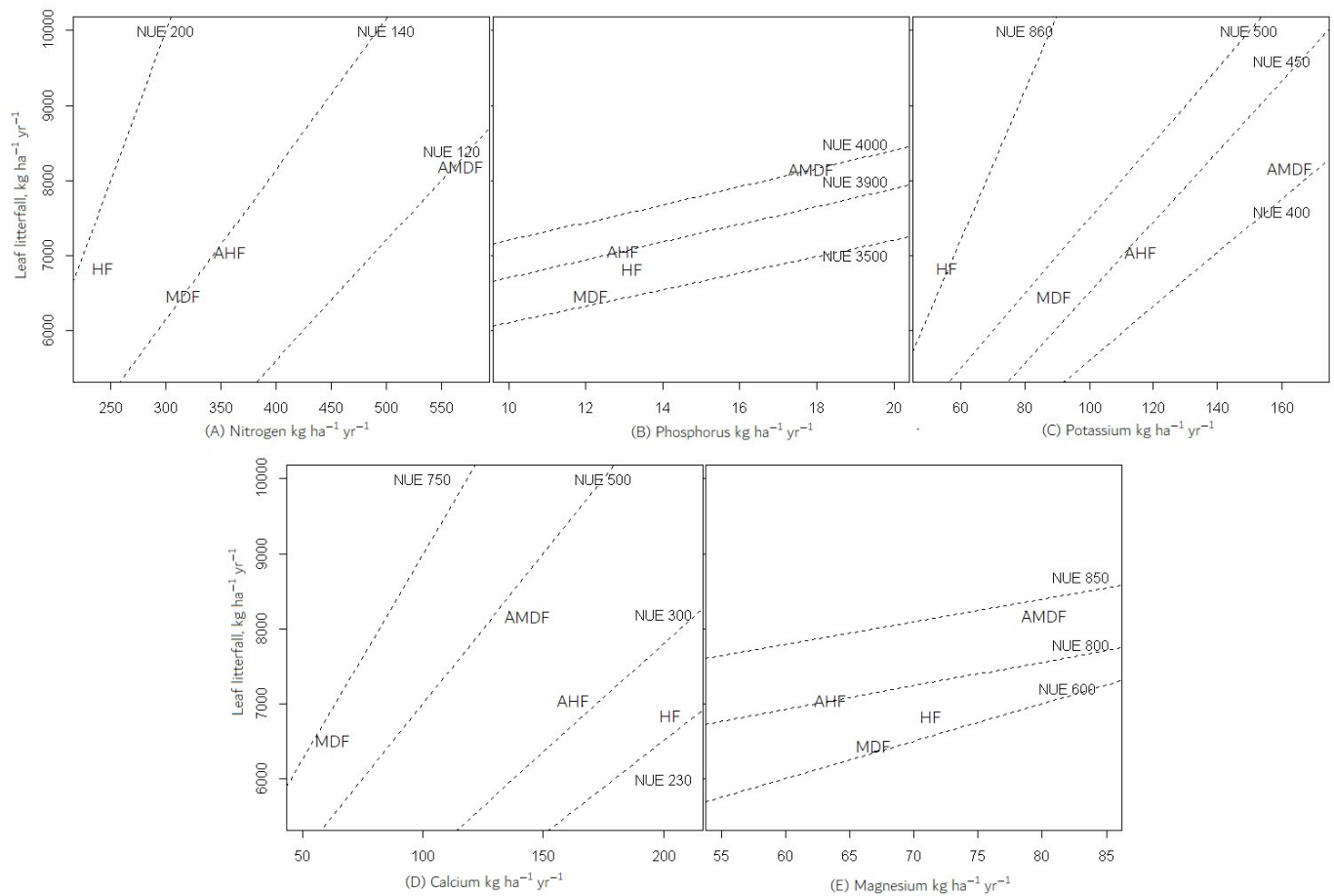


Figure 2. The relationship between the dry mass of leaf litterfall production ($\text{kg ha}^{-1} \text{yr}^{-1}$) and nutrient returns for (A) nitrogen (N), (B) phosphorus (P), (C) potassium (K), (D) calcium (Ca), and (E) magnesium (Mg) through leaf litterfall production ($\text{kg ha}^{-1} \text{yr}^{-1}$) for intact heath forest (HF), *Acacia*-invaded heath forest (AHF), intact mixed dipterocarp forest (MDF), and *Acacia*-invaded mixed dipterocarp forest (AMDF). Dotted lines indicate constant stand-level nutrient use efficiency (NUE).

3.1.5. Variation in Leaf Litter Decomposition Rates

The mean percentages of remaining litter mass at the end of the experiment did not differ significantly between the intact and invaded heath forest habitats for either *Acacia* litter or mixed-species litter ($p > 0.05$; Table 4; Figure S2). However, the mean percentage of *Acacia* litter mass remaining was higher, the decay coefficient value was lower, and the half-life was longer by 56 days ($t_{0.5} = 201$ days) in AMDF than the corresponding MDF across the 336 days of the decomposition experiment (Table 4). Mixed-species litter in AMDF also showed a higher mean percentage of litter mass remaining ($p < 0.001$), lower decay coefficient (K) values ($K \text{ day}^{-1}$ and yr^{-1} ; $p < 0.01$), and longer half-life ($t_{0.5} = 237$ days) compared to the corresponding MDF (Table 4).

Table 4. Mean percentages (%) of litter mass remaining, annual litter decomposition rates (decay coefficients or $K \text{ day}^{-1}$ and yr^{-1}), and half-lives ($t_{0.5}$ in days) at heath forest (intact and *Acacia*-invaded) and mixed dipterocarp forest (intact and *Acacia*-invaded) at the end of litter decomposition experiment using two litter types (*Acacia mangium* litter and mixed-species litter).

Litter Type	Forest Type	Habitat Type	Mean % of Litter Mass Remaining	Decay Coefficient ($K \text{ Day}^{-1}$)	$K \text{ yr}^{-1}$	Half-Life, $t_{0.5}$ (Days)
<i>Acacia</i>	Heath	Intact	22.8 ± 2.16	0.005 ± 0.001	1.73	146
		Invaded	31.8 ± 3.92	0.004 ± 0.001	1.32	192
	Mixed Dipterocarp	Intact	23.9 ± 4.40	0.005 ± 0.001	1.75	145
		Invaded	37.1 ± 4.57 ***	0.003 ± 0.001 **	1.26	201
Mixed-species	Heath	Intact	31.8 ± 1.48	0.004 ± 0.001	1.28	198
		Invaded	35.4 ± 2.92	0.003 ± 0.001	1.18	215
	Mixed Dipterocarp	Intact	31.5 ± 4.59	0.004 ± 0.001	1.36	185
		Invaded	39.8 ± 3.88 ***	0.003 ± 0.001 **	1.07	237

Values for % litter mass remaining and the decay coefficient are means ± standard error, SE. Significant differences between habitat type within forest and litter type were detected after a linear mixed effects (LME) analysis followed by an lsmeans pairwise comparisons test at $\alpha = 0.05$ level (** $p < 0.01$; *** $p < 0.001$). Values in bold indicate a significant difference in response to *Acacia* invasion within a forest type for a specific litter type.

3.1.6. Variation in Litter pH and Nutrients Release

Mean pH values and percentages of nutrients (N, P, K, Ca, and Mg) remaining at day 336 in both *Acacia* litter and mixed-species litter buried in HF did not differ significantly in response to *Acacia* invasion ($p > 0.05$; Table 5). *Acacia* litter buried in AMDF recorded a significantly higher percentage of Ca and Mg remaining than when buried in MDF ($p < 0.001$; Table 5). Mixed-species litter in AMDF had greater pH ($p < 0.001$) and percentages of N ($p < 0.001$), P ($p < 0.05$), Ca ($p < 0.001$), and Mg ($p < 0.001$) remaining than the MDF (Table 5).

Table 5. Mean pH values and mean percentage of nutrients (N, P, K, Ca, and Mg) remaining in litter at day 336 for the litter decomposition experiment. Litter bags containing *Acacia mangium* litter and mixed-species litter were deployed in heath forest (intact and *Acacia*-invaded) and mixed dipterocarp forest (intact and *Acacia*-invaded).

Litter Type	Forest Type	Habitat	pH	N (%)	P (%)	K (%)	Ca (%)	Mg (%)
<i>Acacia</i>	Heath	Intact	2.99 ± 0.11	28.7 ± 2.89	60.9 ± 13.7	2.73 ± 0.27	31.8 ± 5.72	5.45 ± 0.89
		Invaded	3.29 ± 0.19	41.1 ± 4.39	60.4 ± 15.0	4.07 ± 0.39	69.2 ± 13.8	13.5 ± 2.82
	Mixed Dipterocarp	Intact	3.13 ± 0.06	26.6 ± 5.52	41.1 ± 10.6	6.88 ± 1.62	22.7 ± 5.64	8.41 ± 2.76
		Invaded	3.55 ± 0.15	42.5 ± 5.33	48.3 ± 5.07	6.54 ± 0.73	82.6 ± 9.42 ***	23.7 ± 2.80 ***
Mixed-species	Heath	Intact	3.38 ± 0.32	41.7 ± 1.86	57.9 ± 5.98	14.6 ± 1.61	30.5 ± 8.48	10.9 ± 2.87
		Invaded	3.38 ± 0.22	40.0 ± 4.61	77.3 ± 17.3	11.8 ± 2.93	29.6 ± 9.30	16.2 ± 4.68
	Mixed Dipterocarp	Intact	3.18 ± 0.05	32.7 ± 4.41	25.6 ± 7.25	13.9 ± 3.07	29.5 ± 6.63	5.33 ± 1.33
		Invaded	3.28 ± 0.22 ***	45.9 ± 5.43 ***	63.5 ± 12.3 *	6.39 ± 0.73	55.1 ± 7.46 ***	22.8 ± 4.85 ***

Values are means ± standard error, SE, at day 336 of the experiment. Significant differences between habitat types within forest and litter types were detected after a linear mixed effects (LME) analysis followed by an lsmeans pairwise comparisons test at $\alpha = 0.05$ level (* $p < 0.05$; *** $p < 0.001$). Values in bold indicate significant differences in response to *Acacia* invasion within a forest type for a specific litter type.

4. Discussion

4.1. Effects of *Acacia* Invasion on Litterfall Production and the Influence of Rainfall

Consistent with other studies on invasive *Acacia* species [25,41,70], *Acacia* invasion increased total litterfall production and leaf litterfall production in AMDF. However, a similar increase was not observed for AHF, contrary to our hypothesis. We suggest several possible interpretations for this finding. Firstly, stand-level productivity in HF may be limited by low nutrient supply [71], which then constrains additional litter production here as compared to MDF. Additionally, habitat differences may result in *Acacia* allocating more resources below-ground into root production and other mechanisms of supporting nutrient uptake from low nutrient HF soils, which then reduces allocation to canopy Net Primary Production (NPP; [72]), thus decreasing total litterfall production. In a related study at the same site, we found that *Acacia* invasion resulted in significant nutrient enrichment of AMDF soils, indicating that the impact of *Acacia* invasion may be more pronounced in MDF [32].

We also recorded higher reproductive output in both *Acacia*-invaded habitats in contrast to intact forest habitats, similar to findings by Milton [73] and Suhaili [41] on litterfall production of *Acacia cyclops*, *A. longifolia*, *A. melanoxylon*, and *A. saligna* in the South-western Cape of South Africa and *A. mangium* in Brunei, respectively. Invasive species are well-known to possess a high reproductive output (i.e., larger seeds and/or many seeds per unit of time) compared to native species [72–74], which helps to explain their rapid colonization and establishment in new habitats [42].

We found significant effects of rainfall (expressed as STDT) on the production of leaf litter and reproductive parts, indicating that rainfall plays an important role in regulating both leaf production and flowering periods in these forest types and for both intact and invaded habitats. This is consistent with findings from an MDF site in Lambir Hills, Sarawak [65], and global patterns in litterfall production for tropical aseasonal forests [64], where rainfall was the most important environmental influence on litterfall production. *Acacia mangium* typically exhibits high total litterfall production during dry seasons [75], resulting from natural leaf senescence due to drought stress [76,77]. This is consistent with the temporal pattern of litterfall production observed in our study, suggesting that this may be an expression of their inherent response to the seasonality of their native range, even when growing in an environment where moisture availability is unlikely to limit leaf function or lifespan.

Our findings of high reproductive output in the *Acacia*-invaded habitats during low rainfall periods contrast with those of Gaol and Fox [78] and Suhaili [41], who found that reproductive materials peaked during wet seasons at their study sites. Tropical rainforest ecosystems in Southeast Asia typically exhibit episodic patterns of flowering and fruiting [79], so reproductive litterfall patterns may not be solely linked to rainfall [48]. Litterfall production may also be influenced by other environmental factors, such as temperature and radiation, the occurrence of storms or high winds, soil fertility, and biotic factors, such as species composition [80,81]. It is likely that other parameters besides rainfall influence litterfall production to some extent in our tropical forest habitats, though this requires further investigation.

The high leaf litterfall production in the AMDF may inhibit the recruitment of co-occurring native plant species by physically preventing seed germination and seedling establishment [81,82]. High accumulation of *Acacia* litter causes physical damage and mortality to native seedlings [83], and *Acacia* species may release allelopathic compounds that inhibit seed germination and growth [84–86] and are likely toxic to soil decomposer organisms [85–87], although these effects are not adequately studied. Allelopathic compounds can persist longer in soil, resulting in legacy effects that then influence the future establishment of native plant species and potentially the entire ecosystem in the long term [88,89].

4.2. Effects of Habitat Types on Nutrient Concentrations in Leaf Litter

Leaf litterfall from both *Acacia*-invaded habitats recorded higher N and K concentrations and lower Mg concentrations than their intact habitats, indicating greater N and K-return from the plant to the soil [25,26,90]. Symbiotic associations with microorganisms enable N-fixation by *Acacia*, thus enhancing soil N supply and tissue N concentrations [91]. Contrasting patterns were evident for Ca concentrations, as AMDF leaf litterfall recorded higher Ca concentrations, while AHF leaf litterfall recorded lower Ca concentrations than their intact habitats. The reduced Mg concentrations in leaf litterfall in both invaded habitats and the contrast recorded for Ca concentrations in leaf litterfall are consistent with patterns of nutrient use efficiency (NUE; Section 4.4) in these habitats. Distinct patterns in Ca concentrations in leaf litterfall from the two *Acacia*-invaded habitats may be due to the effects of pH on Ca mobilization from soil [50]. *Acacia* invasion into heath forests significantly elevates soil pH, which can increase soil Ca availability [32,92], potentially allowing increased Ca uptake [92]. Further, low soil pH has been linked to decreased cation

stocks in biomass [93], which could also explain the contrasting patterns we recorded in leaf litterfall Ca concentrations.

4.3. Effects of *Acacia* Invasion on Nutrient Addition from Leaf Litter Production

In both forest types, *Acacia* invasion increased N and K nutrient supply via litterfall production. *Acacia*-mediated additions of N and K in leaf litterfall may relieve limitations on productivity by N and K in the nutrient-poor HF and also add N and K to the nutrient-rich MDF. Enhanced leaf litter production in the AMDF also added greater P, Ca, and Mg concentrations, further enriching the MDF soil and enabling greater stand-level productivity. In contrast, leaf litter production in the AHF resulted in lower Ca addition. Calcium is typically a non-limiting nutrient in tropical rainforests, and plants will only take up Ca when needed for cell metabolism [52,94]. However, Ca is a potentially limiting nutrient in HF [95], and the presence of *Acacias* which can utilize Ca^{2+} ions to enhance the structure of their cell walls and membranes [96], appears to have impacted Ca dynamics in our HF sites.

The enhanced returns of N and K in *Acacia*-invaded forests could influence plant growth [97], particularly in N-fixing species of the Fabaceae, such as *Acacia*, because adequate K fertility contributes to efficient N-fixation [92,98]. Increased production of litter with high nutrient concentrations in the two *Acacia*-invaded habitats implies that *Acacia* invasion has major impacts on biogeochemical cycling [24,99], resulting in both high litter accumulation and an up-regulation of net primary productivity. One effect of the increased production of N-rich litter may be a transition to the more open biogeochemical cycling of N and increased organic and available N concentrations in the soil [32,99–101] in response to *Acacia* invasion.

4.4. Effects of *Acacia* Invasion on Stand-Level Nutrient Use Efficiency (NUE) of Leaf Litter Production

HF displayed high stand-level N and K use efficiencies, but AHF displayed high stand-level Ca and Mg use efficiencies. This high stand-level NUE for N in HF is consistent with high N limitation for tropical heath forests overlying spodosols [33,95,102]. Forests with nutrient-poor soils containing low levels of Ca, Mg, and K are typically more efficient in their use of these nutrients than forests overlying nutrient-rich soils [103]. The high Ca and Mg NUE for AHF is, therefore, indicative of efficient recycling of these nutrients and a closed nutrient cycle [104], and these two elements appear to be actively taken up and conserved by *Acacia* for their own use in metabolism and growth. Similarly, AMDF showed high Mg use efficiency only but low NUE for other nutrients. These patterns suggest that *Acacia* may have developed adaptations that enable efficient uptake of selected nutrients [105] or adaptations that minimize nutrient losses after uptake through nutrient resorption prior to leaf senescence to maintain their high level of productivity [103].

Foliar P concentration and inputs of P from leaf litterfall were consistently low compared to other nutrients, resulting in high P use efficiencies across all habitats. Silver [57] compared NUE and soil nutrient status of tropical forests and found significant negative correlations between NUE and total soil P concentrations. Forrester et al. [106] also recorded high cycling of P in annual leaf litterfall production in an *Acacia mearnsii* plantation. The high addition of P in AMDF and P use efficiency indicates a high P demand, common in areas with N-fixing species [107]. Inagaki et al. [26] found a positive correlation between the production of reproductive parts with soil P availability, consistent with our findings of high reproductive output in both *Acacia*-invaded habitats. It is possible that the enhanced inputs of P from leaf litterfall and the inherently high P use efficiency of *Acacia* contributed to the production of reproductive materials in the *Acacia*-invaded habitats, as P is important for plant reproduction, particularly flowering [108].

Although the concentrations of K (and Mg) produced from leaf litterfall can be an indicator of K (and Mg) cycling in tropical rain forests, K (and, to a lesser extent, Mg) are highly mobile elements that are easily leached and readily returned to the forest floor via throughfall, rather than through leaf litterfall [31,33,52]. The higher K concentrations in

leaf litterfall in our invaded plots, coupled with the low K use efficiency in AHF, AMDF, and MDF, suggest that K is rapidly recycled in these habitats. Only HF exhibited high NUE for K, likely due to the lower K concentrations in leaf litterfall and high rates of K leaching from the well-drained HF soils.

4.5. Cumulative Impacts of *Acacia* Invasion on Leaf Litterfall Nutrient Concentrations, Nutrient Addition, and NUE

We detected commonalities in the impacts of *Acacia* invasion on leaf litterfall nutrient concentrations, nutrient addition, and NUE for several elements in our four habitat types. Increased leaf litterfall nutrient concentrations and nutrient addition for N and K, but decreased NUE for N only, were observed in both AHF and AMDF. Inconsistent patterns were seen for Ca and Mg. AHF recorded decreased leaf litterfall Ca and Mg concentrations and the addition of these nutrients and increased NUE, while AMDF recorded increased leaf litterfall Ca concentrations and additions of both Ca and Mg and decreased NUE of both nutrients. *Acacia* invasion resulted in decreased Mg leaf litterfall concentrations and increased NUE in both AHF and AMDF but only increased Mg nutrient addition in the latter. For P, a significantly increased P nutrient addition was recorded only for AMDF, but no significant effects were found for leaf litterfall concentrations and NUE for all other habitat type comparisons.

Here, we suggest that *Acacia* invasion has significantly and similarly impacted N, K, and Mg nutrient cycles in both invaded forest types. *Acacia* invasion elevates N and K concentrations in leaf litterfall, resulting in higher N and K addition in leaf litter, which then decreases NUE as these *Acacia*-invaded forests are relieved from N and K limitations on stand-level productivity [109]. However, *Acacia* invasion appears to exert the opposite effect for Mg, resulting in decreased Mg concentrations in leaf litterfall and increased NUE for both invaded forest types. In contrast, the impacts of *Acacia* invasion upon Ca appear to be more complex, as seen from the distinct patterns we observed. For the Ca-limited HF, *Acacia* invasion seemed to aggravate further Ca limitations in this forest type through decreased Ca leaf litterfall concentration, decreased nutrient addition in litter, and increased NUE. In the MDF, *Acacia* invasion enriched Ca concentrations in leaf litterfall and leaf litter, resulting in the removal of Ca limitations, as was similarly observed for N and K in this forest type. The higher Mg NUE in both invaded forest types and higher Ca NUE in AHF potentially means *Acacia* invasion drives increased cation (Ca and Mg) deficiency. This enhanced cation deficiency can further impact the circulation of these nutrients in the forest ecosystem [56].

In both HF and MDF, N and P are considered the most limiting nutrients [110,111] and are known to influence nutrient mineralization rates [112] and carbon sequestration [113] in lowland tropical forests. Our results have demonstrated that *Acacia* invasion impacted N cycling but did not appear to significantly impact P cycling except for causing increased P addition in AMDF. We suggest that elevated N produced by *Acacia* invasion can result in an N/P imbalance [101] in the invaded habitats. This imbalance affects nutrient mineralization rates and carbon sequestration but may also impact soil microbial communities and nutrient pools [114]. We predict that if the *Acacia* invasion progresses unchecked in our sites, this imbalance will worsen, impacting N and P dynamics and other ecosystem processes in both invaded forests.

4.6. Effects of *Acacia* Invasion on Leaf Litter Decomposition Rates and Nutrient Release Patterns

Our study has demonstrated that *Acacia* invasion induced a slower rate of leaf litter decomposition in MDF but not in HF, which translated to lower nutrient release for selected nutrients in MDF. We suggest that this may be largely due to differences in litter quality, as *Acacia* litter is known to contain high levels of secondary compounds (phenolics and tannins) compared to native species [45,115]. *Acacia* phyllodes also exhibit xeromorphic qualities (thick, hard, with low specific leaf area and high lignin concentrations; [45]), all of which can further lower litter decomposition rates and impede nutrient release. Yelenik et al. [99]

similarly found that the N-rich litter of *A. saligna* invading South African fynbos was slow to decompose, while Suhaili [41] reported *A. mangium* litter decomposed and released nutrients significantly slower than mixed heath forest litter, especially in the *Acacia*-invaded heath forest. It is likely that microbial and mesofaunal decomposers in MDF are not well-adapted to consuming and digesting *Acacia* litter, as MDF tree species typically record lower foliar levels of secondary compounds and non-xeromorphic foliar characteristics [116]. In contrast, native HF tree species show xeromorphic foliar characteristics [116], similar to invasive *Acacia* species.

Differences in tree species composition between invaded and non-invaded plots may have also influenced litter decomposition and nutrient release patterns. Although we did not determine tree species composition in our study plots, *Acacia*-invaded MDF and HF in related studies within the Andulau FR [117,118] and at other sites [28,29] have documented a significantly lower abundance of native tree species. A proportionally lower abundance of dipterocarp trees in our invaded plots could result in a decreased density of ectomycorrhizal fungi [119], further affecting nutrient mineralization. Additionally, invading tree species can alter microsite properties, specifically below their canopy [120,121], and impact soil decomposer communities [122–124], thus affecting leaf litter decomposition rates and nutrient release in the invaded habitats.

5. Conclusions

This study reported the differential effects of *Acacia* invasion on nutrient fluxes via litterfall production and litter decomposition rates between two distinct lowland tropical forest types, MDF and HF, in Brunei Darussalam. In contrast to our hypothesis, we detected stronger overall effects of *Acacia* invasion in MDF, including a greater magnitude of increase in total litterfall; increased leaf litterfall N, K, and Ca concentrations; increased nutrient addition in leaf litterfall; and slower rates of litter decomposition and nutrient release. Conversely, HF appeared less impacted by *Acacia* invasion, with significant effects detected only upon N, K, Ca, and Mg cycles. Our results indicate that nutrient-rich forests may be more vulnerable to invasive *Acacia* through greater modifications to biogeochemical cycles. It is crucial to supplement these findings through future investigations focusing on other determinants of nutrient fluxes such as climatic, soil, and biotic factors; quantifications of above-ground and below-ground biomass; as well as studies of plant traits and soil microbial and decomposer communities that may help to explain the differential patterns in nutrient fluxes uncovered by our work. Our study has demonstrated the complex impacts of *Acacia* invasion on nutrient cycling processes in these contrasting forest types, highlighting an urgent need to fully assess the harmful impacts of invasive *Acacias* on the overall ecosystem functioning and biodiversity of tropical lowland forests.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f13122101/s1>, Table S1: Results of ANOVA from the linear mixed effects model analysis of estimated dry masses of mean total litterfall and its fractions of leaves, small woods, reproductive and trash productions ($\text{t ha}^{-1} \text{yr}^{-1}$) showing the effects of forest, *Acacia* and rainfall (expressed as sliding thirty days totals, STDT) and their interactions. Significant *p*-values are highlighted in bold. Figure S1: Seasonality of mean monthly total litterfall, leaf litterfall, small woods, reproductive and trash productions (kg ha^{-1}), and sliding thirty days total rainfall (STDT; mm) for each litterfall collection month over a 12-month period (October 2016–September 2017) in intact and *Acacia*-invaded heath forest (A–E) and mixed dipterocarp forest (F–J). Values on bar graphs are mean \pm standard error, SE. Sliding 30 days total rainfall (STDT; mm) was calculated by summing the rainfall recorded for a particular sampling day and the preceding 29 days. Figure S2: Mean percentage of original litter mass remaining in litter decomposition bags over time (from day 0 to day 336). Two types of litter (*Acacia* litter and mixed species litter) were deployed in four different habitats: intact heath forest (HF), *Acacia*-invaded heath forest (AHF), intact mixed dipterocarp forest (MDF), and *Acacia*-invaded mixed dipterocarp forest (AMDF). All values are mean \pm standard error, SE.

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resources, R.S.S., F.M. and D.F.R.P.B.; data curation, S.M.J.; writing—original draft preparation, S.M.J. and R.S.S.; writing—review and editing, S.M.J., R.S.S., S.N.S.N., N.E.S., N.A., F.M. and D.F.R.P.B.; supervision, R.S.S. and F.M.; project administration, R.S.S.; funding acquisition, R.S.S. All authors have read and agreed to the published version of the manuscript.

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