Foliar Trait and Nutrient Differences Between Invasive *Acacia* and Native Species in Disturbed Coastal *Kerangas* Forests of Brunei Darussalam

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Abstract

Invasive *Acacia* species are fast-growing exotic trees that were introduced to Brunei Darussalam in the 1990s for plantation forestry and land rehabilitation. Over time, several *Acacia* species have spread beyond planted areas and are now invading disturbed coastal *Kerangas* (tropical heath) forests, raising concerns about their impacts on native vegetation adapted to nutrient-poor conditions. However, information on the functional traits associated with *Acacia* invasion in Brunei's *Kerangas* ecosystems remains limited. This study investigated differences in selected foliar traits and foliar nutrient concentrations among three invasive *Acacia* species (*Acacia auriculiformis*, *Acacia holosericea* and *Acacia mangium*) and six co-occurring native species (*Buchanania arborescens*, *Calophyllum soulattri*, *Dillenia suffruticosa*, *Melastoma malabathricum*, *Ploiarium elegans* and *Symplocos polyandra*,), which represent a range of functional strategies present in disturbed *Kerangas* habitats. Measured foliar traits included leaf thickness, specific leaf area (SLA), leaf dry matter content (LDMC) and green leaf tissue pH, while foliar nutrients assessed were leaf nitrogen content (LNC) and leaf phosphorus content (LPC). Results showed that invasive *Acacia* species, particularly *Acacia auriculiformis* and *Acacia mangium*, exhibited significantly higher SLA, thinner leaves and higher foliar nutrient concentrations compared to native *Kerangas* species. These traits indicate a resource-acquisitive strategy associated with rapid growth and competitive ability under disturbed conditions. In contrast, native *Kerangas* species displayed lower SLA, higher LDMC and greater investment in leaf structural traits, reflecting conservative resource-use strategies consistent with adaptation to nutrient-poor environments. *Dillenia suffruticosa* exhibited trait characteristics similar to invasive *Acacia* species, while *Melastoma malabathricum* showed mixed strategies. Other native species were associated with more conservative trait syndromes. Overall, the findings indicate that differences in foliar traits and nutrient allocation strategies are likely to contribute to the invasion success of *Acacia* species in coastal *Kerangas* forests, with potential implications for the persistence of Brunei's increasingly rare *Kerangas* ecosystems.

Index Terms: leaf nitrogen and phosphorus; plant functional traits; plant invasions; resource-use strategies; specific leaf area

1. Introduction

Invasive alien species are widely recognised as one of the major drivers of biodiversity loss and ecosystem degradation globally, alongside habitat destruction.[1-3] Invasive alien plants are defined as non-native species that establish, spread and cause ecological, economic or social harm in their introduced ranges.[4,5] Their success is often facilitated by anthropogenic disturbance, which creates open niches and reduces the competitive ability of native species.[6,7]

Plant invasions are increasingly interpreted through a functional trait framework, where differences in morphological and physiological traits influence competitive ability, resource acquisition and survival.[8-10] Traits such as specific leaf area (SLA), leaf dry matter content (LDMC), leaf thickness and foliar nutrient concentrations are closely linked to plant strategies along the resource acquisition-conservation spectrum.[11,12] Species with high SLA and elevated foliar nitrogen and phosphorus contents typically exhibit rapid growth and high photosynthetic capacity, whereas species with thicker leaves and higher LDMC tend to adopt conservative strategies suited to nutrient-poor and stressful environments.[9,13]

Among invasive woody plants, Australian *Acacia* species are considered some of the most successful invaders globally.[14] Their invasion success has been attributed to traits such as rapid growth, high nutrient uptake efficiency, nitrogen fixation, and tolerance of disturbance.[15-17] However, while the impacts of *Acacia* invasion on soil processes and nutrient cycling have been widely studied[18-25], comparatively fewer studies have focused explicitly on foliar functional traits as mechanisms underpinning invasion success, particularly in Southeast Asian ecosystems.

In Brunei Darussalam, *Acacia auriculiformis*, *Acacia holosericea* and *Acacia mangium* were introduced in the late 1980s and early 1990s for timber production and land rehabilitation following large-scale infrastructure development.[26] These species have since spread into disturbed habitats and are increasingly encroaching into coastal tropical heath (*Kerangas*) forests.[27,28] *Kerangas* forests are characterised by highly acidic, sandy and nutrient-poor soils, and support a distinctive flora adapted to resource limitation and periodic drought.[29-31] Due to their restricted distribution, frequent fire disturbance and ongoing land-use pressure, coastal *Kerangas* forests in Brunei are particularly vulnerable to invasion.[27]

Native *Kerangas* species typically exhibit xeromorphic leaf traits such as thick, leathery leaves and high structural investment, reflecting conservative resource-use strategies suited to infertile conditions.[32,33] In contrast, invasive *Acacia* species are likely to possess foliar traits that favour rapid resource capture and growth, together with ecological characteristics such as nitrogen fixation that can enhance nutrient acquisition, potentially conferring a competitive advantage over native species in disturbed *Kerangas* habitats. However, investigations comparing foliar traits and nutrient concentrations among invasive *Acacia* and native species in Brunei remain scarce.

This study therefore examined differences in selected foliar traits (SLA, LDMC, leaf thickness and leaf tissue pH) and foliar nutrient concentrations (leaf nitrogen and phosphorus) between three known invasive *Acacia* species and six native species (including *Kerangas* forest species) in disturbed coastal *Kerangas* forests of Brunei Darussalam. By adopting a trait-based approach, this study aims to improve understanding of the functional strategies associated with *Acacia* invasion in nutrient-poor *Kerangas* ecosystems and to inform management and restoration of these increasingly threatened forests.

2. Experimental approach

2.1 Study area and sampling design

Foliar samples were collected from disturbed coastal *Kerangas* forest (*Kerangas* forest; KF) sites in Rimba, Tungku and Berakas, Brunei Darussalam (see ***Figure 1***), during the rainy season (September - October 2014). During this period, mean maximum and minimum air temperatures were 32.1°C and 23.9°C, respectively based on meteorological records from Brunei International Airport.[34] Sampling locations were predominantly roadside margins, open areas and fragmented *Kerangas* patches that had been invaded by *Acacia* and were subject to recurrent anthropogenic disturbance (*e.g.* fire, vegetation clearance). Within these sampling locations, sites were selected where target species were present.

A total of 20 sampling points were established across the study sites, each separated by a distance of >10 m. At each sampling point, foliar samples were collected from all target species present. For each species, foliar material was obtained from five sampling points. Within each sampling point, five mature individuals were selected (individuals spaced >5 m apart). From each individual, five to six sun-exposed, mature, healthy leaves (or phyllodes for *Acacia*) with no visible damage or discolouration were collected as twig sections, sealed in plastic bags and transported to the laboratory for processing. In total, 225 individual plant samples were obtained (9 species × 5 sampling points × 5 individuals = 225).

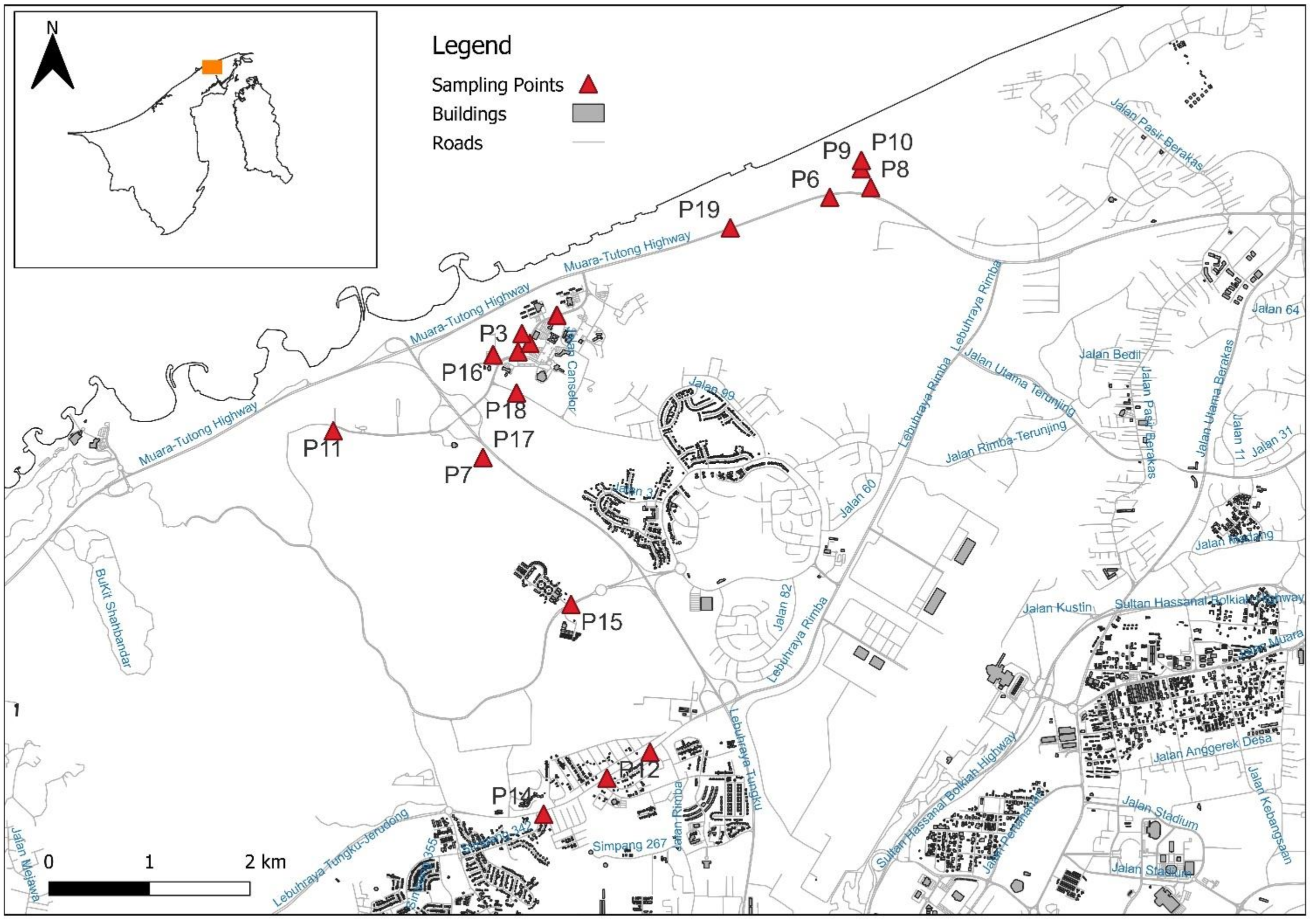

Figure 1. Locations of the 20 sampling points (P1 - P20) in disturbed coastal *Kerangas* forests of Brunei Darussalam. Sampling points were distributed across Rimba, Tungku and Berakas and were separated by a minimum distance of 10 m.

2.2 Species selection and identification

Nine common co-occurring species were selected, comprising three invasive *Acacia* species and six native species. Invasive *Acacia species* comprised *Acacia auriculiformis* A.Cunn. ex Benth., *Acacia holosericea* A.Cunn. ex G.Don and *Acacia mangium* Willd. (Fabaceae), all of which have been recorded as invasive in Brunei Darussalam.[26] Native species comprised tree species typically found in the coastal landscapes where the study was conducted and included *Buchanania arborescens* (Blume) Blume (Anacardiaceae), *Calophyllum soulattri* Burm.f. (Calophyllaceae), *Dillenia suffruticosa* (Griff. ex Hook.f. & Thomson) Martelli (Dilleniaceae), *Melastoma malabathricum* L. (Melastomataceae), *Ploiarium elegans* Korth. (Bonnetiaceae) and *Symplocos polyandra* (Blanco) Brand (Symplocaceae). Of the six native species selected, *C. soulattri* and *S. polyandra* are typically found in intact *Kerangas* forests.[27,35]

Voucher specimens were collected for all taxa and identified at the Brunei National Herbarium (BRUN) with assistance from BRUN staff. *Acacia* identifications were additionally verified by a specialist (Bruce Maslin, *personal communications*). Because *Acacia* phyllodes function as leaves, phyllodes are referred to as "leaves" throughout this study.[36]

2.3 Foliar trait measurements

Four foliar traits were measured: specific leaf area (SLA), leaf dry matter content (LDMC), leaf thickness, and pH of leaf tissue. Trait measurements followed standardised protocols,[37] with minor modifications described below.

For each sampled individual, five fresh leaves were randomly selected for trait measurements. Leaves were gently cleaned (tissue wipe and distilled water) to remove surface contaminants. Leaf area (cm^2) was measured using a leaf area meter (AM300, ADC Bioscientific Ltd., USA). Leaf thickness (mm) was measured with a micrometer screw gauge at three points per leaf lamina and averaged per leaf to the nearest 0.01 mm. Fresh mass (g) was recorded prior to drying. Leaves were oven-dried (65°C) for 48 h to obtain dry mass (g). SLA was calculated as leaf area divided by dry mass, and LDMC as oven-dry mass divided by water-saturated fresh mass, following rehydration of leaves in distilled water for 12 h.[37]

To determine leaf tissue pH, oven-dried leaves were ground using a ball mill (Retsch Mixer Mill MM 400, Germany). Ground material was mixed with distilled water at an 8:1 (water:powder, v/w) ratio following a method modified from Pérez-Harguindeguy *et al*.[37] Samples were shaken for 1 h on a rotary shaker, centrifuged to separate particulate material from the supernatant, and the pH of the supernatant was measured using a calibrated pH meter (Hanna Instruments Ltd., UK).

2.4 Foliar nutrient analysis

Leaf nitrogen content (LNC) and leaf phosphorus content (LPC) were quantified using a micro-Kjeldahl digestion followed by flow injection analysis (FIAstar 5000, Höganäs, Sweden), following the FIAstar 5000 user manual. Briefly, 0.1 g of ground oven-dried leaf material was digested in 5 mL of concentrated H_2SO_4 (96%) using a block digester (Digester BD-46, Lachat Instruments, USA) for 1 h 30 min. Digests were filtered and made up to 50 mL with distilled water prior to analysis for total N and total P. Analytical accuracy was ensured through the use of certified reference materials and procedural blanks included with each digestion batch.

2.5 Statistical analysis

Differences in foliar traits and nutrient concentrations among species were initially explored using one-way analysis of variance (ANOVA) with Tukey's HSD for post-hoc comparisons. Where ANOVA assumptions were violated, data were $\log_{10}$- or Box–Cox-transformed prior to analysis to meet assumptions of normality and homoscedasticity.

To summarise multivariate trait-nutrient relationships among species, all measured variables were further analysed using principal component analysis (PCA). All variables were standardised (mean = 0, SD = 1) prior to PCA to account for differences in measurement units. Species groupings were interpreted post hoc based on their positions within the multivariate trait space revealed by PCA rather than being imposed a priori. To evaluate relationships between leaf functional traits and nutrient concentrations independently of species classification, multiple linear regression analyses were conducted. Leaf nitrogen content (LNC) and leaf phosphorus content (LPC) were modelled as response variables, with foliar traits (specific leaf area, leaf dry matter content, leaf thickness and leaf tissue pH) included as explanatory variables. All statistical analyses were conducted in R.[38]

3. Results

3.1 Differences in foliar traits and nutrients among species in disturbed Kerangas forests

All measured foliar traits differed significantly among the nine study species (one-way ANOVA,

$p < 0.001$; see ***Table 1***). Mean leaf dry mass varied among species ($p < 0.001$; see ***Table 1***), with comparatively higher values in *D. suffruticosa* and *S. polyandra*, while *A. mangium*, *A. holosericea*, *B. arborescens* and *C. soulattri* exhibited overlapping values. Leaf thickness was greatest in *P. elegans*, *A. holosericea*, and *S. polyandra* (see ***Table 1***), whereas the remaining species exhibited comparatively thinner leaves ($p < 0.01$).

Table 1. One-way ANOVA results for differences in foliar traits (leaf thickness, leaf dry mass, leaf dry matter content (LDMC), leaf tissue pH and specific leaf area (SLA)) and foliar nutrient concentrations (leaf nitrogen content (LNC) and leaf phosphorus content (LPC)) among plant species in disturbed coastal *Kerangas* forests. Values are mean ± SE. Different letters within each column indicate significant differences among species based on Tukey's HSD test ($p < 0.05$). Leaf thickness was measured in mm ($\times 10^{-1}$), leaf dry mass in g, SLA in cm^2 g^{-1}, and foliar nutrient concentrations in mg g^{-1}. Where necessary, data were log$_{10}$- or Box–Cox-transformed prior to statistical analysis to meet assumptions of normality and homoscedasticity; untransformed values are presented. Overall significance was determined at $\alpha = 0.05$.

Species	**Thickness**	**Dry mass**	**LDMC**	**pH**	**SLA**	**LNC**	**LPC**
Acacia auriculiformis	29.7 ± 1.0^{b}	0.4 ± 0.1^{c}	414.1 ± 22.3^{a}	5.7 ± 0.1^{a}	99.4 ± 3.6^{b}	23.7 ± 0.5^{a}	0.8 ± 0.1^{a}
Acacia holosericea	39.8 ± 1.5^{a}	0.5 ± 0.1^{c}	399.6 ± 20.9^{a}	5.6 ± 0.1^{a}	68.1 ± 2.5^{c}	23.4 ± 0.5^{a}	0.8 ± 0.1^{a}
Acacia mangium	26.6 ± 0.6^{b}	0.6 ± 0.1^{c}	394.6 ± 28.3^{a}	5.6 ± 0.1^{a}	106.9 ± 5.0^{b}	21.2 ± 0.4^{a}	0.6 ± 0.1^{b}
Buchanania arborescens	27.5 ± 1.2^{b}	0.7 ± 0.1^{c}	457.9 ± 8.9^{a}	5.0 ± 0.1^{b}	77.7 ± 0.4^{c}	10.2 ± 0.5^{d}	0.4 ± 0.1^{c}
Calophyllum soulattri	28.4 ± 0.4^{b}	0.6 ± 0.4^{c}	495.7 ± 17.7^{a}	4.4 ± 0.4^{c}	78.2 ± 0.4^{c}	10.8 ± 0.4^{c}	0.3 ± 0.4^{c}
Dillenia suffruticosa	32.3 ± 1.4^{b}	4.1 ± 0.4^{a}	315.0 ± 10.3^{b}	5.4 ± 0.1^{a}	102.1 ± 3.5^{b}	16.9 ± 0.7^{b}	0.7 ± 0.1^{a}
Melastoma malabathricum	27.1 ± 1.8^{b}	0.1 ± 0.1^{c}	469.5 ± 64.7^{a}	3.4 ± 0.1^{d}	131.7 ± 7.5^{a}	12.1 ± 1.3^{c}	0.5 ± 0.1^{b}
Ploiarium elegans	42.8 ± 2.3^{a}	0.2 ± 0.1^{c}	331.9 ± 41.2^{b}	3.3 ± 0.3^{d}	96.5 ± 5.1^{b}	12.1 ± 0.4^{c}	0.4 ± 0.1^{c}
Symplocos polyandra	39.5 ± 0.4^{a}	1.8 ± 0.4^{b}	398.0 ± 17.7^{a}	5.1 ± 0.4^{b}	72.0 ± 0.4^{c}	9.4 ± 0.4^{d}	0.4 ± 0.4^{c}
P-value	**< 0.001**	**< 0.001**	**< 0.01**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**

Leaf tissue pH differed significantly among species ($p < 0.001$; see ***Table 1***), with the lowest values recorded for *P. elegans* (3.3 ± 0.3) and *M. malabathricum* (3.4 ± 0.1). Most species exhibited high leaf dry matter content (LDMC), with significantly lower values observed only in *D. suffruticosa* and *P. elegans* (p < see 0.01; see ***Table 1***).

Specific leaf area (SLA) was highest in *M. malabathricum*, followed by relatively high values in *A. mangium*, *A. auriculiformis*, *D. suffruticosa* and *P. elegans*. In contrast, lower SLA values were observed in *A. holosericea*, *S. polyandra*, *B. arborescens* and *C. soulattri* (see ***Table 1***). Specific leaf area (SLA) differed markedly among species ($p < 0.001$; see ***Table 1***).

Foliar nutrient concentrations also differed among species ($p < 0.001$; see ***Table 1***). Leaf nitrogen content (LNC) was highest in the invasive *Acacia* species (*A. mangium*: 21.2 ± 0.4 mg g^{-1}; *A. auriculiformis*: 23.7 ± 0.5 mg g^{-1}; *A. holosericea*: 23.4 ± 0.5 mg g^{-1}), intermediate in *D. suffruticosa*: 16.9 ± 0.7 mg g^{-1}; *P. elegans*:

12.1 ± 0.4 mg g^{-1}; *M. malabathricum*: 12.1 ± 1.3 mg g^{-1}, and lowest in *B. arborescens:* 10.2 ± 0.5 mg g^{-1}; *S. polyandra*: 9.4 ± 0.4 mg g^{-1}; *C. soulattri*: 10.8 ± 0.4 mg g^{-1}.

Leaf phosphorus content (LPC) was significantly higher in all *Acacia* species and *D. suffruticosa* (*A. mangium*: 0.6 ± 0.1 mg g^{-1}; *A. auriculiformis*: 0.8 ± 0.1 mg g^{-1}; *A. holosericea*: 0.8 ± 0.1 mg g^{-1}; *D. suffruticosa*: 0.7 ± 0.1 mg g^{-1}; see ***Table 1***) compared to the remaining native species examined, which exhibited consistently lower LPC values.

3.2 Multivariate variation in foliar traits and nutrients among species groups

Principal component analysis (PCA) based on five foliar traits (leaf dry mass, leaf thickness, LDMC, SLA and leaf tissue pH) and two foliar nutrients (LNC and LPC) explained 77.5% of the total variation in the dataset across the first three axes (see ***Table 2***). The first principal component (PC1; 36.1%) represented a gradient associated with foliar nutrient status and leaf chemistry, with strong negative loadings for leaf nitrogen content (LNC), leaf phosphorus content (LPC) and leaf tissue pH (see ***Table 2***). The second principal component (PC2) explained 23.2% of the variation and represented a structural leaf trait gradient characterised by increasing leaf thickness and dry mass, while the third principal component (PC3) explained 18.2% of the variation and was associated with increasing LDMC and decreasing SLA.

Table 2. Principal component analysis (PCA) loadings of five foliar traits (leaf dry mass, leaf thickness, leaf tissue pH, specific leaf area (SLA) and leaf dry matter content (LDMC)) and two foliar nutrient variables (leaf nitrogen content (LNC) and leaf phosphorus content (LPC)) for invasive and native species in disturbed coastal *Kerangas* forests. The percentage of total variation explained by each principal component axis is shown. Loadings represent correlation coefficients between variables and principal components; variables with the highest absolute loadings on each axis are indicated in bold.

Parameters	Principal component axes		
	1	2	3
% of total variation explained	36.1	23.2	18.2
Cumulative % variation explained	36.1	59.3	77.5
Loadings of foliar traits and foliar nutrients properties			
Thickness	0.04	**0.63**	-0.14
Dry mass	-0.22	**0.37**	-0.20
Leaf dry matter content, LDMC	0.25	-0.33	**0.62**
Specific leaf area, SLA	-0.02	-0.54	**-0.60**
pH of leaf tissues, pH	**-0.49**	0.09	0.43

Leaf nitrogen content, LNC	**-0.56**	-0.20	0.02
Leaf phosphorus content, LPC	**-0.58**	-0.11	-0.03

The PCA ordination (PC1 vs PC2) revealed multivariate variation in foliar traits and nutrient among species (see ***Figure 2***). *Acacia mangium* and *A. auriculiformis* were associated with higher SLA and elevated foliar nutrient concentrations (LNC and LPC), whereas *B. arborescens* and *C. soulattri* aligned with higher LDMC values. *Ploiarium elegans* and *S. polyandra* were characterised by greater leaf thickness, while *A. holosericea* and *D. suffruticosa* occupied intermediate positions associated with variation in dry mass and leaf tissue pH. *Melastoma malabathricum* formed a distinct cluster in ordination space, reflecting its unique foliar trait combination.

3.3 Relationships between foliar traits and nutrient concentrations

Multiple regression analysis was used to examine how foliar traits predicted nutrient concentrations across species without pre-classifying species into ecological groups. Leaf nitrogen content (LNC) was significantly explained by the combined effects of leaf traits ($R^2 = 0.53$, $F = 11.21$, $p < 0.001$). Specific leaf area (SLA) and leaf tissue pH showed strong positive relationships with LNC ($p < 0.001$), while leaf thickness had a smaller but significant positive effect ($p < 0.05$). Leaf dry matter content (LDMC) did not significantly contribute to the model.

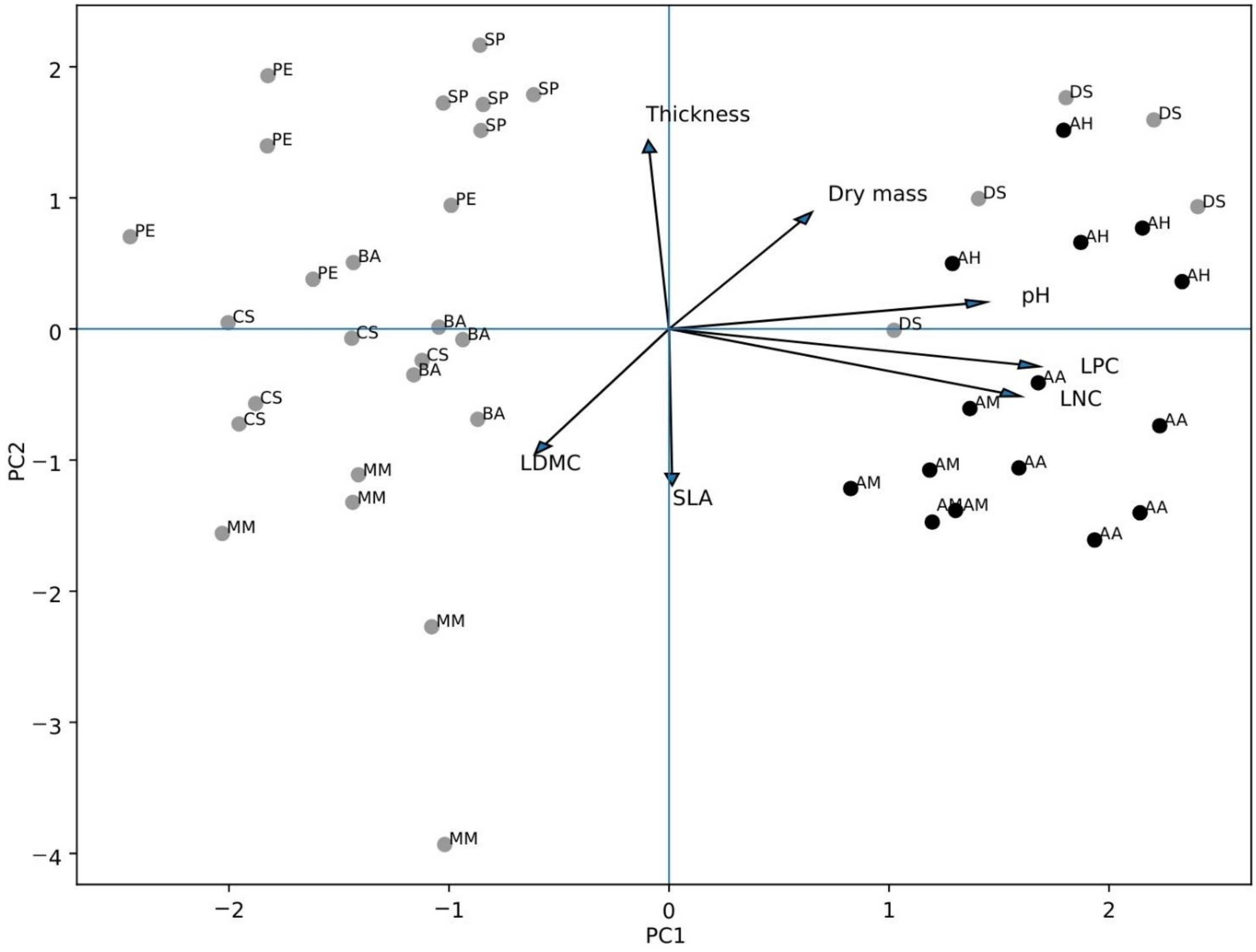

Figure 2. Principal component analysis (PCA) of foliar traits and nutrient concentrations based on individual replicate measurements. Each point represents an individual sample and is labelled according to species abbreviations: AA = *Acacia auriculiformis*, AH = *Acacia holosericea*, AM = *Acacia mangium*, BA = *Buchanania arborescens*, CS = *Calophyllum soulattri*, DS = *Dillenia suffruticosa*, MM = *Melastoma malabathricum*, PE = *Ploiarium elegans*, and SP = *Symplocos polyandra*. Points are coloured to distinguish invasive *Acacia* species (black) from native species (grey). Arrows indicate the direction and relative contribution of foliar traits and nutrient variables.

Similarly, leaf phosphorus content (LPC) was significantly related to foliar traits ($R^2 = 0.54$, $F = 11.68$, $p < 0.001$). SLA and leaf tissue pH again showed strong positive relationships with LPC ($p < 0.001$), while leaf thickness had a smaller but significant effect ($p < 0.05$). LDMC was not a significant predictor. Regression analysis showed that SLA and leaf tissue pH were the strongest predictors of both leaf nitrogen and phosphorus concentrations (***Table 3***). These results indicate that acquisitive leaf traits, particularly higher specific leaf area (SLA) and higher leaf tissue pH, are strongly associated with increased foliar nutrient concentrations across species, supporting the functional gradients subsequently observed in the PCA ordination.

Table 3. Results of multiple linear regression analyses examining relationships between foliar traits (specific leaf area, leaf dry matter content, leaf thickness and leaf tissue pH) and foliar nutrient concentrations (leaf nitrogen content, LNC; leaf phosphorus content, LPC) across nine species in disturbed coastal *Kerangas* forests. β represents regression coefficients. Significant predictors are indicated by asterisks (*p < 0.05; **p < 0.01; ***p < 0.001), while ns indicates non-significant results.

Predictor	**LNC β**	**t**	**Sig.**	**LPC β**	**t**	**Sig.**
Constant	-36.259	-3.03	ns	-1.282	-2.95	ns
SLA	**0.160**	4.04	***	**0.0058**	4.01	***
LDMC	0.007	0.81	ns	0.000075	0.24	ns
Thickness	**0.284**	2.21	*	**0.0108**	2.31	*
Leaf tissue pH	**5.188**	6.40	***	**0.188**	6.40	***
Response variable	**R²**	**Adjusted R²**	**F**	**Sig.**		
LNC	0.529	0.481	11.21	***		
LPC	0.539	0.493	11.68	***		

4. Discussions

4.1 Foliar trait variation and implications for Acacia invasion

The invasive *Acacia* species, particularly *A. auriculiformis* and *A. mangium*, exhibited foliar traits characteristic of a resource-acquisitive strategy, including higher specific leaf area (SLA) and elevated foliar nitrogen and phosphorus concentrations, coupled with relatively lower investment in structural leaf traits such as leaf thickness. High SLA is strongly associated with rapid resource capture, high photosynthetic capacity and fast growth rates.[9,39,40] These traits are consistent with, and likely facilitate, the rapid establishment and spread of *A. auriculiformis* and *A. mangium* observed in disturbed *Kerangas* forests in Brunei.

Although thinner leaves and lower LDMC may reduce mechanical defense against herbivory and environmental stress,[9,39] the growth advantages conferred by high SLA may outweigh these costs in disturbed habitats where light and space are readily available.[41,42] Similar trait syndromes have been reported for invasive *Acacia* species in South Africa and Europe, where high SLA and elevated foliar nutrient contents were linked to invasion success.[16,17,43]

In contrast, *A. holosericea* exhibited lower SLA and greater leaf thickness, indicating a more conservative growth strategy relative to *A. auriculiformis and A. mangium*. This species was also less frequently encountered at the study sites and has also been recorded at lower abundance in invaded areas within the coastal landscape of the study site,[27] which appears to be consistent with its comparatively slower growth strategy. This intra-generic variation suggests that not all *Acacia* species share identical invasion strategies. Greater investment in tissue protection rather than rapid growth may partly contribute to the comparatively lower abundance of *A. holosericea* observed at the study sites, consistent with previous findings that slower-growing *Acacia* species tend to be less invasive.[44]

4.2 Trait-based strategies among native species in disturbed Kerangas forests

Native species exhibited substantial variation in foliar traits, reflecting a range of resource-use strategies associated with disturbance conditions in *Kerangas* forests. These traits are characteristic of plants adapted to the highly acidic, sandy and nutrient-poor soils of *Kerangas* forests.[31-33] Investment in thicker, tougher leaves enhances tissue longevity and resistance to environmental stress but typically results in slower growth rates.[37,45]

The observed foliar traits of native species in this study are consistent with previous studies in Brunei, Sarawak and Kalimantan, which reported xeromorphic leaf characteristics as key adaptations to drought, low nutrient availability and high irradiance in heath forests.[30,46,47] While these traits favour persistence under harsh conditions, they may place native species at a competitive disadvantage when confronted with fast-growing invasive species following disturbance.

Native species exhibited substantial variation in foliar traits, reflecting differences in functional strategies within disturbed *Kerangas* environments. Patterns observed in the PCA indicated that *D. suffruticosa* grouped closely with the invasive *Acacia* species, suggesting convergence in trait syndromes associated with rapid resource acquisition. Similar to *Acacia*, *D. suffruticosa* exhibited relatively high SLA and elevated foliar nutrient concentrations, supporting a resource-acquisitive strategy that facilitates rapid establishment. This is consistent with its well-documented ability to colonise open and degraded habitats, where it often acts as an early successional or pioneer species.[48]

In contrast, several native species (*B. arborescens*, *C. soulattri*, *P. elegans* and *S. polyandra*) were associated with more conservative trait combinations, characterised by lower SLA, greater investment in structural traits and comparatively lower foliar nutrient concentrations. These traits are indicative of strategies favouring persistence under nutrient-poor and stressful conditions typical of *Kerangas* ecosystems.[31-33] *Melastoma malabathricum* occupied a distinct position in trait space, reflecting a unique combination of relatively high SLA and moderately high LDMC, suggesting efficient resource capture combined with a degree of leaf tissue durability, which may explain its widespread distribution in disturbed habitats in Brunei.[26] Although frequently associated with disturbed environments, its trait profile does not align closely with either strongly acquisitive or conservative strategies, highlighting its functional versatility. Lower leaf tissue pH observed in *M. malabathricum* and *P. elegans* may also function as a defense against herbivory, as acidic leaf tissues are often less palatable.[37] Previous studies have linked low leaf tissue pH in *M. malabathricum* to high concentrations of acidic polysaccharides and phenolic compounds, which are associated with increased chemical defence against herbivores.[49-50] Such traits suggest greater investment in defence rather than rapid resource acquisition.

4.3 Foliar nutrient concentrations and competitive advantage

Regression analysis showed that higher specific leaf area and leaf tissue pH were strongly associated with elevated foliar nitrogen and phosphorus concentrations across species, indicating that acquisitive leaf traits are closely linked to enhanced nutrient status, which may contribute to competitive advantage. Foliar nitrogen and phosphorus concentrations were generally higher in invasive *Acacia* species than in native species, supporting the hypothesis that nutrient acquisition plays a central role in *Acacia* invasion success. However, *D. suffruticosa* exhibited relatively high foliar nutrient concentrations, particularly for phosphorus, where it did not differ significantly from *Acacia* species (see ***Table 1***). This suggests that *D. suffruticosa* shares similar nutrient acquisition strategies with invasive *Acacia*, consistent with its positioning in the PCA. High leaf nitrogen content is closely linked to photosynthetic capacity due to its association with Rubisco and other photosynthetic proteins,[9,51] while phosphorus is essential for energy transfer during photosynthesis.[52,53] Elevated foliar nutrient concentrations may therefore enhance growth and competitive ability of *Acacia* species in disturbed *Kerangas* forests. Such advantages are likely amplified in the inherently nutrient-poor *Kerangas* environment, where even modest differences in nutrient acquisition can translate into substantial competitive effects. Species capable of maintaining higher foliar nutrient concentrations, such as *Acacia* and *D. suffruticosa*, may therefore be better positioned to exploit disturbed conditions. This convergence further supports the trait-based grouping observed in the PCA, where *D. suffruticosa* clustered with *Acacia* species.

The ability of *Acacia* species to fix atmospheric nitrogen likely contributes to their higher foliar nitrogen content.[26] As the other species examined in this study do not possess nitrogen-fixing capabilities, this trait may provide *Acacia* species with an additional advantage in nutrient-poor systems. Similar patterns have been reported in invaded ecosystems elsewhere, where nitrogen-fixing invaders increased their competitive dominance through enhanced nutrient uptake and allocation to leaves.[54,55]

4.4 Implications and future research

Overall, the results indicate that the invasion success of *A. auriculiformis* and *A. mangium* in disturbed *Kerangas* forests is strongly associated with a combination of high SLA, elevated foliar nutrient concentrations and low investment in tissue protection. However, *A. holosericea* appears to possess leaf traits that do not favour successful invasion to the same extent as *A. mangium* and *A. auriculiformis.* In contrast, many native *Kerangas* species rely on conservative strategies that favour survival over rapid growth, potentially increasing their vulnerability to displacement following disturbance. However, this pattern is not uniform across all native species. *Dillenia suffruticosa* exhibited trait characteristics similar to invasive *Acacia*, including relatively high foliar nutrient concentrations and SLA, indicating a more resource-acquisitive strategy. *Melastoma malabathricum* displayed a combination of acquisitive and conservative traits, suggesting greater functional flexibility. These variations highlight that responses of native species to disturbance are heterogeneous and depend on their underlying trait syndromes.

While this study focused on foliar traits, future research should integrate measurements of relative growth rates, photosynthetic capacity and leaf lifespan to further elucidate trait-function relationships. Expanding sampling to include additional *Kerangas* forest species and true pioneer species, as well as other forest types (e.g. mixed dipterocarp, peat swamp and mangrove forests), would improve understanding of how habitat context influences invasion strategies.[56,57]

In conclusion, this study provides novel insights into the functional trait mechanisms underpinning *Acacia* invasion in Brunei's coastal *Kerangas* forests. Understanding these trait-based differences is critical for predicting invasion dynamics and informing management and restoration strategies aimed at conserving these increasingly rare and vulnerable ecosystems.

5. Conclusion

This study demonstrates clear differences in foliar traits and nutrient concentrations among invasive *Acacia* species and co-occurring native species in disturbed coastal *Kerangas* forests of Brunei Darussalam. Invasive *A. mangium* and *A. auriculiformis* exhibited resource-acquisitive strategies characterised by high specific leaf area and elevated foliar nitrogen and phosphorus concentrations, coupled with reduced investment in structural leaf traits. Trait-based analyses further revealed that not all native species followed conservative strategies. *Dillenia suffruticosa* exhibited trait characteristics similar to invasive *Acacia*, including relatively high foliar nutrient concentrations, consistent with its ability to colonise disturbed environments. *Melastoma malabathricum* displayed a combination of acquisitive and conservative traits, indicating greater functional flexibility, while other native species were associated with more conservative trait syndromes linked to persistence under nutrient-poor conditions. These findings highlight that invasion success in *Kerangas* ecosystems is not solely determined by the presence of acquisitive traits, but also by the capacity to sustain these strategies under nutrient-limited conditions. In this context, the ability of *Acacia* species to fix atmospheric nitrogen, a trait absent in the native species examined, likely provides a key advantage by enabling consistently higher foliar nitrogen concentrations and supporting more competitive growth strategies in nutrient-poor environments.

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