Journal of Tropical Ecology

www.cambridge.org/tro

Research Article

Cite this article: Jaafar SM, Metali F, and Sukri RS (2022) *Acacia* invasion differentially impacts soil properties of two contrasting tropical lowland forests in Brunei Darussalam. *Journal of Tropical Ecology* **38**, 259–266. https://doi.org/10.1017/S0266467422000141

Received: 16 March 2020
Revised: 1 September 2021
Accepted: 20 February 2022
First published online: 28 March 2022

Keywords:
Acacia; Borneo; edaphic properties; exotic plants; heath forests; invasive species; Kerangas forests; mixed dipterocarp forests

Author for correspondence:
Rahayu Sukmaria Sukri,
Email: rahayu.sukri@ubd.edu.bn

Acacia invasion differentially impacts soil properties of two contrasting tropical lowland forests in Brunei Darussalam

Salwana Md. Jaafar[1,2], Faizah Metali[1] and Rahayu Sukmaria Sukri[2]

[1]Environmental and Life Sciences Programme, Faculty of Science, Universiti Brunei Darussalam, Jln Tungku Link, BE 1410, Brunei Darussalam and [2]Institute for Biodiversity and Environmental Research, Universiti Brunei Darussalam, Jln Tungku Link, BE 1410, Brunei Darussalam

Abstract

Invasive *Acacia* species are known to modify soil properties, although effects are often site-specific. We examined the impact of *Acacia* species on the soils of intact and invaded habitats of two contrasting tropical lowland rain forest types in Brunei Darussalam: heath forest (HF) and mixed dipterocarp forest (MDF). Impacts on soil properties differed between the two forest types. Overall, *Acacia*-invaded HF soil recorded significantly higher gravimetric water content, pH and total P, K and Ca compared to the intact HF soil. In contrast, invaded MDF soil exhibited significantly higher organic matter content and total soil N, P, K and Mg compared to its intact habitat. *Acacia*-invaded MDF soils were more nutrient-enriched than *Acacia*-invaded HF soils by the addition of threefold, threefold and fourfold total soil P, K and Mg, respectively. The positive effect of addition of total soil Ca was, however, fourfold greater in HF soil than MDF soil, indicating that the magnitude of impact on soil properties was strongly site-specific. Overall, *Acacia* invasion significantly impacted soil properties in nutrient-rich MDF more than those of nutrient-poor HFs, indicating a potential vulnerability of MDFs to invasion.

Introduction

Many plant invasion studies focus on the impact of invasive plants on ecosystem functions, such as nutrient and hydrological cycles (Morris *et al.* 2011, Yelenik & D‘Antonio 2013). Invasive plant species can also modify edaphic properties, including soil pH (Kourtev *et al.* 2003), organic matter content and nutrient concentrations (Inagaki *et al.* 2011, Koutika *et al.* 2014), and their impact on soil properties vary due to inherent soil differences even at small scales. Studies have reported increased soil nutrients availability in invaded areas (Liao *et al.* 2008), the opposite or no change patterns (Tanaka *et al.* 2015) or the same invasive species may have different impacts depending on local conditions (Dassonville *et al.* 2008). Further, modifications in soil properties in invaded areas are influenced by the composition of invasive species and pre-invasion state of the soil (Ehrenfeld 2003).

Among invasive plants, the genus *Acacia* contains some of the top plant invaders worldwide (Richardson & Rejmanek 2011). Exotic *Acacia* species have spread and established in tropical Southeast Asia, where they were widely utilised in timber plantations (Koutika & Richardson 2019, Peh 2010). The ability of *Acacia* to fix atmospheric N (Nsikani *et al.* 2018, Perreira *et al.* 2018) enable them to grow and establish in acidic soils with poor nutrient conditions (Peh 2010). Invasive Acacias alter soil nutrient availability (Wang *et al.* 2015), enriching resources in nutrient-poor invaded habitats (Marchante *et al.* 2009, Nsikani *et al.* 2018), resulting in a competitive advantage over native species.

Acacia invasion often increase organic matter and total N concentrations and elevates inorganic N availability in soils (Yelenik *et al.* 2007). Although most *Acacia*-invaded habitats have nutrient-poor soils characterised by low pre-invasion levels of N (Marchante *et al.* 2009), nutrient-rich soils can also become prone to invasion (Witkowski 1991, Zefferman *et al.* 2015). In nutrient-rich soils, invasive species preferentially utilise available resources first rather than manufacturing their own nutrients through N-fixation and *Rhizobium* or microbes do not initiate N-fixing as the plants are not nutrient-deprived (Morris *et al.* 2011, Witkowski 1991).

In Brunei Darussalam, Northwest Borneo, *Acacia* species were introduced in the 1990s and currently have an established population, often present as the dominant tree species along major highways and roadsides (Osunkoya *et al.* 2005). Since this initial introduction, Acacias have spread into degraded, burnt areas and secondary forest habitats in both tropical heath and mixed dipterocarp forests (Jambul *et al.* 2020, Osunkoya & Damit 2005, Tuah *et al.* 2020). Heath forests (HFs) and mixed dipterocarp forests (MDFs) are two lowland tropical rain forest types in Borneo, with the latter comprising the main forest type in Brunei Darussalam (Ashton *et al.* 2003). Heath forest soils are sandy, well-drained with low nutrient and organic matter content and poor water-holding capacity (Jaafar *et al.* 2016, Metali *et al.* 2015). In contrast, mixed dipterocarp forest soils are clayey, poorly drained with high nutrient content and water-holding capacity (Jaafar *et al.* 2016, Sukri *et al.* 2012).

Investigating the impacts of invasion on soil properties is a key first step into quantifying *Acacia* invasion effects on these two distinct tropical forests. Within Brunei Darussalam, most studies to date focus on the impact of *Acacia* invasion on HFs (Ibrahim *et al.* 2021, Jambul *et al.* 2020, Le *et al.* 2018, Osunkoya *et al.* 2005, Suhaili *et al.* 2015, Tuah *et al.* 2020, Yusoff *et al.* 2019) which are highly vulnerable to fire and drought and are increasingly disturbed for urbanisation (Din *et al.* 2015). However, the spread of *Acacia mangium* into disturbed MDFs in Brunei (RS Sukri, unpubl. data) indicate an urgent need to study the effects of invasive Acacias on MDF soils. Our study therefore aimed to assess the impact of *Acacia* invasion on soil physicochemical properties of HFs and MDFs in Brunei Darussalam. We formulated two research questions:

1. Does *Acacia* invasion alter soil physicochemical properties (gravimetric water content, organic matter, bulk density and concentrations of total N, P, K, Ca and Mg) in heath and mixed dipterocarp forests?
2. Does the magnitude of changes in soil properties caused by *Acacia* invasion differ between heath and mixed dipterocarp forests?

Methods

Study sites

Four habitat types within the Andulau Forest Reserve (4°37’60.00”N, 114°31’60.00”E) in Brunei Darussalam were compared: heath forest (HF), *Acacia*-invaded heath forest (AHF), mixed dipterocarp forest (MDF) and *Acacia*-invaded mixed dipterocarp forest, (AMDF; Figure 1). The Andulau Forest Reserve primarily contains MDFs with undulating topography and elevation range of 2.7° – 27.6° (Sukri *et al.* 2012) with pockets of HFs (Davies & Becker 1996). The climate of Brunei Darussalam is aseasonal with mean monthly rainfall of 162.6 mm and mean monthly temperature of 28.2°C recorded at the Sungai Liang Agricultural station (c. 2 km away from Andulau) in 2016 (Department of Agriculture and Agrifood, unpubl. data).

Intact forest (HF and MDF) plots represented areas with no *Acacia* invasion and were selected from within primary forest areas with no previous history of logging or man-made disturbance (Forestry Department, pers. comm.). The *Acacia*-invaded (AHF and AMDF) plots were selected based on the presence of *Acacia* trees inside and outside the study plots. Both AHF and AMDF plots selected showed comparatively similar degree of invasion, with similar density and total number of *Acacia* trees (n = 4 to 7 trees) of the same estimated age (≤ 20 years) in all the established plots. AHF and AMDF plots had more open canopies than HF and MDF plots (SM Jaafar, pers. obs.). Plots within the same forest type (i.e. MDF and AMDF plots and HF and AHF plots) were located c. 1 km apart.

Soil sampling

Fieldwork was carried out in February until March 2016 during the wet season (rainfall ≥ 100 mm, Becker 1992). To investigate habitat variation in soil physicochemical properties, six 20 × 20 m plots were randomly set up within accessible locations in each habitat type. Distances between plots within the same habitat range from c. 50 to 100 m. The 20 × 20 m plots were further subdivided into 10 × 10 m subplots. Within each subplot, one soil core was sampled at a random position using a soil auger at two depths: topsoil (0 – 15 cm) and subsoil (30 – 50 cm). The litter layer was cleared prior to soil sampling. A total of 192 soil samples were collected (n = 96 subplots × 2 depths) from 24 plots at the four habitat types.

Measurements of soil parameters

Fresh soils were analysed for pH in distilled water, gravimetric water content (GWC) and bulk density (Allen *et al.* 1989). The remaining fresh soil samples were air-dried, ground and passed through a 2.0 mm sieve and stored at room temperature. Air-dried soil samples were analysed for concentrations of total N, P, K, Ca and Mg as well as organic matter (OM) content (Allen *et al.* 1989). Total N and P concentrations were determined using the Kjeldahl method by digesting each soil sample in concentrated H_2SO_4 and analysed using a Flow Injector Analyser (FIAstar 5000, Hoganas, Sweden). For analysis of total K, Ca and Mg concentrations, air-dried soil samples were acid-digested using a block digestor with 70% H_2SO_4 and H_2O_2, following a procedure modified from Allen *et al.* (1989) and measured using a Flame Atomic Absorption Spectrophotometer (AAS; Thermo Scientific iCE 3300, Sydney, Australia).

Statistical analyses

All statistical analyses were conducted in R 3.5.1 software (R Development Core Team 2018). The effects of forest type, habitat type and sampling depth on nine soil physicochemical properties (GWC, OM, bulk density, pH and nutrient concentrations; total N, P, K, Ca and Mg) were tested via a linear mixed-effects (LME) model using the nlme version 3.1-137 package (Pinheiro *et al.* 2018). Where necessary, soil physicochemical variables were either arcsine or $\log_{10}$-transformed prior to analysis. Forest type, habitat type and sampling depth were modelled as fixed-effects, the transformed values of soil physicochemical properties were modelled as response variables and sampling points were modelled as random effects. Each response variable was tested using separate LME models. In each LME model, pair-wise comparisons between habitat type within each forest type were performed by obtaining the least-square means using the lsmeans version 2.3 package (Lenth 2018).

All nine soil physicochemical variables (GWC, OM, bulk density, pH and nutrient concentrations; total N, P, K, Ca and Mg) for only the topsoil depth (0 – 15 cm) between the four different habitat types were then subjected to a principal component analysis (PCA) to determine which variables account for most of the variation in the data set. Since most soil nutrients accumulate in the first 15 cm of soil depth (Jaafar *et al.* 2016), only the topsoil variables were subjected to PCA and presented.

The changes in soil physicochemical properties (Δ GWC, Δ OM, Δ bulk density, Δ pH and Δ nutrient concentrations; total N, P, K, Ca and Mg) were calculated by subtracting mean values of the intact habitat from mean values of the invaded habitat for each soil physicochemical variable. The variable Δ thus represents how different the invaded habitat was from the intact habitat in terms of mean values of soil variables, as a way of expressing the change in

https://doi.org/10.1017/S0266467422000141 Published online by Cambridge University Press

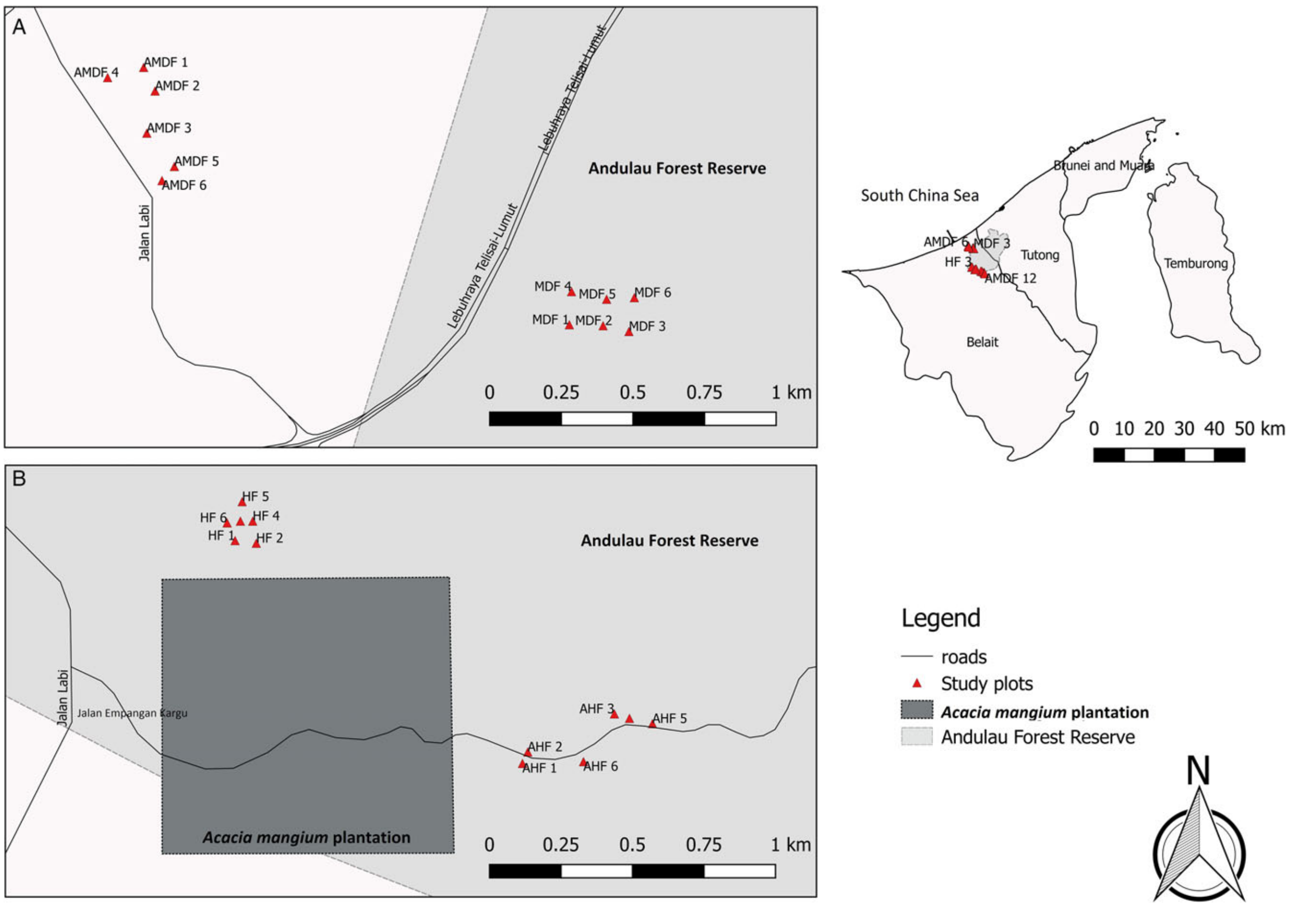

Figure 1. Locations of the study sites consisting six plots in the intact heath forest (HF 1-6), six plots in *Acacia*-invaded heath forest (AHF 1-6), six plots in intact mixed dipterocarp forest (MDF 1-6) and six plots in *Acacia*-invaded mixed dipterocarp forest (AMDF 1-6), within compartments 7 and 8 of the Andulau Forest Reserve in the Belait District, Brunei Darussalam. AHF plots were set up along the Jalan Empangan Kargu roadsides, whereas AMDF plots were set up along Jalan Labi roadsides and both AHF and AMDF plots were invaded by *Acacia* trees. Distances between plots within the same habitat type range from c. 50 to 100 m. **A** represents the inset of plots MDF 1-6 and AMDF 1-6 and **B** represent the inset of plots HF 1-6 and AHF 1-6.

soil properties caused by the presence of *Acacia* in invaded habitats while taking into account potential variation in localities, age range and vegetation type, following Majalap (2000). Similarly, the effects of forest type and sampling depth on changes in soil physicochemical properties were tested separately using LME models. Transformed values of changes in soil physicochemical properties were modelled as response variables, forest type and sampling depth as fixed effects with sampling points included as random effects. All LME models' selection followed Pinheiro and Bates (2004) and Zuur *et al.* (2009). In each of the LME model, pair-wise comparisons between forest type and between sampling depth were performed by obtaining the least-square means. Although sampling depth was included in the LME models, most soil physicochemical variables did not show significant effects for sampling depth (Supplementary Table 1), and so we focussed on presenting and discussing findings on the main effects of forest and habitat types.

Results

Soil physicochemical properties

Acacia invasion either increased or decreased soil physicochemical properties in both forest types. Significant effects of forest type were detected on soil OM, bulk density, pH and concentrations of total N, P, K and Mg ($P < 0.05$; Supplementary Table 1). Habitat type significantly influenced GWC, bulk density and concentrations of total P, K, Ca and Mg ($P < 0.05$; Supplementary Table 1). Soil OM, pH and concentrations of total N, K, Ca and Mg displayed significant forest type by habitat-type interactions ($P < 0.05$; Supplementary Table 1).

Within HF, regardless of sampling depth, AHF plots recorded significantly higher GWC, pH and concentrations of total P, K and Ca than plots in the intact habitat ($P < 0.05$; Table 1), while the intact habitat plots exhibited significantly higher OM content than the invaded habitat plots ($P < 0.05$; Table 1). In contrast, within the MDF, also regardless of sampling depth, AMDF plots recorded significantly higher soil OM and concentrations of total N, P, K and Mg compared to its intact habitat plots ($P < 0.05$; Table 1). The intact habitat, however, recorded significantly higher values of soil bulk density and pH than its invaded habitat ($P < 0.05$; Table 1).

Topsoil (0 – 15 cm) variation in physicochemical properties created a clear separation of plots from HF and MDF into two distinct clusters (Figure 2). The MDF plots were strongly influenced by PC2 (pH), while the HF plots were strongly influenced by PC1 (Bulk density) and PC2 (OM; Supplementary Table 2). In contrast, AHF and AMDF plots were scattered within the biplot (Figure 2),

Table 1. Mean values for nine soil physicochemical properties (gravimetric water content, organic matter, bulk density, pH and nutrient concentrations; total N, P, K, Ca and Mg) at forest type and habitat type levels regardless of the sampling depth of the soil samples at heath and mixed dipterocarp forests of two habitat types (intact or *Acacia*-invaded). Values are means ± standard error, SE. The mean values presented in this table were calculated averaging the 48 samples per habitat type. Significant differences between each forest and within each habitat types were detected after a linear mixed effects (LME) analysis followed by an lsmeans pairwise comparisons test at $\alpha = 0.05$ level (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$)

Forest	Habitat	Gravimetric water content (%)	Organic matter (%)	Bulk density (g cm^{-3})	pH	Total N (mg g^{-1})	Total P (mg g^{-1})	Total K (mg g^{-1})	Total Ca (mg g^{-1})	Total Mg (mg g^{-1})
Heath	Intact	7.52 ± 0.71	3.66 ± 0.35	1.18 ± 0.03	3.44 ± 0.05	0.52 ± 0.05	0.04 ± 0.01	0.07 ± 0.02	0.02 ± 0.01	0.03 ± 0.01
	Invaded	9.80 ± 1.06*	2.73 ± 0.35*	1.06 ± 0.04	3.82 ± 0.06***	0.52 ± 0.06	0.07 ± 0.01***	1.59 ± 0.24***	0.06 ± 0.01***	0.04 ± 0.01
Mixed dipterocarp	Intact	9.00 ± 0.34	2.15 ± 0.12	1.02 ± 0.05	3.93 ± 0.03	0.44 ± 0.03	0.08 ± 0.01	2.01 ± 0.16	0.04 ± 0.01	0.03 ± 0.01
	Invaded	10.49 ± 0.74	2.94 ± 0.21*	0.89 ± 0.03*	3.58 ± 0.05***	0.71 ± 0.05**	0.15 ± 0.01***	6.53 ± 0.41***	0.05 ± 0.01	0.08 ± 0.01***

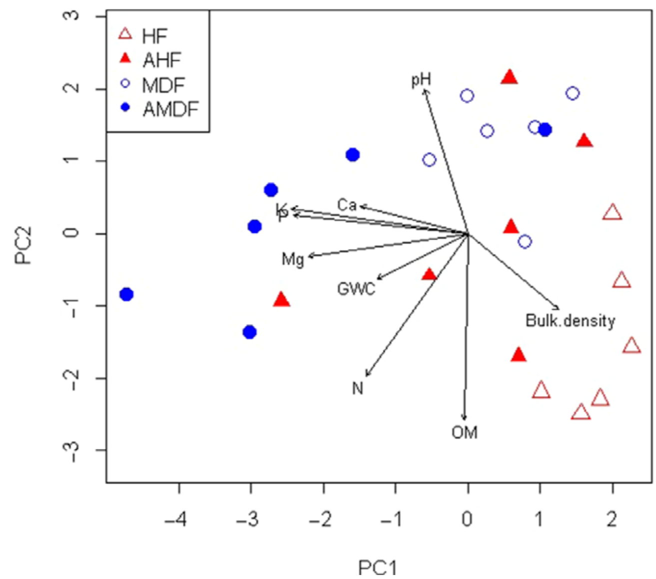

Figure 2. Biplot of principal component (PC) axes 1 and 2 from principal component analysis (PCA) of nine topsoil (0 – 15 cm) physicochemical variables (gravimetric water content, organic matter, bulk density, pH and nutrient concentrations; total N, P, K, Ca and Mg) across 24 plots from heath forest (HF), *Acacia*-invaded heath forest (AHF), mixed dipterocarp forest (MDF) and *Acacia*-invaded mixed dipterocarp forest (AMDF). PC1 and PC2 accounted for 41.7% and 23.4% of the total variation, respectively. The arrows show the loadings of each variable on the first two PC axes. GWC, OM, nulk density, pH, N, P, K, Ca, Mg are gravimetric water content, organic matter, bulk density, pH, total N, P, K, Ca and Mg concentrations, respectively. Note the overlapping arrows for the loadings of K and P.

indicating that *Acacia*-invaded plots were equally influenced by most of the topsoil physicochemical variables.

Changes in soil properties (Δ) in each forest type

Acacia-invaded HF and AMDF soils showed significant changes in all soil properties (Δ OM, Δ pH and, Δ total N, P, K, Ca and Mg concentrations; $P < 0.05$) except for Δ GWC and Δ bulk density ($P > 0.05$; Supplementary Table 3). Changes in soil properties (Δ) in both forest types were either positive or negative (Table 2). Heath forest, when invaded by *Acacia* species, decreased in OM, bulk density and total N concentration (negative change; Table 2), but increased in GWC, soil pH and total P, K, Ca and Mg (positive change; Table 2). In contrast, MDF decreased in bulk density and soil pH (negative change; Table 2) but increased in GWC, soil organic matter and total N, P, K, Ca and Mg (positive change; Table 2) when invaded by *Acacia*. The positive changes of total P, K and Mg were greater in MDF than HF by threefold, threefold and fourfold, respectively, while only positive change of total Ca concentration was greater in HF than MDF by fourfold (Table 2).

Discussion

Effects of Acacia invasion on heath forest soils

For HF soils, *Acacia* invasion significantly increased soil pH, GWC and concentrations of total P, K and Ca and significantly decreased soil OM content. Increased soil pH was similarly recorded in invaded coastal HF in Brunei (Ibrahim *et al.* 2021). The significant increase in soil pH in our AHF plots may reflect the impact of Acacias on the balance between soil nitrification and ammonification processes in tropical heath soils, resulting in changes to soil pH

https://doi.org/10.1017/S0266467422000141 Published online by Cambridge University Press

Table 2. Mean values for the change of soil properties (Δ gravimetric water content, Δ organic matter, Δ bulk density, Δ pH and Δ nutrient concentrations; total N, P, K, Ca and Mg) between two forest types (heath and mixed dipterocarp forests) and between two sampling depths (topsoil 0 – 15 cm and subsoil 30 – 50 cm). Values were calculated by subtracting the average values of the intact habitat from the values of invaded habitat for each of the soil physicochemical variable. Values are means ± standard error, SE. The mean values presented in this table were calculated averaging the 24 samples per forest type and per sampling depth. Significant differences between each forest type and sampling depths were detected after a linear mixed effects (LME) analysis followed by an lsmeans pairwise comparisons test at α = 0.05 level (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Note the NA (not available) for Δ bulk density column at sampling depth level. Bulk density was only sampled at topsoil depth (0 – 15 cm), hence sampling depth was not used as part of the fixed effects in the model. The (−) sign before the mean values indicates a decrease and no sign before the mean values indicate an increase in soil physicochemical properties in the presence of *Acacia*

Effect	Type	Δ Gravimetric water content (%)	Δ Organic matter (%)	Δ Bulk density ($g\ cm^{-3}$)	Δ pH	Δ Total N ($mg\ g^{-1}$)	Δ Total P ($mg\ g^{-1}$)	Δ Total K ($mg\ g^{-1}$)	Δ Total Ca ($mg\ g^{-1}$)	Δ Total Mg ($mg\ g^{-1}$)
Forest	Heath	2.28 ± 1.06	−0.93 ± 0.33	−0.11 ± 0.04	0.38 ± 0.06	−0.003 ± 0.06	0.02 ± 0.01	1.52 ± 0.24	0.04 ± 0.01	0.01 ± 0.005
	Mixed dipterocarp	1.49 ± 0.74	0.79 ± 0.21***	−0.13 ± 0.03	−0.35 ± 0.05***	0.27 ± 0.05**	0.06 ± 0.01*	4.52 ± 0.41**	0.01 ± 0.01**	0.04 ± 0.01*
Sampling depth	Topsoil (0 – 15 cm)	1.76 ± 0.97	−0.21 ± 0.37	NA	0.09 ± 0.08	0.13 ± 0.07	0.05 ± 0.01	3.21 ± 0.44	0.03 ± 0.01	0.04 ± 0.01
	Subsoil (30 – 50 cm)	2.02 ± 0.86	0.08 ± 0.21		−0.07 ± 0.08***	0.13 ± 0.04	0.04 ± 0.01	2.84 ± 0.36	0.03 ± 0.01	0.02 ± 0.01**

(Xiong *et al.* 2008). Our AHF plots recorded higher soil GWC, which is inconsistent with findings of Yusoff *et al.* (2019) and Ibrahim *et al.* (2021) in coastal HF in Brunei. *Acacia* typically reduce soil GWC (Ibrahim *et al.* 2021, Le Maitre *et al.* 2011, Matali & Metali 2015), as their large aboveground biomass requires more water from soil (Morris *et al.* 2011). Here, we suggest that instead of an effect caused by *Acacia* invasion, our finding was more likely due to waterlogged conditions at three out of six plots during our wet season sampling (SM Jaafar, pers. obs.). It is crucial that future studies should consider sampling soils during both the dry and wet seasons, as these can impact soil properties (Xiong *et al.* 2008).

Regardless of sampling depths, intact HF recorded significantly higher OM content compared to AHF. The PCA biplots clearly showed a separation of the HF and AHF plots due to the high influence of bulk density and organic matter. Bulk density and OM content are interrelated (Shiri *et al.* 2017), and lower OM content in AHF may be due to changes in the physical structure of these invaded soils caused by the extensive *Acacia* root systems. These changes could have impacted soil texture and porosity, resulting in further modifications to bulk density and OM content.

Our findings of significantly higher soil nutrient concentrations (total P, K and Ca) in AHF are consistent with observations of soil nutrient enrichment within *Acacia* plantations or *Acacia*-invaded habitats (e.g. Castro-Diez *et al.* 2014, Perreira *et al.* 2018, van Bich *et al.* 2018). However, our findings of no difference in total N concentrations and higher total Ca concentrations contradict those of Matali and Metali (2015) who compared soil properties at the same intact HF site as our study, versus soil properties in an adjacent *A. mangium* plantation, located approximately c. 500 m away from our AHF plots. Their *A. mangium* plantation soils recorded significantly higher total N concentrations and reduced total Ca concentrations (Matali & Metali 2015). These contradicting results could be attributed to tree abundance and diversity differences between the two habitats, as *A. mangium* trees dominated the plantation (about 80%), while the AHF showed a mix of *A. mangium* and native shrub HF tree species (RS Sukri, unpubl. data). Elsewhere in Brunei, no significant differences in soil properties between coastal HF and AHF were reported, except for increased topsoil available P and subsoil exchangeable Ca concentrations (Yusoff *et al.* 2019). Heath forest soils or soil solutions are typically richer in total Ca (Jaafar *et al.* 2016) and exchangeable Ca concentrations (Metali *et al.* 2015) than other nutrients. Here, we reported that *Acacia* invasion increased Ca concentrations in HF soils, which could further impact these forests.

Interestingly, our study did not record increased soil total N concentration when the HF was invaded by these N-fixing *Acacia* species. Similarly, no significant increase in total soil N concentration was recorded in *Acacia*-invaded coastal HF (Yusoff *et al.* 2019). We suggest the absence of soil total N increase was because our invaded HF plots contained young *Acacia* seedlings and saplings, rather than older and more established trees. Uptake of soil N by *Acacia* trees is generally higher during the first three years after planting (Huong *et al.* 2015), possibly contributing to the lack of elevated soil N. Pre-invasion soil nutrient status of heath soils could have further affected the N-fixing ability of invasive *Acacia* (Ehrenfeld 2003). Additionally, allelochemicals produced by invasive *Acacia* species (Ismail & Metali 2014, Lorenzo *et al.* 2013) may inhibit activities of soil decomposer organisms, affecting soil mineralisation (Xiong *et al.* 2008), thus further reducing N release from litter into soil in invaded HF habitats.

Effects of Acacia invasion on mixed dipterocarp forest soils

Acacia invasion effects on MDF soils contrasted with those observed on nutrient-poor HF soils. Invaded MDF soils were more acidic with decreased bulk density and increased organic matter content and total N, P, K and Mg concentrations. The biplots of PCA also supported this result and clearly showed a separation of intact MDF plots from the AMDF plots.

Acacias increased soil nutrient (total N, P, K and Mg) concentrations in invaded MDF plots, consistent with soil nutrients enrichment following *Acacia* invasion (Pereira *et al.* 2018, van Bich *et al.* 2018). The increase in total soil N concentration in MDF was expected due to the N-fixing ability of *Acacia*, leading to the production of N-rich litter and elevated total soil N concentration (Jeddi & Chaieb 2012, Morris *et al.* 2011). Increased total P concentrations in invaded MDF are important as these forests are P-limited (Paoli *et al.* 2006, Sukri *et al.* 2012), and *Acacia* invasion can potentially impact their P balance. Increased total soil K concentrations in the AMDF may be due to leaching of this highly mobile ion via throughfall from *Acacia* foliar biomass, accumulation of K-rich leaf litter and K deposition into soil (Ampitan *et al.* 2021, Dent *et al.* 2006). AMDF soil also recorded higher total Mg concentrations than its intact habitat. Decomposing materials are usually high in total Mg (Powers *et al.* 2009), and the presence of several dead and fallen *Acacia* trees in our AMDF plots, coupled with the naturally nutrient-rich soil, could have resulted in high Mg accumulation.

Bulk density of MDF soil was decreased by *Acacia* invasion. The increase in organic matter content in the AMDF soil likely contributed to lower bulk density (Lindsay & French 2005). Further, faster leaf litter decomposition in AMDF than invaded HF (Jaafar 2020) could have released more OM into the soil. This increase in OM could further elevate total N concentrations (Lindsay & French 2005) as seen in our AMDF soils. Additionally, higher accumulation of OM content often occurs in nutrient-rich soil, such as MDF soil, due to high abundance and diversity of decomposer organisms (Tsukamoto & Sabang, 2005).

Contrasting magnitude of impacts of Acacia invasion on soils

We found that *Acacia* invasion either positively or negatively impacted several soil variables, as quantified by changes in soil properties (Δ) for OM, pH, total N, P, K, Ca and Mg concentrations. The magnitude of changes differed between forest types, with up to 1.4-, 1.6-, 1.9-, 3.2-, 1.3- and 2.7-folds increase in OM, total N, P, K, Ca and Mg concentrations, respectively, for MDF soils and the magnitude of changes for HF soils were up to 1.8-, 22.7-, 3.0- and 1.3-folds increase in total P, K, Ca and Mg concentrations, respectively, and up to 1.3-fold decrease in OM.

Consistent with the significantly higher mean pH values in AHF than in AMDF, we recorded increased pH for the former but decreased pH for the latter. Habitats with the lowest bulk density often show lower soil pH (Lindsay & French 2005), and MDF soils are generally less sandy, and thus have lower bulk density, than HF soils (Jaafar *et al.* 2016). Further, nitrification process that generates H^+ can affect soil acidity (Li *et al.* 2001, Majalap 2000), and increased soil acidity for our AMDF could be caused by relatively high nitrification processes (Yamashita *et al.* 2008). Indeed, nitrification process in our MDF soils was 45-fold higher than in our HF soils (Jaafar 2020).

Acacia invasion consistently increased total P, K, Ca and Mg concentrations in both forest types, but the positive effects of total soil P (threefold), K (threefold) and Mg (fourfold) additions were greater in MDF soil than in HF soil. In contrast, the positive effect of addition of total Ca concentration was four times greater in HF soil than MDF soil. Plant invasions often result in elevated nutrient levels (Keet *et al.* 2021). Additionally, tropical lowland rain forest soils are strongly P-limited (Paoli *et al.* 2006, Sukri *et al.* 2012), and *Acacia* may overcome this limitation by enriching soils with P.

Interestingly, *Acacia* invasion showed contrasting effects of increased OM and total N concentration for AMDF, but decreased OM and total N for AHF. This may be linked to slower litter decomposition rates in HF compared to MDF, which remained slower in the presence of invasive *Acacia* (Jaafar 2020). Notably, we detected a significant decrease in total N (as measured by Δ total N) for AHF compared to the intact HF, despite not recording a significant difference in mean values of total N concentrations between intact and AHF. This suggests that *Acacia* invasion did cause a decrease in total N concentrations for HF in our study. We highlight that this finding illustrates the importance of quantifying Δ change in soil properties as a direct measure of the impact of *Acacia* invasion on soil properties, rather than only relying on comparing mean values between intact and invaded habitats.

The greater magnitude of nutrient increase in MDF than HF soils might reflect differences in pre-invasion soils (Stock *et al.* 1995), with MDF being inherently nutrient-rich compared to HF soils (Jaafar *et al.* 2016). The three- to fourfold increases in nutrients for MDF soils may reflect higher litterfall production and nutrient release triggered by *Acacia* invasion. Further, low resource utilization by native HF species adapted to nutrient-poor conditions could have benefitted nutrient uptake by invasive *Acacia* species (Werner *et al.* 2010).

The higher magnitude of changes in soil nutrients recorded for the nutrient-rich MDF soils compared to the nutrient-poor HF soils provides further evidence that nutrient-rich sites may be more impacted by plant invasions than nutrient-poor sites (Witkowski 1991, Zefferman *et al.* 2015). This is an important finding as it is often presumed that nutrient-rich MDF are more resistant to *Acacia* invasion because of differences in species diversity, soil physicochemical properties, topography and underlying geology compared to HF. We suggest that *Acacia* may be able to easily utilise the readily available nutrients in nutrient-rich MDF soils, and in the process, significantly modify soil properties to facilitate their own growth, to the detriment of native plant species.

Conclusion

Our study provides evidence of distinct impacts of *Acacia* invasion on soil properties at two contrasting lowland forest sites in northwest Borneo, which appear to be influenced by pre-invasion soil nutrient status as well as by inherent pre-invasion differences in other soil properties. Associated differences include elevated gravimetric water content, pH and total P, K and Ca concentrations in AHF and higher organic matter content and concentrations of total soil N, P, K and Mg in AMDF. We detected stronger effects of *Acacia* invasion in the MDF soil via higher magnitude of nutrient additions (except for total Ca), compared to HF soil, indicating that nutrient-rich forests may be more vulnerable to invasive *Acacia*. With increasing urban development and extensive road networks where invasive *Acacia* can readily establish, intact MDFs in Brunei and elsewhere in Borneo face increasing pressure from *Acacia* invasion and subsequently may be more affected than the nutrient-poor HFs.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/S0266467422000141

Acknowledgements. The authors thank the Brunei Forestry Department for granting entry permit (Ref no. [99]/JPH/UND/17 PT.1), the Department of Agriculture and Agrifood for providing rainfall data, Nur Khalish Hafizhah Ideris and Muhammad Abdul Hakeem Julaihi for field assistance, David Burslem for advice and Dennis Ting for assistance with the map. We are grateful to the Associate Editor and reviewer for critical feedback that have significantly improved our paper.

Financial support. The research was funded by the Brunei Research Council [Grant No. UBD/BRC/11] and Universiti Brunei Darussalam [Grant Nos. UBD/RSCH/1.4/FICBF(b)/2018/005 and UBD/PNC2/2/RG/1(204)]). SMJ was supported by a University Graduate Scholarship (UGS) from Universiti Brunei Darussalam.

Competing interest. The authors declare that we have no conflicts of interest.

References

Allen SE, Grimshaw HM, Parkinson JA and Quarmby C (1989) *Chemical Analysis of Ecological Materials*. Oxford: Blackwell Publishing.

Ampitan TA, Ampitan AA, Muhammad SA and Ibrahim AO (2021) Effect of litter mineralisation on soil under *Acacia senegal* (Wild L) plantation in the semi-arid zone of Nigeria. *Ethiopian Journal of Environmental Studies and Management* **14**, 74–83.

Ashton PS, Kamariah AS and Idris MS (2003) *A field guide to the forest and trees of Brunei Darussalam and The Northeast Borneo Hotspot*, Vol. **1**. Bandar Seri Begawan: Universiti Brunei Darussalam.

Becker P (1992) Seasonality of rainfall and drought in Brunei Darussalam. *Brunei Museum Journal* **7**, 99–109.

Castro-Díez P, Godoy O, Alonso A, Gallardo A and Saldaña A (2014) What explains variation in the impacts of exotic plant invasions on the nitrogen cycle? A meta-analysis. *Ecology Letters* **17**, 1–12.

Dassonville N, Vandrhoeven S, Vanparys V, Hayez M, Gruber W and Meerts P (2008) Impacts of alien invasive plants on soil nutrients are correlated with initial site conditions in NW Europe. *Oecologia* **157**, 131–140.

Davies SJ and Becker P (1996) Floristic composition and stand structure of mixed dipterocarp and heath forests in Brunei Darussalam. *Journal of Tropical Forest Science* **8**, 542–569.

Dent DH, Bagchi R, Robinson D, Majalap-Lee N and Burslem DFRP (2006) Nutrient fluxes via litterfall and leaf litter decomposition vary across a gradient of soil nutrient supply in lowland tropical rain forest. *Plant and Soil* **288**, 197–215.

Din H, Metali F and Sukri RS (2015) Tree diversity and community composition of the Tutong white sands, Brunei Darussalam: a rare tropical heath forest ecosystem. *International Journal of Ecology*. doi: 10.1155/2015/807876.

Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* **6**, 503–523.

Huong VD, Nambiar ES, Quang LT, Mendham DS and Dung PT (2015) Improving productivity and sustainability of successive rotations of *Acacia auriculiformis* plantations in South Vietnam. *Southern Forest* **77**, 51–58.

Ibrahim MH, Sukri RS, Tennakoon KU, Le QV and Metali F (2021) Photosynthetic responses of *Acacia mangium* and co-existing native heath forest species to elevated temperature and CO_2 concentrations. *Journal of Sustainable Forestry* **40**, 573–593.

Inagaki M, Kamo K, Miyamoto K, Titin J, Jamalung L, Lapongan J and Miura S (2011) Nitrogen and phosphorous retranslocation and N:P ratios of litterfall in three tropical plantations: luxurious N and efficient P use by *Acacia mangium*. *Plant and Soil* **341**, 295–307.

Ismail NAN and Metali F (2014) Allelopathic effects of invasive *Acacia mangium* germination and growth of local paddy varieties. *Journal of Agronomy* **13**, 158–168.

Jaafar S (2020) Investigating the effects of invasive Acacia species on the nutrient cycling of Brunei's tropical lowland rain forests. PhD Thesis Universiti Brunei Darussalam, Brunei Darussalam.

Jaafar S, Sukri RS and Procheş Ş (2016) An investigation of soil physico-chemical variables across different lowland forest ecosystems of Brunei Darussalam. *Malaysian Journal of Science* **35**, 148–166.

Jambul R, Limin A, Ali AN and Slik F (2020) Invasive *Acacia mangium* dominance as an indicator for heath forest disturbance. *Environmental and Sustainability Indicators* **8**. doi: 10.1016/j.indic.2020.100059.

Jeddi K and Chaieb M (2012) Restoring degraded arid Mediterranean areas with exotic tree species: influence of an age sequence of *Acacia salicina* on soil and vegetation dynamics. *Flora-Morphology Distribution Functional Ecology of Plants* **207**, 693–700.

Keet JH, Ellis AG, Hui C, Novoa A and Le Roux JJ (2021) Impacts of invasive Australian Acacias on soil bacterial community composition, microbial enzymatic activities, and nutrient availability in Fynbos Soils. *Microbial Ecology*. doi: 10.1007/s00248-021-01683-1

Kourtev PS, Ehrenfeld JG and Haggblom M (2003) Experimental analysis of the effect of exotic and native plant species on the structure and function of soil microbial communities. *Soil Biology and Biochemistry* **35**, 895–905.

Koutika L, Epron D, Bouillet K and Mareschal L (2014) Changes in N and C concentrations, soil acidity and P availability in tropical mixed *Acacia* and *Eucalypt* plantations on a nutrient poor sandy soil. *Plant and Soil* **379**, 205–216.

Koutika LS and Richardson DM (2019) *Acacia mangium* Willd: benefits and threats associated with its increasing use around the world. *Forest Ecosystems* **6**, 1–13.

Le Maitre DC, Gaertner M, Marchante E, Ens EJ, Holmes PM, Pauchard A, O'Farrell PJ, Rogers AM, Blanchard R, Blignaut J and Richardson DM (2011) Impacts of invasive Australian Acacias: implications for management and restoration. *Diversity and Distributions* **17**, 1015–1029.

Le QV, Tennakoon KU, Metali F and Sukri RS (2018) Photosynthesis in co-occurring invasive *Acacia* spp. and native Bornean Heath forest trees at the post-establishment invasion stage. *Journal of Sustainable Forestry* **38**, 230–243.

Lenth RV (2018) Least-squares means: the R package lsmeans. *Journal of Statistical Software* **69**, 1–33.

Li Z, Peng S, Rae DJ and Zhou G (2001) Litter decomposition and nitrogen mineralization of soils in subtropical plantation forests of southern China, with special attention to comparisons between legumes and non-legumes. *Plant and Soil* **229**, 105–116.

Liao CZ, Peng RH, Luo YQ, Zhou XH, Wu XW and Fang CM (2008) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytologist* **177**, 706–714.

Lindsay EA and French K (2005) Litterfall and nitrogen cycling following invasion by *Chrysanthemoides monilifera ssp. rotundata* in coastal Australia. *Journal of Applied Ecology* **42**, 556–566.

Lorenzo P, Pereira CS and Rodríguez-Echeverría S (2013) Differential impact on soil microbes of allelopathic compounds released by the invasive *Acacia dealbata* Link. *Soil Biology and Biochemistry* **57**, 156–163.

Majalap N (2000) Does *Acacia mangium* improve soils in Sabah? *Proceedings of the 15th SITE Seminar - Exotics: Potentials, Issues & Challenges; Kota Kinabalu, Sabah.*

Marchante E, Kjoller A, Struwe S and Freitas H (2009) Soil recovery after removal of the N_2-fixing invasive *Acacia longifolia*: consequences for ecosystem restoration. *Biological Invasions* **11**, 813–823.

Matali S and Metali F (2015) Selected soil physio-chemical properties in the *Acacia mangium* plantation and the adjacent heath forest at Andulau Forest Reserve. *Malaysian Journal of Soil Science* **19**, 45–58.

Metali F, Salim KA, Tennakoon K and Burslem DFRP (2015) Controls on foliar nutrient and Al concentrations in a tropical tree flora: phylogeny, soil chemistry and interactions among elements. *New Phytologist* **205**, 280–292.

Morris TL, Esler KJ, Barger NN, Jacobs SM and Cramer MD (2011) Ecophysiological traits associated with the competitive ability of invasive Australian acacias. *Diversity and Distributions* **17**, 898–910.

Nsikani MM, van Wilgen BW, Bacher S and Gaertner M (2018) Re-establishmnet of *Protea repens* after clearing invasive *Acacia saligna*: consequences of soil legacy effects and on native nitrophilic weedy species. *South African Journal of Botany* **116**, 103–109.

Osunkoya OO and Damit N (2005) Population dynamics of the invasive Acacias in Brunei Darussalam using matrix modelling. *Journal of Physical Science* **16**, 115–126.

Osunkoya OO, Othman FE and Kahar RS (2005) Growth and competition between seedlings of an invasive plantation tree, *Acacia mangium*, and those of a native Borneo heath-forest species, *Melastoma beccarianum*. *Ecological Research* **20**, 205–214.

Paoli GD, Curran LM and Zak DR (2006) Soil nutrients and beta diversity in the Bornean Dipterocarpaceae: evidence for niche partitioning by tropical rain forest trees. *Journal of Ecology* **94**, 157–170.

Peh KSH (2010) Invasive species in Southeast Asia: the knowledge so far. *Biodiversity Conservation* **19**, 1083–1099.

Perreira APA, Zagatto MRG, Brandani CB, Mescolotti DDL, Cotta SR, Goncalves JLM and Cardoso EJBN (2018) *Acacia* changes microbial indicators and increases C and N in soil organic fractions in intercropped *Eucalyptus* plantations. *Frontiers in Microbiology* **9**, 655. doi: 10.3389/fmicb.2018.00655

Pinheiro J, Bates D, DebRoy S, Sarkar D and R Core Team (2018) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-137, http://CRAN.R-project.org/package=nlme.

Pinhero JC and Bates DM (2004) *Mixed-effects Models in S and S-Plus*. New York: Springer.

Powers JS, Motgometry RA, Adair EC, Brearley FQ, DeWalt SJ, Castanho CT, Chave J, Deiner E, Ganzhorn JU, Gilbert ME, Gonzalez-Iturbe JA, Bunyavejchewin S, Grau HR, Harms KE, Hiremath A, Iriarte-Vivar S, Manzane E, de Oliveira AA, Poorter L, Ramanamanjato J, Salk C, Varela A, Weiblen G and Lerdau MT (2009) Decomposition in tropical forests: a pan-tropical study of the effects of litter type, litter placement and mesofaunal exclusion across a precipitation gradient. *Journal of Ecology* **97**, 801–811.

R Development Core Team (2018) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Richardson DM and Rejmánek M (2011) Trees and shrubs as invasive alien species: a global review. *Diversity and Distribution* **17**, 788–809.

Shiri J, Keshavarzi A, Kisi O, Karimi S and Iturraran-Viveros U (2017) Modelling soil bulk density through a complete data scanning procedure: heuristic alternatives. *Journal of Hydrology* **549**, 592–602.

Stock WD, Wienand KT and Baker AC (1995) Impacts of N_2 fixing *Acacia* species on patterns of nutrient cycling in two Cape ecosystems: evidence from soil incubation studies and ^{15}N natural abundance values. *Oecologia* **101**, 375–382.

Suhaili ALR, Tennakoon KU and Sukri RS (2015) Soil seed bank of an exotic *Acacia* sp. plantation and an adjacent tropical heath forest in Brunei Darussalam. *Biotropia* **22**, 140–150.

Sukri RS, Wahab RA, Salim KA and Burslem DFRP (2012) Habitat associations and community structure of Dipterocarps in response to environment and soil conditions in Brunei Darussalam, Northwest Borneo. *Biotropica* **44**, 595–605.

Tanaka S, Kano S, Lat J, Mohd Effendi WM, Tan NP, Arifin A, Sakurai K and Kendawang JJ (2015) Effects of *Acacia mangium* on morphological and physicochemical properties of soil. *Journal of Tropical Forest Science* **27**, 357–368.

Tsukamoto J and Sabang J (2005) Soil macro-fauna in an *Acacia mangium* plantation in comparison to that in a primary mixed dipterocarp forest in the lowlands of Sarawak, Malaysia. *Pedobiology* **49**, 69–80.

Tuah WH, Tenakoon KU, Jaafar SM and Sukri RS (2020) Post-fire impacts on tree diversity in coastal heath forests of Brunei Darussalam. *Scientia Bruneiana* **19**, 19–32.

van Bich N, Eyles A, Mendham D, Dong TL, Ratkowsky D, Evans KJ, Hai VD, Thanh HV, Thinh NV and Mohammed C (2018) Contribution of harvest residues to nutrient cycling in a tropical *Acacia mangium* Willd. plantation. *Forests* **9**, 577. doi: 10.3390/f9090577

Wang C, Xiao H, Liu J, Wang L and Du D (2015) Insights into ecological effects of invasive plants on soil nitrogen cycles. *American Journal of Plant Science* **6**, 34–46.

Werner C, Zumkier U, Beyschlag W and Maguas C (2010) High competitiveness of a resource demanding invasive *Acacia* under low resource supply. *Plant Ecology* **206**, 83–96.

Witkowski ETF (1991) Effects of alien Acacias on nutrient cycling in coastal lowlands of the Cape Fynbos. *Journal of Applied Ecology* **28**, 1–15.

Xiong Y, Xia H, Li Z, Cai X and Fu S (2008) Impacts of litter and understory removal on soil properties in a subtropical *Acacia mangium* plantations in China. *Plant and Soil* **304**, 179–188.

Yamashita N, Ohta S and Hardjono A (2008) Soil changes induced by *Acacia mangium* plantation establishment: comparison with secondary forest and *Imperata cylindrica* grassland soils in South Sumatra, Indonesia. *Forest Ecology and Management* **254**, 362–370.

Yelenik SG and D'Antonio CM (2013) Self-reinforcing impacts of plant invasions change over time. *Nature* **503**, 517–520.

Yelenik SG, Stock WD and Richardson DM (2007) Functional group identity does not predict invader impacts: differential effects of nitrogen fixing exotic plants on ecosystem function. *Biological Invasions* **9**, 117–125.

Yusoff A, Tennakoon KU, Jaafar S, Zaman DNAN and Sukri RS (2019) Effects of *Acacia* invasion on leaf litter nutrient and soil properties of coastal Kerangas forests in Brunei Darussalam. *Scientia Bruneiana* **18**, 1–10.

Zefferman E, Stevens JT, Charles GK, Dunbar-Irwin M, Emam T, Fick S, Morales LV, Wolf KM, Young DJN and Young TP (2015) Plant communities in harsh sites are less invaded: a summary of observations and proposed explanations. *AoB PLANTS* **7**. doi: 10.1093/aobpla/plv056

Zuur AF, Ieno EN, Walker NJ, Savaliev AA and Smith GM (2009) *Mixed Effects Models and Extensions in Ecology with R*. New York: Springer.