

RESEARCH ARTICLE

Differential nutrient limitation and tree height control leaf physiology, supporting niche partitioning in tropical dipterocarp forests

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Abstract

1. Revealing the mechanisms of environmental niche partitioning within lowland tropical forests is important for understanding the drivers of current species distributions and potential vulnerability to environmental change. Tropical forest structure and species composition change across edaphic gradients in Borneo over short distances. However, our understanding of how edaphic conditions affect tree physiology and whether these relationships drive niche partitioning within Bornean forests remains incomplete.
2. This study evaluated how leaf physiological function changes with nutrient availability across a fine-scale edaphic gradient and whether these relationships vary according to tree height. Furthermore, we tested whether intraspecific leaf trait variation allows generalist species to populate a wider range of environments.
3. We measured leaf traits of 218 trees ranging in height from 4 to 66 m from 13 dipterocarp species within four tropical forest types (alluvial, mudstone, sandstone and kerangas) occurring along an <5 km edaphic gradient in North Borneo. The traits measured included saturating photosynthesis (A_{sat}), maximum photosynthetic capacity (V_{cmax}), leaf dark respiration (R_{leaf}), leaf mass per area (LMA), leaf thickness, minimum stomatal conductance (g_{dark}) and leaf nutrient concentrations (N, P, Ca, K and Mg).
4. Across all species, leaf traits varied consistently in response to soil nutrient availability across forest types except $R_{\text{leaf_mass}}$, $[\text{Mg}]_{\text{leaf}}$ and $[\text{Ca}]_{\text{leaf}}$. Changes in photosynthesis and respiration rates were related to different leaf nutrients across forest types, with greater nutrient-use efficiency in more nutrient-poor environments. Generalist species partially or fully compensated reductions in mass-based photosynthesis through increasing LMA in more nutrient-poor environments.

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5. Leaf traits also varied with tree height, except $V_{\text{cmax_mass}}$, but only in response to height-related modifications of leaf morphology (LMA and leaf thickness). These height-trait relationships did not vary across the edaphic gradient, except for A_{sat} , $[N]_{\text{leaf}}$, $[P]_{\text{leaf}}$ and $[K]_{\text{leaf}}$.
6. Our results highlight that modification of leaf physiological function and morphology act as important adaptations for Bornean dipterocarps in response to edaphic and vertical environmental gradients. Meanwhile, multiple nutrients appear to contribute to niche partitioning and could drive species distributions and high biodiversity within Bornean forest landscapes.

KEYWORDS

Borneo, generalist, leaf traits, leaf respiration, ontogeny, photosynthetic capacity, rainforest, trait plasticity

INTRODUCTION

Partitioning of limiting resources among coexisting species has been suggested as one of the mechanisms maintaining high biodiversity in tropical forests (Brokaw & Busing, 2000; Kitajima & Poorter, 2008; Paoli et al., 2006; Queenborough et al., 2007; Ricklefs, 1977). There is significant evidence in support of environmental niche partitioning as an important process determining the assembly of tropical forest communities (Baldeck et al., 2013; Chuyong et al., 2011; Davis & Richards, 1933; Johnson et al., 2017; Katabuchi et al., 2012; Paoli et al., 2006; Queenborough et al., 2007). However, the determinants of differential niche breadth among tropical forest trees are poorly understood. Specifically, it remains unknown whether generalist species (i.e. those which are found in a range of environmental settings) have evolved a capacity to be more plastic in their functional processes (Dewitt et al., 1998; Sultan, 2000; Van Tienderen, 1991) and/or if they have evolved genetically distinct ecotypes in different habitats (van Tienderen, 1997). Moreover, we lack a mechanistic understanding of the specific abiotic drivers of environmental niche partitioning in tropical forests, although access to and use of light, water and nutrients have all been suggested (D'Andrea et al., 2020; Esquivel-Muelbert, Baker, et al., 2017; Esquivel-Muelbert, Galbraith, et al., 2017; Katabuchi et al., 2012; Kitajima & Poorter, 2008; Paoli et al., 2006). Improving our understanding of the processes underlying environmental niche partitioning is fundamental for understanding species distribution patterns in primary forests, the maintenance of species richness and predicting tolerance to future environmental change.

The lowland tropical forests of South-East Asia are dominated by the Dipterocarpaceae family, which typically comprise at least 20% of stems in a forest (Brearley et al., 2017; Slik et al., 2003). Borneo contains 267 named dipterocarp species, and many of these are known to be specialised to specific habitats (Brearley et al., 2017; Davies et al., 2005; Nilus, 2004; Paoli et al., 2006; Sukri et al., 2012), resulting in rapid species turnover across fine-scale environmental gradients (Bongalov et al., 2019; Jucker, Bongalov, et al., 2018; Slik et al., 2003). These changes in species composition and forest

structure occur over small spatial scales without dramatic changes in climate, suggesting topographic or edaphic niche partitioning to be important (Jucker, Bongalov, et al., 2018). Most studies detailing how plant function is tied to habitat specialisation in tropical forest trees have, however, been undertaken in Amazonia or elsewhere in the Neotropics (e.g. Brum et al., 2018; Fontes et al., 2020; Oliveira et al., 2019; Vleminckx et al., 2018), while the few studies conducted in Asian tropical forests focus on seedlings or small tree size classes, or a more limited subset of demographic or leaf traits (e.g. Baltzer et al., 2005; Dent & Burslem, 2016; Palmiotto et al., 2004; Russo et al., 2010). Many of the studies that have tried to understand how edaphic conditions affect plant function in the Neotropics take place over large spatial extents and encompass gradients in climate as well as soil conditions (e.g. Esquivel-Muelbert, Baker, et al., 2017; Esquivel-Muelbert, Galbraith, et al., 2017; Fyllas et al., 2009; Patiño et al., 2012; Soong et al., 2020). Consequently, we still do not fully understand the functional mechanisms that drive environmental niche partitioning at small spatial scales in tropical forests.

To survive and compete effectively for resources, plants must adapt their physiology and resource investment in response to their environment. Plants typically follow a fast-slow leaf economics spectrum across environmental gradients (Wright et al., 2004), having more acquisitive traits, such as high photosynthetic capacity and low leaf mass per area (LMA), in resource-rich environments and more conservative traits in resource-poor environments. The ability to express different traits in response to resource availability has been identified as a key mechanism that may allow some species to compete across a wider range of environmental conditions (Russo & Kitajima, 2016; Whitlock, 1996).

Across large edaphic gradients, leaf physiological and structural traits follow predictions from the leaf economics spectrum (Baker et al., 2003; Fyllas et al., 2009; Patiño et al., 2012; Turner et al., 2000). Phosphorus is traditionally considered the predominant limiting nutrient in tropical forests located on old soils (Vitousek, 1984; Vitousek & Farrington, 1997), but more recent evidence suggests nitrogen and other nutrients may also limit forest productivity (Santiago, 2015; Sayer & Banin, 2016;

TABLE 1 Summary of traits measured for each dipterocarp species in each forest. Data presented are mean \pm standard error of the mean.

Species	Forest	Specialist/ Generalist	$A_{\text{sat_mass}}$ ($\mu\text{mol kg}^{-1} \text{s}^{-1}$)	$A_{\text{sat_area}}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	$V_{\text{cmax_mass}}$ ($\mu\text{mol kg}^{-1} \text{s}^{-1}$)	$V_{\text{cmax_area}}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	$R_{\text{leaf_mass}}$ ($\mu\text{mol kg}^{-1} \text{s}^{-1}$)
<i>Cotylelobium melanoxylon</i>	Kerangas	Specialist	39.33 \pm 2.82	5.86 \pm 0.37	483.93 \pm 41.3	72.88 \pm 6.50	5.68 \pm 0.53
<i>Dipterocarpus acutangulus</i>	Sandstone	Specialist	48.59 \pm 4.00	5.89 \pm 0.68	543.78 \pm 43.9	65.90 \pm 7.62	6.38 \pm 0.69
<i>Dipterocarpus caudiferus</i>	Alluvial	Specialist	86.86 \pm 4.96	6.79 \pm 0.54	881.18 \pm 56.21	65.42 \pm 5.72	7.76 \pm 0.78
<i>Dipterocarpus grandiflorus</i>	Sandstone	Specialist	46.75 \pm 5.27	5.87 \pm 0.78	508.37 \pm 73.46	63.08 \pm 10.36	5.42 \pm 0.55
<i>Dipterocarpus kunstleri</i>	Alluvial	Specialist	70.10 \pm 5.49	6.41 \pm 0.71	692.13 \pm 65.53	62.49 \pm 6.81	5.96 \pm 0.48
<i>Hopea beccariana</i>	Sandstone	Generalist	61.19 \pm 4.80	5.25 \pm 0.34	857.07 \pm 51.74	73.13 \pm 4.28	5.55 \pm 0.34
<i>Hopea beccariana</i>	Kerangas	Generalist	42.11 \pm 1.56	4.38 \pm 0.16	505.26 \pm 46.83	52.32 \pm 4.31	5.71 \pm 0.72
<i>Parashorea tomentella</i>	Alluvial	Generalist	70.97 \pm 8.06	7.63 \pm 0.94	849.10 \pm 129.03	87.19 \pm 11.43	6.23 \pm 0.33
<i>Parashorea tomentella</i>	Mudstone	Generalist	79.37 \pm 7.65	8.18 \pm 0.85	869.17 \pm 86.00	90.13 \pm 9.95	5.85 \pm 0.56
<i>Shorea johorensis</i>	Alluvial	Specialist	130.17 \pm 12.64	13.69 \pm 1.77	1429.99 \pm 142.03	151.27 \pm 21.65	8.05 \pm 0.58
<i>Shorea macroptera</i>	Mudstone	Generalist	59.74 \pm 11.17	10.02 \pm 1.81	549.40 \pm 118.83	117.83 \pm 32.22	4.73 \pm 0.54
<i>Shorea macroptera</i>	Sandstone	Generalist	61.10 \pm 5.76	7.18 \pm 0.71	731.72 \pm 172.23	74.56 \pm 8.06	6.27 \pm 0.53
<i>Shorea multiflora</i>	Sandstone	Generalist	62.91 \pm 7.81	5.20 \pm 0.63	797.53 \pm 110.07	67.58 \pm 9.25	6.84 \pm 0.68
<i>Shorea multiflora</i>	Kerangas	Generalist	45.76 \pm 5.21	4.78 \pm 0.44	531.51 \pm 60.55	53.61 \pm 5.37	8.82 \pm 1.19
<i>Shorea smithiana</i>	Mudstone	Generalist	130.55 \pm 15.38	14.02 \pm 1.57	1503.97 \pm 125.03	167.85 \pm 20.65	4.86 \pm 0.59
<i>Shorea smithiana</i>	Sandstone	Generalist	93.66 \pm 6.22	13.10 \pm 0.94	938.86 \pm 64.54	131.17 \pm 9.41	6.13 \pm 0.68
<i>Shorea xanthophylla</i>	Mudstone	Specialist	51.43 \pm 3.02	4.86 \pm 0.28	606.07 \pm 53.91	58.25 \pm 5.31	3.91 \pm 0.97
<i>Vatica micrantha</i>	Kerangas	Specialist	29.38 \pm 3.13	3.39 \pm 0.29	297.90 \pm 39.83	34.56 \pm 4.44	3.92 \pm 0.44

Wright, 2019; Wright et al., 2011). The high turnover of dipterocarp species along edaphic gradients in Borneo may be associated with specialised nutrient requirements, and other edaphic factors affecting nutrient uptake such as pH, soil particle size (Sellan et al., 2019) and mycorrhizal associations (Liu et al., 2018; Peay et al., 2015; Weemstra et al., 2020). In Bornean lowland forests, leaf nutrient concentrations correlate with soil nutrient availability (Baltzer et al., 2005; Dent & Burslem, 2016; Katabuchi et al., 2012; Weemstra et al., 2020), with potential implications on leaf physiological processes. However, our understanding of canopy metabolism in Bornean forests is limited to settings spanning a narrow range of soil fertility (Kenzo et al., 2004; Kenzo et al., 2006; Kurokawa & Nakashizuka, 2008), montane forests (Hidaka & Kitayama, 2011) or disturbed forests (Both et al., 2019).

Leaf traits additionally vary with tree height (Cavaleri et al., 2010; Kenzo et al., 2006; Kenzo et al., 2015). These changes arise from vertical gradients in light availability, air temperature, vapour pressure deficit, and height-related effects of hydraulic resistance and gravity on water transport that collectively alter leaf trait expression (Ambrose et al., 2016; Chazdon & Fetcher, 1984; England & Attiwill, 2006; Kenzo et al., 2015). In response to height-related environmental shifts, tropical forest trees increase area-based photosynthetic capacity and LMA with increasing tree height (Cavaleri et al., 2010; Kenzo et al., 2015; Lloyd et al., 2010; Meir et al., 2002). Increases in

LMA are generally associated with greater hydraulic stress (England & Attiwill, 2006), greater water-use efficiency (Poorter et al., 2009) and or thermal tolerance (Fauset et al., 2018; Sastry & Barua, 2017) in taller trees. While this may serve to increase photosynthesis on an area basis, increases in LMA tend to be associated with lower total leaf area (Mencuccini et al., 2019), which may reduce total photosynthetic assimilation if it is not offset by higher light exposure in taller trees. The average maximum canopy height of lowland dipterocarp forests generally lies in the range 60–80m, which exceeds the typical height of Neotropical and African forests by 20–30m (Banin et al., 2012). Given these differences in height between regions, it is important to understand how leaf traits vary with height when hydraulic limitations may reduce leaf expansion and turgor (Woodruff & Meinzer, 2011) and trees begin to reach physical limits on leaf shape and size (Jensen & Zwieniecki, 2013).

Across Bornean forest landscapes, forest structure, including maximum canopy height, canopy gap fraction and basal area, vary according to soil nutrient availability (Banin et al., 2014; Jucker, Bongalov, et al., 2018). These differences in forest structure result in greater light penetration, measured by the frequency and intensity of sunflecks, to lower canopy layers on nutrient-poor soils (Russo et al., 2011). We might therefore expect variation in leaf traits with height to be steeper in nutrient-rich forests if light acts as a key control, because the greater leaf area index of these forests confers greater light attenuation between the canopy and understory.

$R_{\text{leaf_area}}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	LMA (g m^{-2})	Leaf thickness (mm)	g_{dark} ($\text{mol m}^{-2} \text{s}^{-1}$)	[N] _{leaf} (g kg^{-1})	[P] _{leaf} (g kg^{-1})	[Ca] _{leaf} (g kg^{-1})	[K] _{leaf} (g kg^{-1})	[Mg] _{leaf} (g kg^{-1})
0.86 ± 0.09	150.76 ± 5.58	0.24 ± 0.01	0.02 ± 0.00	12.26 ± 0.21	0.49 ± 0.02	3.63 ± 0.24	5.80 ± 0.28	1.07 ± 0.10
0.73 ± 0.10	115.28 ± 8.65	0.19 ± 0.01	0.02 ± 0.00	12.64 ± 0.19	0.50 ± 0.02	1.93 ± 0.17	5.22 ± 0.27	1.65 ± 0.12
0.65 ± 0.08	80.99 ± 5.65	0.15 ± 0.01	0.08 ± 0.02	16.38 ± 0.36	0.96 ± 0.04	6.09 ± 0.37	8.95 ± 0.91	1.81 ± 0.14
0.65 ± 0.08	126.04 ± 10.90	0.24 ± 0.01	0.02 ± 0.00	12.96 ± 0.42	0.53 ± 0.03	1.78 ± 0.09	6.18 ± 0.29	2.26 ± 0.12
0.54 ± 0.05	87.76 ± 3.86	0.17 ± 0.00	0.06 ± 0.01	14.51 ± 0.27	0.94 ± 0.03	6.06 ± 0.47	7.51 ± 0.33	2.12 ± 0.15
0.51 ± 0.04	88.14 ± 4.11	0.12 ± 0.01	0.01 ± 0.00	14.56 ± 0.23	0.53 ± 0.02	2.75 ± 0.19	6.95 ± 0.41	2.30 ± 0.10
0.53 ± 0.06	100.38 ± 4.95	0.14 ± 0.01	0.01 ± 0.00	13.28 ± 0.26	0.44 ± 0.01	2.40 ± 0.22	7.36 ± 0.27	2.00 ± 0.08
0.65 ± 0.08	105.57 ± 9.57	0.21 ± 0.02	0.04 ± 0.01	16.02 ± 0.38	1.10 ± 0.06	7.99 ± 0.74	6.64 ± 0.41	1.19 ± 0.08
0.63 ± 0.09	103.17 ± 8.22	0.20 ± 0.01	0.04 ± 0.01	15.20 ± 0.29	1.00 ± 0.05	9.68 ± 1.36	5.72 ± 0.27	1.12 ± 0.12
0.81 ± 0.05	104.52 ± 10.96	0.19 ± 0.02	0.02 ± 0.00	18.72 ± 0.45	1.24 ± 0.04	6.20 ± 0.72	8.53 ± 0.32	1.74 ± 0.26
0.61 ± 0.06	130.23 ± 11.61	0.28 ± 0.02	0.02 ± 0.00	13.91 ± 0.37	0.75 ± 0.02	5.10 ± 0.42	7.42 ± 0.14	1.54 ± 0.13
0.87 ± 0.10	131.29 ± 7.36	0.28 ± 0.02	0.05 ± 0.02	14.21 ± 0.30	0.61 ± 0.04	2.67 ± 0.36	7.50 ± 0.33	1.79 ± 0.19
0.65 ± 0.09	88.75 ± 4.94	0.12 ± 0.01	0.02 ± 0.00	14.81 ± 0.33	0.54 ± 0.03	3.51 ± 0.17	4.76 ± 0.34	2.85 ± 0.09
0.96 ± 0.13	111.91 ± 5.25	0.17 ± 0.01	0.02 ± 0.00	14.32 ± 0.32	0.55 ± 0.03	3.93 ± 0.31	5.02 ± 0.32	2.76 ± 0.18
0.50 ± 0.04	108.23 ± 7.08	0.26 ± 0.01	0.06 ± 0.02	16.85 ± 0.92	1.08 ± 0.11	5.54 ± 0.83	8.43 ± 0.72	1.33 ± 0.13
0.79 ± 0.07	138.22 ± 3.96	0.32 ± 0.01	0.02 ± 0.01	14.80 ± 0.52	0.65 ± 0.04	2.98 ± 0.30	6.75 ± 0.22	1.32 ± 0.07
0.39 ± 0.08	102.89 ± 5.50	0.20 ± 0.01	0.02 ± 0.00	14.44 ± 0.30	0.71 ± 0.03	7.21 ± 0.55	6.16 ± 0.28	1.31 ± 0.07
0.44 ± 0.05	116.42 ± 5.27	0.19 ± 0.01	0.03 ± 0.01	12.50 ± 0.29	0.42 ± 0.03	1.66 ± 0.17	5.26 ± 0.25	0.73 ± 0.06

However, to date, studies measuring how photosynthetic capacity changes with tree height have not assessed how these vertical gradients in plant function change across forest types with different soil nutrient availabilities and maximum canopy heights. This limits our understanding of whole-plant responses to environmental conditions.

The Kabili-Sepilok Forest Reserve (hereafter Sepilok) in northern Borneo represents an ideal system to study the role of soil nutrients, tree height and forest structure on the expression of leaf traits. This forest is composed of four distinct lowland forest types within close proximity (<5km) and the same climatic space: alluvial floodplain forests containing emergent mudstone hills (Born et al., 2014), sandstone forests and kerangas heath forest (Jucker, Bongalov, et al., 2018; Nilus, 2004). Soil nutrient and water availability, leaf area index, topography, canopy height and gap fraction, species distribution, biomass and above-ground wood production all vary along this gradient (Banin et al., 2014; Coomes et al., 2017; Dent & Burslem, 2016; Jucker, Bongalov, et al., 2018). Dipterocarp niche breadth also varies, with some species specialised to one forest type and more generalist species inhabiting two forest types (Nilus, 2004).

Here we evaluate how edaphic conditions, tree height and the degree of edaphic specialism control leaf-level eco-physiological strategies of 218 trees from 13 species of Dipterocarpaceae (eight highly specialist species and five more generalist species) in Sepilok. Specifically, we tested the following predictions:

- Trees growing in habitats richer in soil nutrients possess more acquisitive leaf traits (higher A_{sat} , higher V_{cmax} , higher R_{leaf} , lower LMA, higher g_{dark}).
- A_{sat} , V_{cmax} and R_{leaf} increase with foliar nutrient concentrations within and across forest types.
- Values of leaf traits (A_{sat} , V_{cmax} , R_{leaf} , LMA, leaf thickness and leaf nutrient concentrations) generally increase with tree height, but the magnitude of the increase is greater for species specialised to nutrient-rich soils, because of the greater maximum height of trees in this environment.
- Species found across more than one forest type have different leaf trait expression on soils differing in nutrient availability and thus have greater intraspecific variability in traits than specialist species.

MATERIALS AND METHODS

Study site

This study was carried out in Sepilok, Sabah, Malaysia (5°10'N 117°56'E). This 4,500ha reserve was founded in 1931 by the Sabah Forestry department and is a remnant of lowland tropical rainforest situated in north-east Borneo. Sepilok has complex topographic variation, with elevation ranging from 0 to 250 m a.s.l. (Fox, 1973). Mean annual precipitation in Sepilok is 3,098mm, mean annual

temperature is 26.7°C and mean solar radiation is 13.6 MJ m⁻² d⁻¹ (Banin et al., 2014). Much of the reserve has never been logged, although surrounding areas were selectively logged until 1957 (Dent et al., 2006). Sepilok is composed of four distinct forest types: alluvial mixed dipterocarp forest in the lowland valleys, which can be further divided into sporadically flooded alluvial floodplains with silty soils and low mudstone hills which are better drained with a higher clay content (Born et al., 2015); sandstone dipterocarp forests located on steep hillsides and ridges; and heath forests known locally as kerangas that occur on podzols associated with cuesta dip slopes (Fox, 1973; Nilus, 2004). There are strong differences across these forest types with respect to species composition, diversity, canopy height, nutrient cycling, above-ground carbon density and forest structure (Coomes et al., 2017; Dent et al., 2006; Dent & Burslem, 2016; Greig-Smith et al., 1967; Jucker, Bongalov, et al., 2018). We took 60 soil samples at three depths (0–5 cm, 5–15 cm and 15–30 cm) across the forests to capture variation in soil conditions across the landscape (see SI Methods section named soil sampling and nutrient analyses). Differences in soil nutrient availability exist between forest types (Figure S1). The alluvial and mudstone forests have higher soil nutrient availability than sandstone and kerangas forests. The alluvial and mudstone forests have tall multi-layered canopies, while the kerangas forest has the shortest canopy of the forest types (Jucker, Bongalov, et al., 2018). Nine permanent 4-ha plots (3 alluvial/mudstone, 3 sandstone and 3 kerangas) were established in 2000 across the distinct forest types and have been intensively monitored since. For more details, see Jucker, Bongalov, et al. (2018) and Nilus (2004).

Tree selection

From June to October 2018, we sampled 218 trees (5–160 cm diameter at breast height (DBH), measured at 1.3 m; height: 4.4–66.1 m) across the four forest types (alluvial: $n = 48$, mudstone: $n = 39$, sandstone: $n = 83$, kerangas: $n = 48$) from six of the permanent 4-ha forest plots (Table S1). Permission to undertake fieldwork was granted by the Sabah Biodiversity Council [Licence Ref. No. JKM/MBS.1000-2/2 JLD.6(88); JKM/MBS.1000-2/2 JLD.9(15)]. We selected individuals from 13 species within the Dipterocarpaceae family that were locally common in one or more of the forest types (*Cotylelobium melanoxylon*, *Dipterocarpus acutangulus*, *D. caudiferus*, *D. grandiflorus*, *D. kunstleri*, *Hopea beccariana*, *Parashorea tomentella*, *Shorea johorensis*, *S. macroptera*, *S. multiflora*, *S. smithiana*, *S. xanthophylla* and *Vatica micrantha*; Table S2). For each species, individual tree selection was designed to cover a range of sizes from 5 cm diameter at breast height (DBH) to the tallest individuals available in the plots (Table S3). The number of individuals sampled per species per forest type ranged from 6 to 17 individuals (median = 12.5). Species were assigned a habitat association (alluvial, mudstone, sandstone and kerangas) according to their relative abundance of mature trees (>30 cm DBH) across the six permanent 4-ha plots. A species was associated to a habitat if mature tree abundance exceeded 1 individual per hectare, except for

S. macroptera that was additionally associated to the mudstone forest, because 20% of the largest trees of this species occurred on this habitat and previous work has classified this species as a mudstone specialist (Born et al., 2015; Table 1). Our habitat associations match previous studies that have classified habitat associations for dipterocarp species in Sepilok (Baltzer et al., 2005; Baltzer & Thomas, 2007; Born et al., 2014; Born et al., 2015; Dent & Burslem, 2009; Dent & Burslem, 2016; Eichhorn et al., 2010; Margrove et al., 2015), except for *D. caudiferus*, *P. tomentella* and *S. xanthophylla* whose habitat associations we align with Margrove et al. (2015). Areas of the alluvial plots were classified as mudstone hills according to elevation using a digital elevation model derived from airborne laser scanning (Jucker, Bongalov, et al., 2018): for each 4-ha plot, a threshold between alluvial and mudstone forests was set at 5 m above the minimum elevation for the plot (approx. 73 m a.s.l.; see Figure S2). Species associated with two forest types were called generalists for the purpose of this analysis, while species associated to just one forest type were classified as specialists. No single species was associated with three or all four forest types (Table 1); our generalist species, and dipterocarps in general, are not as widespread as some generalist tropical tree species described in other studies (Baltzer et al., 2007; Condit et al., 2013; Esquivel-Muelbert, Baker, et al., 2017; Esquivel-Muelbert, Galbraith, et al., 2017), and show a certain degree of habitat specialism, but they do provide a useful contrast to the strict specialists at the study site.

For each tree, height was measured using the sine method with a laser distance meter (Nikon Forestry Pro Rangefinder, Nikon) by standing directly below the canopy and aiming vertically at the highest branch (Larjavaara et al., 2013). Multiple branches were measured with the largest reading taken as overall tree height. For trees <10 m that could not be measured from directly below the canopy, we used the trigonometric tangent method to quantify height (Larjavaara et al., 2013).

Leaf traits

Leaves were sampled from a sunlit branch, or a branch from the top of the crown for understorey trees, using rope-climbing canopy access. Leaves from cut branches were used to measure 14 leaf traits: saturating photosynthesis (A_{sat}), maximum photosynthetic capacity (V_{cmax}) and leaf dark respiration (R_{leaf}) standardised to 25°C, abaxial leaf conductance after 30 min of dark adaptation (g_{dark}), leaf mass per area (LMA), leaf thickness and leaf nutrient concentrations ($[N]_{\text{leaf}}$, $[P]_{\text{leaf}}$, $[Ca]_{\text{leaf}}$, $[K]_{\text{leaf}}$, $[Mg]_{\text{leaf}}$). We present both mass-based and area-based measures of A_{sat} , V_{cmax} and R_{leaf} . Full details of trait measurements are described in the supplementary methods.

Data analysis

To test prediction 1, we used linear models to test for differences among the four forest types in soil properties (pH, total N, total P, soluble P, exchangeable Ca, K, Mg and granulometry; $n = 87$), and

leaf gas exchange, morphological and nutrient concentration traits for all trees sampled ($A_{\text{sat_mass}}$, $A_{\text{sat_area}}$, $V_{\text{cmax_mass}}$, $V_{\text{cmax_area}}$, $R_{\text{leaf_mass}}$, $R_{\text{leaf_area}}$, LMA, leaf thickness, g_{dark} , $[N]_{\text{leaf}}$, $[P]_{\text{leaf}}$, $[Ca]_{\text{leaf}}$, $[K]_{\text{leaf}}$ and $[Mg]_{\text{leaf}}$; $n = 218$). We compared a model with forest type included as a fixed effect to a null model with no fixed effects. We tested for significance of forest type by checking if the model with forest type had a lower AIC score than the null model (Sakamoto, 1994). Data were natural-log, \log_{10} , square-root or square transformed if the assumption of normally distributed residuals was violated when models were applied to untransformed data.

To test prediction 2, we used standardised major axis regression (SMA), using the package *SMATR* (Warton et al., 2012), to test for relationships between $V_{\text{cmax_mass}}$ and $R_{\text{leaf_mass}}$ and leaf nutrient concentrations. Trait values were \log_{10} -transformed and presented at the individual level and using Sidak adjusted p values to account for multiple pairwise comparisons (Šidák, 1967). We compared the intercept and slope of these relationships between different forest types using Wald tests. We additionally tested for bivariate trait relationships between $V_{\text{cmax_mass}}$, $R_{\text{leaf_mass}}$ and LMA within each forest.

To test prediction 3—the effect of tree height on leaf traits—we used linear mixed effects models, using the *LME4* package (Bates et al., 2014). Forest type, tree height and an interaction between forest and tree height on leaf traits were fitted as fixed effects; species was fitted as a random intercept variable. The significance of the random effect was tested using a log-likelihood ratio test (Bolker et al., 2009; Harrison et al., 2018) by comparing the full linear mixed-effects model to an ordinary least squares model using the *NLME* package (Pinheiro et al., 2012), following Zuur et al. (2009). When the species random intercept did not significantly improve the model fit according to log-likelihood tests, linear models were used to test the significance of the fixed effects. For models where residuals were non-normal, we transformed the trait data using a natural-log, inverse natural-log or square-root transformation. In these instances, nonlinear relationships between leaf trait variation and tree height were better predictors than linear relationships. Intraspecific relationships between leaf traits and tree height were tested by comparing a linear model with tree height as a fixed effect to a null model using analysis of variance with the *anova* function in the *STATS* package (R Core Team, 2019).

To test prediction 4, we fitted linear mixed-effects models using forest type, tree height and their interaction as fixed effects and species as a random intercept effect. The best model for each trait was selected based on AIC scores (Sakamoto, 1994). To test for equal variance between generalist and specialist species, we used linear mixed-effect models with forest type and our generalist/specialist classification included as fixed effects and species included as a random effect using the *NLME* package (Pinheiro et al., 2012). Using this model formula, we compared models where (a) the variance was allowed to differ according to the generalist or specialist category versus (b) models with constant variance across the two generalist/specialist classes and tested for the best model using an analysis of

variance. *Shorea johorensis* was removed from this analysis because only large trees were measured for this species.

RESULTS

Variation in soil conditions across the edaphic gradient

Soil nutrient availability differed between forest types (Figure S1). The alluvial and mudstone forests had higher pH, total N, total P, exchangeable Ca and K than sandstone and kerangas forests. These differences between forests were more pronounced at shallower depths (0–5 cm) than at greater depths (15–30 cm). The alluvial and mudstone forest soils did not significantly differ, except for significantly higher total P in alluvial forests at all three depths. The kerangas forest had the highest sand and lowest silt and clay content of all forests. The kerangas was also the most nutrient-poor forest with the lowest total N, total and soluble P, and exchangeable K and Mg at all three depths, as well as the lowest pH. Exchangeable Ca did not differ between sandstone and kerangas forests, with very low concentrations in both. Overall, there was an edaphic fertility gradient from nutrient-rich alluvial and mudstone forests to the nutrient-poor kerangas forest, with sandstone forest typically intermediate.

Variation in leaf traits across the edaphic gradient in nutrient availability

All non-nutrient-based leaf traits ($A_{\text{sat_mass}}$, $A_{\text{sat_area}}$, $V_{\text{cmax_mass}}$, $V_{\text{cmax_area}}$, $R_{\text{leaf_mass}}$, $R_{\text{leaf_area}}$, LMA, leaf thickness, g_{dark}) varied significantly between all forest types (Figure 1a–i; Table 1). Values of $A_{\text{sat_mass}}$, $A_{\text{sat_area}}$, $V_{\text{cmax_mass}}$ and g_{dark} followed the nutrient availability gradient with significantly higher trait values in the nutrient-rich alluvial forest transitioning to significantly lower values in the nutrient-poor kerangas forest ($p < 0.05$). Mean values of LMA displayed the inverse trend (Figure 1d). In contrast, mean $R_{\text{leaf_mass}}$ and $R_{\text{leaf_area}}$ were significantly lower in the mudstone forest compared to all other forest types (Figure 1c,h). We found no significant bivariate trait–trait relationships between $V_{\text{cmax_mass}}$, $R_{\text{leaf_mass}}$ and LMA in any of the four forests (Figure S3).

Leaf nutrient concentrations differed between forest types (Figure 1j–n; Table 1). $[N]_{\text{leaf}}$, $[P]_{\text{leaf}}$ and $[K]_{\text{leaf}}$ followed the same gradient across the forest types: alluvial > mudstone > sandstone > kerangas. Mean $[Ca]_{\text{leaf}}$ was highest in the mudstone forest and lowest in the sandstone forest (Figure 1l), whereas mean $[Mg]_{\text{leaf}}$ was greatest in the sandstone and lowest in the mudstone forest (Figure 1n). Gradients in leaf nutrient concentrations between forests largely reflect the gradient in soil nutrient concentrations, with alluvial and mudstone forests richer in all soil and leaf nutrients when compared with sandstone and kerangas forests, except $[Mg]_{\text{leaf}}$. Despite no significant differences in soil nutrient availability between alluvial and mudstone soils, except total P (Figure S1), we

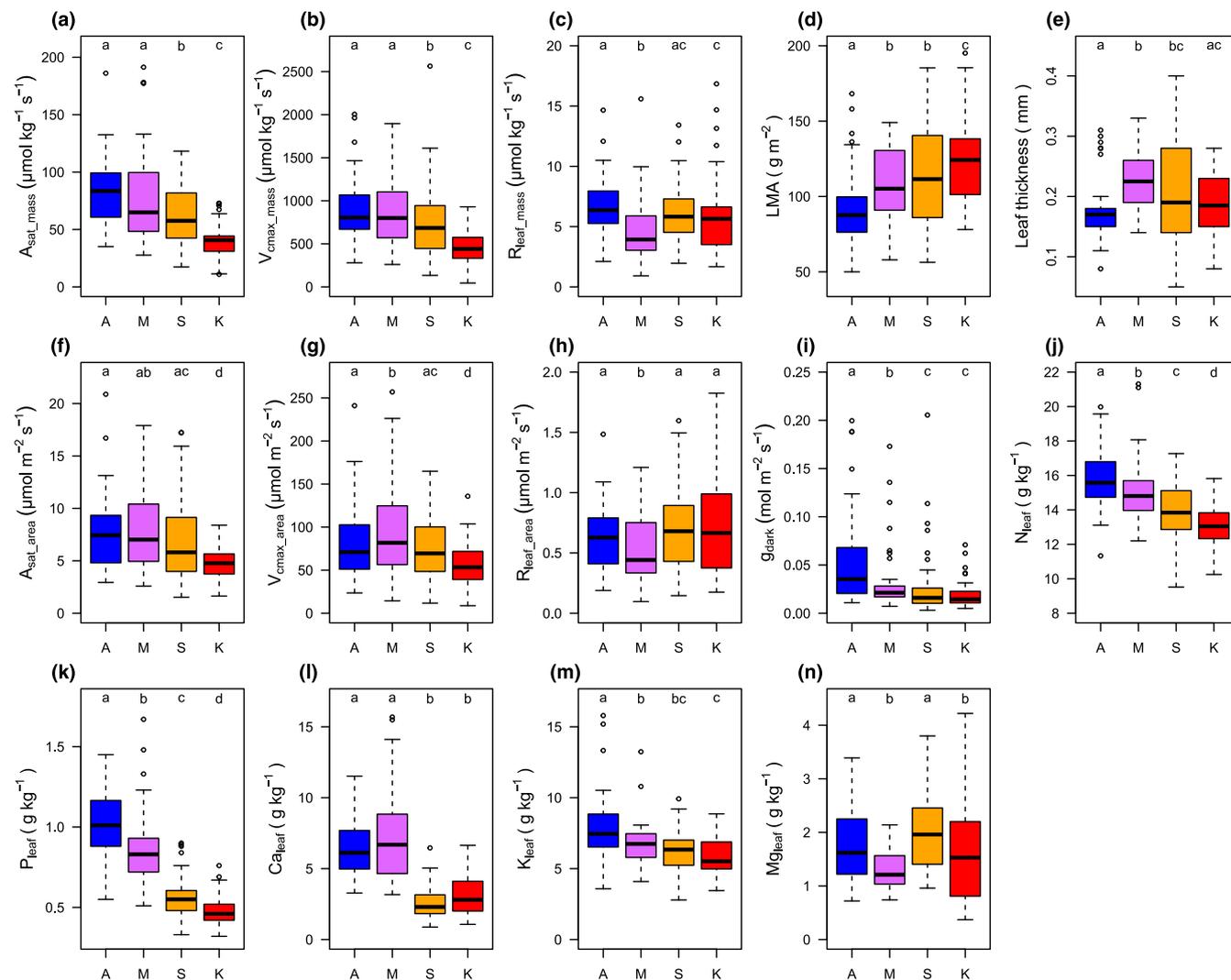


FIGURE 1 Boxplots showing how $A_{\text{sat_mass}}$ (a) $V_{\text{cmax_mass}}$ (b), $R_{\text{leaf_mass}}$ (c), leaf mass per area (LMA; d), leaf thickness (e), $A_{\text{sat_area}}$ (f) $V_{\text{cmax_area}}$ (g), $R_{\text{leaf_area}}$ (h), dark-adapted stomatal conductance (g_{dark} ; i) and leaf nutrient concentrations (j–n), change between the four forests (alluvial (A)—blue, mudstone (M)—purple, sandstone (S)—orange, kerangas (K)—red). Data presented represent individual-level traits (see Figure S9 for presentation at the species level). Identical letters represent categories where there is no significant difference between forests from linear models ($p > 0.05$). Boxes represent the interquartile range with a horizontal line for the median and the whiskers represent 1.5*interquartile range or the maximum and minimum point. Dots represent points outside the extent of the 1.5*interquartile range.

did find significant differences in $[N]_{\text{leaf}}$, $[P]_{\text{leaf}}$, $[K]_{\text{leaf}}$ and $[Mg]_{\text{leaf}}$ between these forests. Moreover, we found significantly lower $[Mg]_{\text{leaf}}$ in kerangas than sandstone forest trees, despite no significant differences in soil exchangeable Mg concentrations between these forests at any sampled depth.

Scaling of photosynthetic capacity and respiration with foliar nutrient concentrations

Using standardised major axis regression (SMA), we found $A_{\text{sat_mass}}$, $V_{\text{cmax_mass}}$ and $R_{\text{leaf_mass}}$ were significantly related to leaf nutrient concentrations (Table 2; Figure 2), but the physiological measures showed significant relationships with different leaf nutrients depending on the forest type. $A_{\text{sat_mass}}$ and $V_{\text{cmax_mass}}$ showed significant

positive relationships in the alluvial forest with $[N]_{\text{leaf}}$ (and $[P]_{\text{leaf}}$ for $A_{\text{sat_mass}}$ only), in the mudstone forest with $[N]_{\text{leaf}}$ and $[P]_{\text{leaf}}$ (and $[K]_{\text{leaf}}$ for $A_{\text{sat_mass}}$ only), in the sandstone forest with $[P]_{\text{leaf}}$, $[Ca]_{\text{leaf}}$ and $[K]_{\text{leaf}}$ and in the kerangas forest with $[Mg]_{\text{leaf}}$ (and $[Ca]_{\text{leaf}}$ for $V_{\text{cmax_mass}}$ only; Table 2; Figure 2a–j). Differences in photosynthetic nutrient-use efficiency between forests were observed by significant shifts in the intercept of the $A_{\text{sat_mass}}$ -nutrient and $V_{\text{cmax_mass}}$ -nutrient SMA relationships. Nitrogen-use efficiency of $V_{\text{cmax_mass}}$ was higher in sandstone than alluvial forest ($p = 0.01$), but did not significantly differ between mudstone and sandstone ($p = 0.485$) or mudstone and alluvial ($p = 0.593$). Phosphorus-use efficiency of $V_{\text{cmax_mass}}$ was higher in sandstone than mudstone forest ($p < 0.001$) and calcium-use efficiency of $V_{\text{cmax_mass}}$ was higher in kerangas than sandstone forest ($p < 0.001$). Phosphorus-use efficiency of $A_{\text{sat_mass}}$ was higher in sandstone than both alluvial ($p < 0.001$) and mudstone

TABLE 2 Summary of standardised major axis regressions between natural log transformed $A_{\text{sat_mass}}$, $V_{\text{cmax_mass}}$ and $R_{\text{leaf_mass}}$ with leaf nutrient concentrations for each of the four forests. Significant correlations between the trait and nutrient concentration are in bold.

Trait	Nutrient	Forest	Intercept	Slope	R^2	p
$A_{\text{sat_mass}}$	[N] _{leaf}	Alluvial	-4.88	-3.34	0.239	<0.001
		Mudstone	-8.20	4.61	0.335	<0.001
		Sandstone	-6.68	4.08	0.232	<0.001
		Kerangas	-6.49	3.96	0.001	0.809
	[P] _{leaf}	Alluvial	4.36	1.98	0.093	0.046
		Mudstone	4.57	2.12	0.498	<0.001
		Sandstone	5.51	2.42	0.322	<0.001
		Kerangas	5.21	2.08	0.022	0.299
	[Ca] _{leaf}	Alluvial	6.40	-1.10	0.031	0.255
		Mudstone	6.28	-1.08	0.000	0.916
		Sandstone	2.97	1.22	0.090	0.006
		Kerangas	2.89	0.74	0.066	0.066
	[K] _{leaf}	Alluvial	1.28	1.54	0.006	0.633
		Mudstone	-0.35	2.44	0.123	0.033
		Sandstone	0.67	1.86	0.148	<0.001
		Kerangas	0.82	1.61	0.017	0.363
[Mg] _{leaf}	Alluvial	4.88	-1.03	0.000	0.983	
	Mudstone	3.85	1.80	0.031	0.300	
	Sandstone	4.91	-1.38	0.033	0.103	
	Kerangas	3.44	0.60	0.176	0.002	
$V_{\text{cmax_mass}}$	[N] _{leaf}	Alluvial	-3.76	3.77	0.151	0.010
		Mudstone	-8.55	5.63	0.203	0.006
		Sandstone	-5.36	4.50	0.244	<0.001
		Kerangas	-7.09	5.15	0.043	0.164
	[P] _{leaf}	Alluvial	6.69	2.25	0.067	0.095
		Mudstone	7.02	2.33	0.311	<0.001
		Sandstone	8.12	2.71	0.249	<0.001
		Kerangas	7.89	2.44	0.053	0.120
	[Ca] _{leaf}	Alluvial	4.32	1.29	0.017	0.398
		Mudstone	9.01	-1.25	0.000	0.996
		Sandstone	5.24	1.42	0.134	<0.001
		Kerangas	5.16	0.90	0.129	0.013
	[K] _{leaf}	Alluvial	3.22	1.75	0.012	0.488
		Mudstone	1.57	2.71	0.072	0.114
		Sandstone	2.77	2.05	0.109	0.003
		Kerangas	2.55	1.98	0.000	0.983
[Mg] _{leaf}	Alluvial	7.29	-1.20	0.003	0.739	
	Mudstone	6.24	2.02	0.003	0.750	
	Sandstone	5.45	1.55	0.001	0.824	
	Kerangas	5.85	0.81	0.224	<0.001	
$R_{\text{leaf_mass}}$	[N] _{leaf}	Alluvial	-5.57	2.69	0.122	0.023
		Mudstone	-15.18	6.13	0.093	0.059
		Sandstone	-7.18	3.39	0.034	0.101
		Kerangas	-11.62	5.20	0.087	0.037

(Continues)

TABLE 2 (Continued)

Trait	Nutrient	Forest	Intercept	Slope	R^2	p
$A_{\text{sat_mass}}$	$[P]_{\text{leaf}}$	Alluvial	1.87	1.62	0.008	0.569
		Mudstone	1.78	2.20	0.202	0.004
		Sandstone	2.95	1.99	0.140	<0.001
		Kerangas	3.82	2.84	0.166	0.003
$[Ca]_{\text{leaf}}$	Alluvial	3.58	-0.92	0.020	0.374	
	Mudstone	-0.98	1.29	0.000	0.973	
	Sandstone	2.58	-0.97	0.024	0.164	
	Kerangas	0.60	1.08	0.039	0.170	
$[K]_{\text{leaf}}$	Alluvial	-0.67	1.27	0.033	0.247	
	Mudstone	-3.80	2.77	0.023	0.362	
	Sandstone	-0.95	1.50	0.012	0.329	
	Kerangas	-1.96	2.09	0.005	0.637	
$[Mg]_{\text{leaf}}$	Alluvial	1.49	0.82	0.001	0.815	
	Mudstone	0.98	1.97	0.014	0.466	
	Sandstone	2.45	-1.09	0.087	0.008	
	Kerangas	1.41	0.91	0.071	0.062	

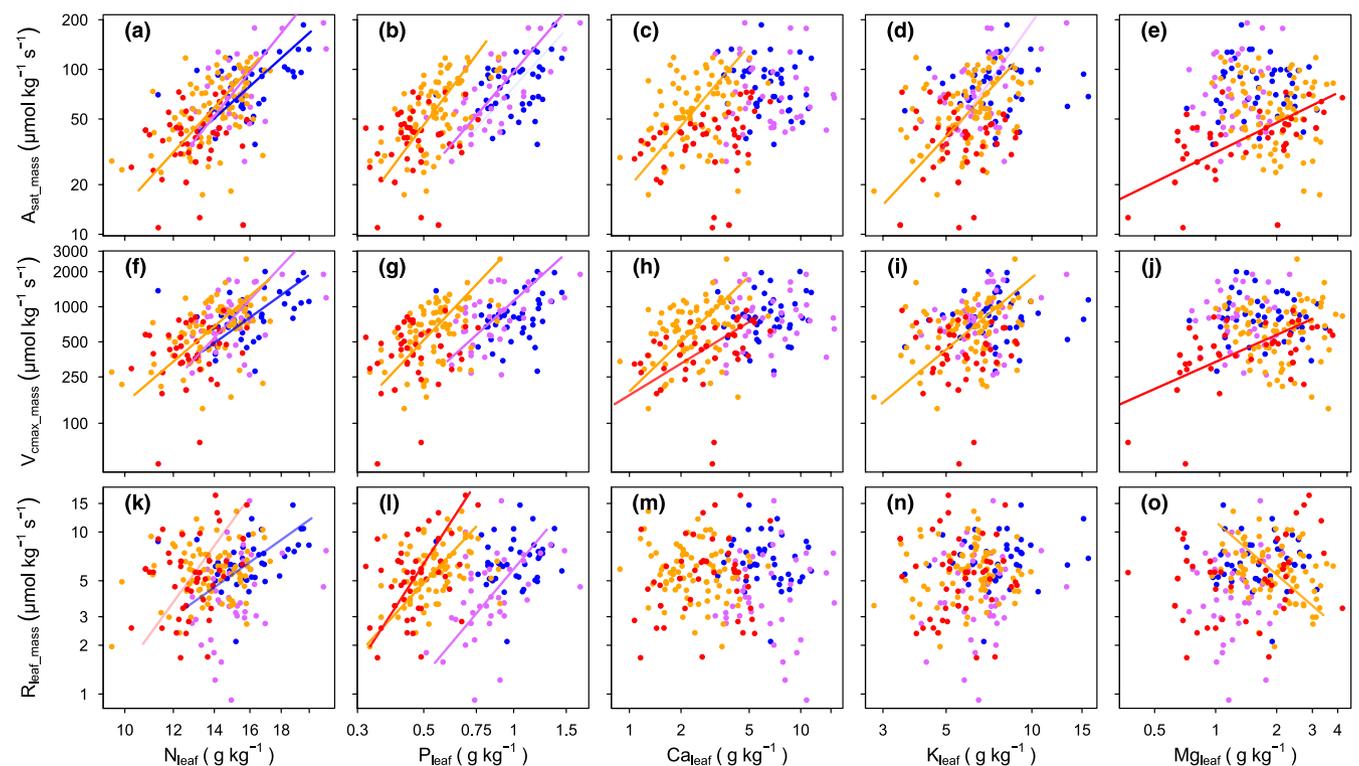


FIGURE 2 Standardised major axis regressions (SMAs) for $A_{\text{sat_mass}}$ (a–e), $V_{\text{cmax_mass}}$ (f–j) and $R_{\text{leaf_mass}}$ (k–o) with leaf nutrient concentrations ($[N]_{\text{leaf}}$ —a, f and k; $[P]_{\text{leaf}}$ —b, g and l; $[Ca]_{\text{leaf}}$ —c, h and m; $[K]_{\text{leaf}}$ —d, i and n; and $[Mg]_{\text{leaf}}$ —e, j and o). Colours represent the four different forests (blue—alluvial, purple—mudstone, orange—sandstone, red—kerangas). Lines are presented for significant SMA relationships ($p < 0.05$), with the degree of transparency scaled to the significance value (greater opacity represents greater significance in the SMA). Most relationships were highly significant, with the exception of the $A_{\text{sat_mass}}$ – $[P]_{\text{leaf}}$ and $R_{\text{leaf_mass}}$ – $[N]_{\text{leaf}}$ relationships that were weakly significant (see Table 2). Note data and axes have been natural log transformed.

forests ($p < 0.001$), but did not differ between alluvial and mudstone forests ($p = 0.289$). No shifts in nitrogen or potassium-use efficiency of $A_{\text{sat_mass}}$ between forests were observed ($p > 0.05$). $R_{\text{leaf_mass}}$

displayed less consistent relationships with leaf nutrients across forest types; it was positively related to $[N]_{\text{leaf}}$ in the alluvial and kerangas forests and to $[P]_{\text{leaf}}$ in the mudstone, sandstone and kerangas

forests. $R_{\text{leaf_mass}}$ also showed a negative relationship with $[\text{Mg}]_{\text{leaf}}$ in the sandstone forest (Table 2; Figure 2k–o). We found a significant shift in the intercept of SMA relationships between $R_{\text{leaf_mass}}$ and leaf nutrient concentrations, which suggest differences in respiratory nutrient-use efficiency between forests. Nitrogen-use efficiency of $R_{\text{leaf_mass}}$ was higher in alluvial than kerangas forest ($p < 0.001$) and phosphorus-use efficiency of $R_{\text{leaf_mass}}$ was higher in both sandstone ($p < 0.001$) and kerangas ($p < 0.001$) than mudstone forest, but did not differ between sandstone and kerangas forests ($p = 0.051$).

Variation in leaf traits with tree height

We tested for the effect of forest type, tree height, forest–height interactions and identity on leaf traits using linear mixed-effects models. We found a significant height effect in all forest types on all leaf traits ($A_{\text{sat_mass}}$, $A_{\text{sat_area}}$, $V_{\text{cmax_area}}$, $R_{\text{leaf_mass}}$, $R_{\text{leaf_area}}$, LMA, leaf thickness, g_{dark} , $[\text{N}]_{\text{leaf}}$, $[\text{P}]_{\text{leaf}}$, $[\text{Ca}]_{\text{leaf}}$, $[\text{K}]_{\text{leaf}}$ and $[\text{Mg}]_{\text{leaf}}$), except $V_{\text{cmax_mass}}$ (Table 3; Figure 3; Figure S4). However, the between-forest differences explained greater variation in leaf traits than tree height, except for $A_{\text{sat_area}}$, $R_{\text{leaf_area}}$, LMA and leaf thickness (Table 3; Figure 4). Significant variation was explained through the inclusion of a species random effect term in models for all leaf traits except g_{dark} (Table 3). Despite these significant species effects, we also observed large intraspecific variation in leaf traits (Figure S5). Intraspecific variation in LMA was largely determined by height, but intraspecific variation in $V_{\text{cmax_mass}}$ and $R_{\text{leaf_mass}}$ was not; when the 12 species were considered individually, no species showed a significant relationship between tree height and $V_{\text{cmax_mass}}$ (Figure S6c), and only five species (*C. melanoxylon*, *D. acutangulus*, *D. caudiferus*, *P. tomentella*, *H. beccariana*) showed significant relationships between tree height and $R_{\text{leaf_mass}}$ (Figure S6e). These species had a positive relationship between $R_{\text{leaf_mass}}$ and tree height except *H. beccariana* (sandstone/kerangas) which had a negative relationship. This suggests that the significant height effect on most leaf traits is driven by strong relationships in a few species rather than a common response across all species and that changes in $V_{\text{cmax_area}}$ are driven by changes in LMA rather than changes in $V_{\text{cmax_mass}}$.

After accounting for interspecific trait variation and height in our models, we found significant forest type effects on all traits except $[\text{Mg}]_{\text{leaf}}$ in our models (Table 3). Moreover, we found a significant interaction suggesting that the effect of tree height on $A_{\text{sat_mass}}$, $A_{\text{sat_area}}$, $[\text{N}]_{\text{leaf}}$, $[\text{P}]_{\text{leaf}}$ and $[\text{K}]_{\text{leaf}}$ varied according to forest type (Table 3). $A_{\text{sat_mass}}$ and $A_{\text{sat_area}}$ increased with tree height in all forests, except for $A_{\text{sat_mass}}$ in kerangas forest. $[\text{N}]_{\text{leaf}}$ and $[\text{K}]_{\text{leaf}}$ both increased with tree height, except for $[\text{K}]_{\text{leaf}}$ in the alluvial forest and $[\text{N}]_{\text{leaf}}$ and $[\text{K}]_{\text{leaf}}$ in the mudstone forest where leaf nutrient concentrations declined with tree height. $[\text{P}]_{\text{leaf}}$ increased with tree height in all forests, but the slope of the relationship varied between forests. For all other traits, the effect of tree height on leaf traits did not differ significantly among forests. Overall, species identity, forest and tree height were able to

explain 19.4–76.6% of the variation in leaf traits, depending on the trait (Table 3; Figure 4).

Trait variation in generalist species

Using linear mixed models, we tested for significant differences in trait values between forest types for the five generalist species. Several traits varied between forest types in generalist species: $A_{\text{sat_area}}$, $V_{\text{cmax_mass}}$, $V_{\text{cmax_area}}$, LMA, $[\text{N}]_{\text{leaf}}$, $[\text{P}]_{\text{leaf}}$, $[\text{Ca}]_{\text{leaf}}$ and $[\text{K}]_{\text{leaf}}$ (Tables 4 and S4). All other traits were conserved between forest types in generalist species. Despite a significant forest effect on several traits, differences in trait values varied depending on which forests the generalists inhabited (Table 4; Figure 5): generalists to alluvial and mudstone forests only had significantly lower $[\text{P}]_{\text{leaf}}$ in mudstone forests (Figure 5a); generalists to mudstone and sandstone forests had significantly higher LMA and lower $A_{\text{sat_area}}$, $V_{\text{cmax_mass}}$, $V_{\text{cmax_area}}$, $[\text{N}]_{\text{leaf}}$, $[\text{P}]_{\text{leaf}}$, $[\text{Ca}]_{\text{leaf}}$ and $[\text{K}]_{\text{leaf}}$ in sandstone forests (Figure 5b); sandstone–kerangas generalists had significantly lower $V_{\text{cmax_mass}}$ and LMA in kerangas forest, but did not have differences in any other traits (Figure 5c). Differences in mean trait values between forest types did not vary with tree height except for LMA, which decreased with height in mudstone–sandstone generalists, but increased with tree height in sandstone–kerangas generalists. Compared to specialist species, standard deviation of five of the nine non-nutrient leaf traits was greater in generalist species: $A_{\text{sat_mass}}$ ($\times 1.60$; $p < 0.001$), $A_{\text{sat_area}}$ ($\times 1.31$; $p = 0.012$), $V_{\text{cmax_mass}}$ ($\times 1.84$; $p < 0.001$), $V_{\text{cmax_area}}$ ($\times 1.42$; $p = 0.003$) and leaf thickness ($\times 1.52$; $p = 0.002$; Figure S5). Standard deviation in leaf nutrients was also greater in generalists for $[\text{N}]_{\text{leaf}}$ ($\times 1.24$, $p = 0.031$), $[\text{P}]_{\text{leaf}}$ ($\times 1.41$, $p < 0.001$) and $[\text{Ca}]_{\text{leaf}}$ ($\times 1.36$, $p = 0.003$) than specialists, while standard deviation in $[\text{K}]_{\text{leaf}}$ was 1.07 times greater in specialists ($p = 0.008$). No significant difference in the standard deviation of $R_{\text{leaf_mass}}$, $R_{\text{leaf_area}}$, LMA, g_{dark} or $[\text{Mg}]_{\text{leaf}}$ was detected between specialist and generalist species. While these differences in trait standard deviation may be explained by differences in mean trait values, similar patterns emerge when analysing the coefficient of variance in traits (Table S5).

DISCUSSION

Our study demonstrates that soil properties and tree height are important controls on dipterocarp leaf physiological strategies in Bornean lowland forests. Across the edaphic gradient we studied, dipterocarp leaf traits shift from an acquisitive strategy when growing in forests with a high nutrient status to a more conservative strategy on nutrient-poor soils. Nutrients limit photosynthetic capacity and respiration across the gradient, with the most limiting nutrient varying with forest type. Dipterocarp species growing on nutrient-poor soils appear to adapt to these conditions by maintaining greater leaf-level nutrient-use efficiency. Generalist species did, however, have greater intraspecific variation in leaf traits, which may enable them to maintain a wider

TABLE 3 Parameter estimates \pm standard error for the minimal adequate model used to explain leaf trait variation. Forest type, tree height and their interaction were included as fixed effects in the models, while species was considered as a random intercept factor. Values for each of the four forests are presented: A—alluvial; M—mudstone; S—sandstone; K—kerangas. A single value for the intercept is given when forest was not significant, and a single value is given for the height slope when no significant interaction between the forest type and tree height was found. The species effect represents the standard deviation of the random intercept slope. Dashes are given when coefficients did not significantly differ from zero and when the species effect was not retained in the minimal adequate model. R^2_m represents the marginal R^2 for all fixed effects combined and R^2_c represents the conditional R^2 for all fixed and random effects combined.

Trait	Data Transformation	Intercept				Height slope				Species effect	R^2_m	R^2_c
		A	M	S	K	A	M	S	K			
$A_{\text{sat_mass}}$	log	4.19 \pm 0.17	4.52 \pm 0.22	3.93 \pm 0.20	4.09 \pm 0.24	0.00 \pm 0.00	-0.01 \pm 0.01	0.00 \pm 0.01	-0.02 \pm 0.01	0.28	0.291	0.546
$A_{\text{sat_area}}$	log	1.54 \pm 0.17	2.02 \pm 0.22	1.44 \pm 0.20	1.81 \pm 0.24	0.01 \pm 0.00	0.00 \pm 0.01	0.01 \pm 0.01	-0.01 \pm 0.01	0.29	0.169	0.485
$V_{\text{cmax_mass}}$	log	6.68 \pm 0.14	6.70 \pm 0.16	6.41 \pm 0.17	5.95 \pm 0.19	—	—	—	—	0.28	0.210	0.413
$V_{\text{cmax_area}}$	log	4.09 \pm 0.16	4.22 \pm 0.16	3.99 \pm 0.16	3.72 \pm 0.19	0.01 \pm 0.00	0.01 \pm 0.00	0.01 \pm 0.00	0.02 \pm 0.00	0.28	0.133	0.360
$R_{\text{leaf_mass}}$	sqrt	2.30 \pm 0.13	1.90 \pm 0.14	2.18 \pm 0.14	2.23 \pm 0.15	0.01 \pm 0.00	0.01 \pm 0.00	0.01 \pm 0.00	0.02 \pm 0.00	0.17	0.100	0.194
$R_{\text{leaf_area}}$	log	-1.03 \pm 0.13	-1.28 \pm 0.13	-0.90 \pm 0.13	-0.77 \pm 0.14	0.02 \pm 0.00	0.02 \pm 0.00	0.02 \pm 0.00	0.02 \pm 0.00	0.17	0.225	0.325
LMA	1/log	0.24 \pm 0.00	0.24 \pm 0.00	0.23 \pm 0.00	0.22 \pm 0.00	0.00	0.395	0.603				
Leaf thickness	—	0.14 \pm 0.02	0.14 \pm 0.01	0.17 \pm 0.02	0.21 \pm 0.02	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.06	0.167	0.767
g_{dark}	log	-2.97 \pm 0.14	-3.45 \pm 0.15	-3.86 \pm 0.13	-3.98 \pm 0.14	-0.01 \pm 0.00	-0.01 \pm 0.00	-0.01 \pm 0.00	-0.01 \pm 0.00	—	0.231	—
$[N]_{\text{leaf}}$	—	14.97 \pm 0.61	15.83 \pm 0.77	13.12 \pm 0.72	12.60 \pm 0.87	0.03 \pm 0.01	-0.02 \pm 0.02	0.03 \pm 0.02	0.02 \pm 0.03	1.00	0.331	0.587
$[P]_{\text{leaf}}$	log	-0.06 \pm 0.08	-0.08 \pm 0.10	-0.77 \pm 0.09	-0.78 \pm 0.11	0.00 \pm 0.00	0.00 \pm 0.00	0.01 \pm 0.00	0.00 \pm 0.00	0.12	0.647	0.761
$[Ca]_{\text{leaf}}$	log	1.92 \pm 0.13	1.94 \pm 0.11	1.15 \pm 0.13	1.06 \pm 0.15	-0.01 \pm 0.00	-0.01 \pm 0.00	-0.01 \pm 0.00	-0.01 \pm 0.00	0.28	0.475	0.720
$[K]_{\text{leaf}}$	log	2.17 \pm 0.10	2.00 \pm 0.12	1.67 \pm 0.12	1.69 \pm 0.14	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.01 \pm 0.00	0.16	0.176	0.498
$[Mg]_{\text{leaf}}$	log	0.56 \pm 0.11	0.56 \pm 0.11	0.56 \pm 0.11	0.56 \pm 0.11	-0.01 \pm 0.00	-0.01 \pm 0.00	-0.01 \pm 0.00	-0.01 \pm 0.00	0.37	0.027	0.704

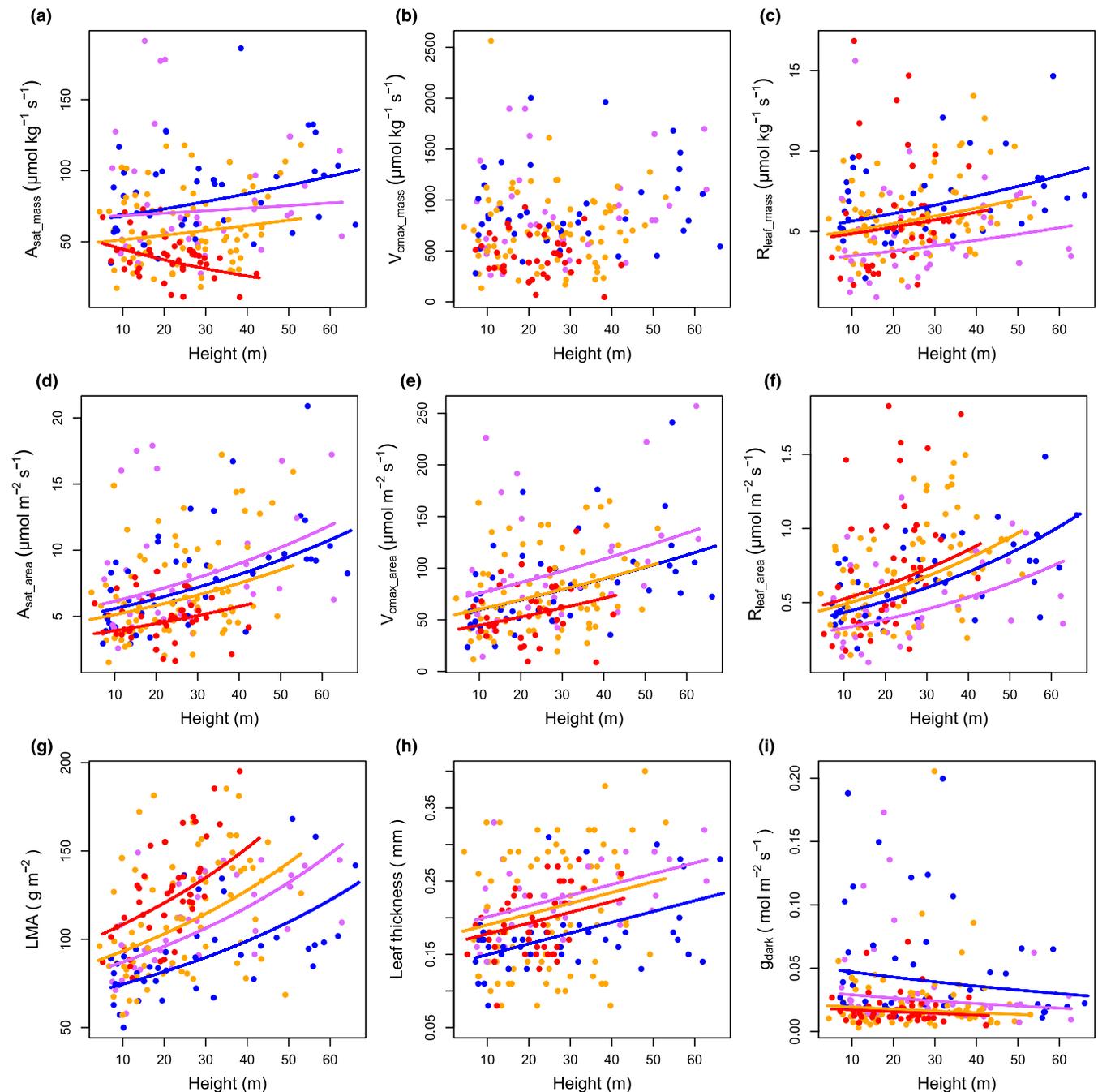


FIGURE 3 Scatterplots showing how $A_{\text{sat_mass}}$ (a), $V_{\text{cmax_mass}}$ (b), $R_{\text{leaf_mass}}$ (c), $A_{\text{sat_area}}$ (d), $V_{\text{cmax_area}}$ (e), $R_{\text{leaf_area}}$ (f), leaf mass per area (g) leaf thickness (h) and g_{dark} (i) change with tree height. Colours represent the four different forests (blue—alluvial, purple—mudstone, orange—sandstone, red—kerangas). Lines represent predicted fits from the minimal adequate general linear model for each trait (see Table 3). For relationships between leaf nutrient concentrations and tree height, see Figure S4.

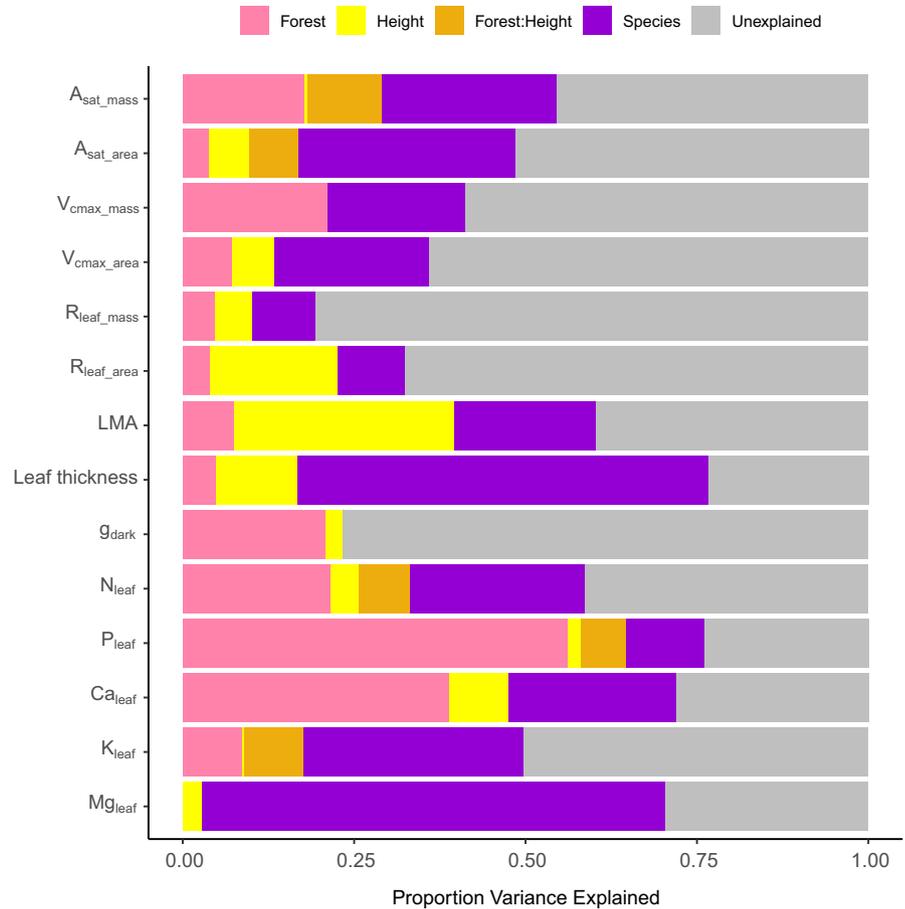
distribution across forest types than specialist species that are isolated to one forest type. Alongside responding to changes in soil conditions, dipterocarp species, which represent some of the world's tallest tropical trees, also altered their leaf traits in response to vertical environmental variations. We find greater light- and water-use efficiency with increasing tree height, although these observed trait variations may reflect increasing hydraulic limitation with tree height. Our results suggest that adaptations to the variation in edaphic and vertical environments may facilitate environmental niche partitioning between

dipterocarps, thus supporting turnover of dipterocarp species across environmental gradients.

Variations in leaf physiology across the edaphic gradient

Most leaf traits, including leaf nutrient concentrations, $V_{\text{cmax_mass}}$, LMA and g_{dark} varied with soil fertility as predicted by the leaf

FIGURE 4 Proportion of variance in leaf traits explained by the minimal adequate linear mixed-effect model for each trait (see Table 3). Forest type (pink), tree height (yellow) and the interaction between them (orange) were included in the models as fixed effects, while species (purple) was included as a random effect. Unexplained variance is presented in grey.



economic spectrum (Wright et al., 2004), being more acquisitive in forests on more fertile soils (alluvial and mudstone) than in forests with lower fertility soils (sandstone and kerangas; Figure 1). Our findings show that canopy dipterocarp trees follow similar soil-related variation in leaf traits to saplings and other tree families in Bornean forests (Katabuchi et al., 2012; Russo et al., 2010; Weemstra et al., 2020; Dent & Burslem, 2016; Baltzer et al., 2005) and that there is significant interspecific variation in leaf traits.

In contrast, $R_{\text{leaf_mass}}$ did not vary with soil fertility as predicted by the leaf economics spectrum (Wright et al., 2004), being lowest in the nutrient-rich mudstone forest. Foliar P concentrations were closely related to $R_{\text{leaf_mass}}$ in all forests except the alluvial forest, where $R_{\text{leaf_mass}}$ was related more closely to $[N]_{\text{leaf}}$. This contrasts patterns observed in other regions of the tropics, where leaf nutrient concentrations scale with variation in $R_{\text{leaf_mass}}$ across forests because of the respiratory costs typically associated with increases in photosynthetic capacity (Rowland et al., 2017; Atkin et al., 2015). We found no relationship between $R_{\text{leaf_mass}}$ and $V_{\text{cmax_mass}}$ (Figure S3), suggesting leaf respiration is not driven by increases in photosynthetic capacity. Instead, the greater $R_{\text{leaf_mass}}$ in the nutrient-poor sandstone and kerangas forests may suggest that other factors are driving variation in $R_{\text{leaf_mass}}$ in these Bornean lowland forests. As $R_{\text{leaf_mass}}$ is known to increase in drier environments (Atkin et al., 2015), one potential hypothesis is that increased water shortage driven by differences in topography and soil texture select for higher $R_{\text{leaf_mass}}$ in

the sandstone and kerangas forests, independent of maximum photosynthetic capacity. The gradient in water availability across the four forest types (Figure S7) may also explain the variation in g_{dark} , as drier conditions select for water conservation traits and lower leaf conductance (Duursma et al., 2019; Russo et al., 2010; Machado et al., 2021; Schuster et al., 2016). Overall, the variation in dipterocarp leaf traits across forest types largely reflects the leaf economics spectrum, although our results highlight how local environmental conditions can modify expectations derived from this framework.

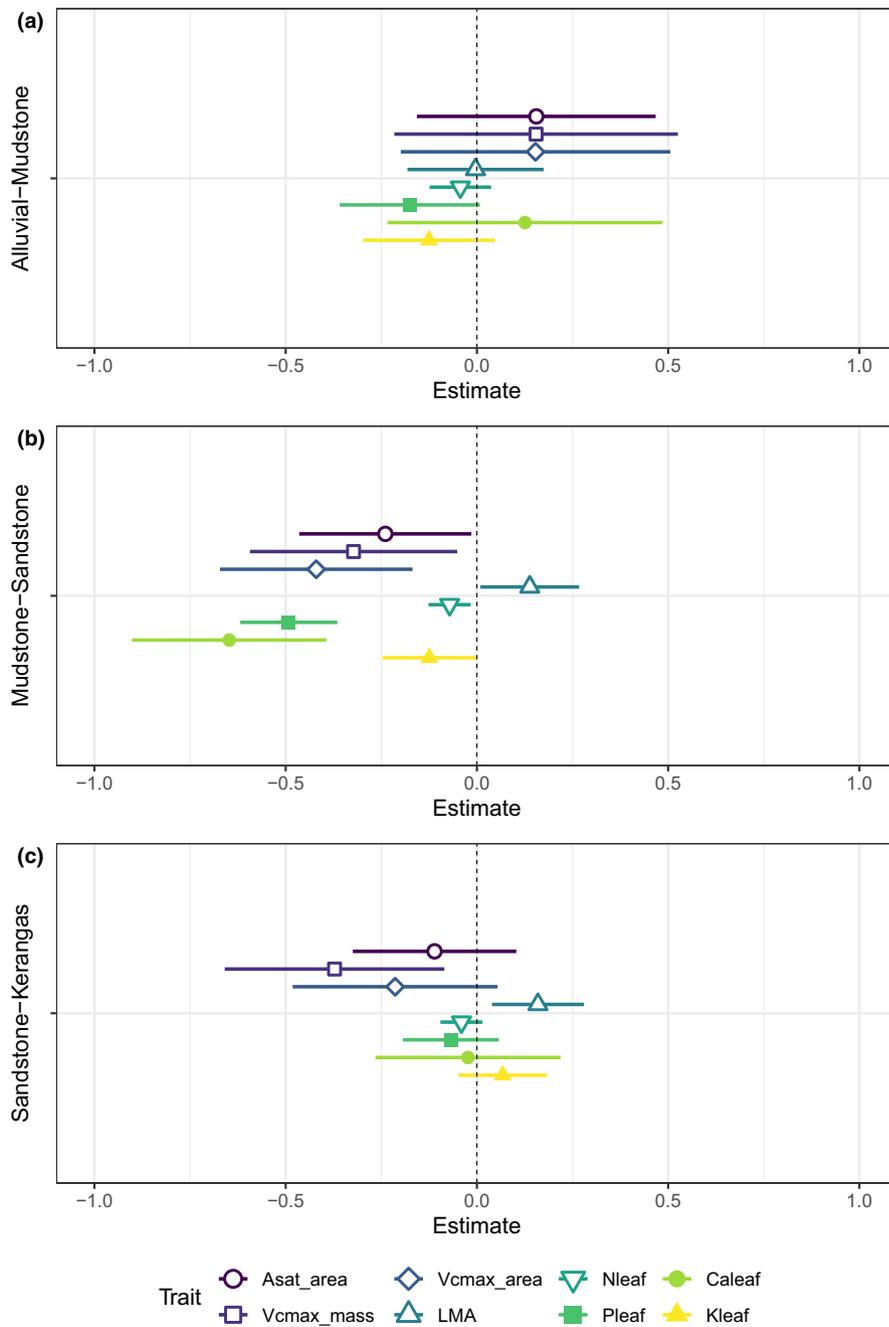
Nutrient limitation of photosynthesis varies with edaphic conditions

Highly contrasting relationships between leaf nutrient concentrations and both saturating photosynthesis and maximum photosynthetic capacity were found across our study gradient (Figure 2). We observed strong relationships of $A_{\text{sat_mass}}$ and $V_{\text{cmax_mass}}$ with $[N]_{\text{leaf}}$ and $[P]_{\text{leaf}}$ in the nutrient-rich alluvial and mudstone forests, whereas $A_{\text{sat_mass}}$ and $V_{\text{cmax_mass}}$ in the nutrient-poor kerangas forest was related to cation availability, particularly $[Mg]_{\text{leaf}}$, but also $[Ca]_{\text{leaf}}$ for $V_{\text{cmax_mass}}$ (Figure 2). Saturating photosynthesis and photosynthetic capacity of trees in the sandstone forest, which was intermediate in terms of soil nutrient concentrations, showed strong relationships with leaf N, P and cations (Figure 2). Our results support the notion that photosynthetic rates

TABLE 4 Parameter estimates \pm standard error for the minimal adequate model used to explain leaf trait variation in generalist species. Forest type, tree height and their interaction were included as fixed effects in the models, while species was considered as a random intercept factor. Parameter estimates for the forests represent the differences in the trait value in the more nutrient-poor forest compared to the more nutrient-rich forest type. Parameter estimates for height represent how the difference in trait values between forest types changes per metre tree height. The species effect represents the standard deviation of the random intercept slope. Dashes are given when forest and/or height were not retained in the best minimal adequate model. R_m^2 represents the marginal R^2 for all fixed effects combined and R_c^2 represents the conditional R^2 for all fixed and random effects combined. Asterisks represent the significance level: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. For units, see [Table 1](#).

Trait	Forest			Height			Species	Marginal R^2	Conditional R^2
	Δ Alluvial – Mudstone	Δ Mudstone – Sandstone	Δ Sandstone – Kerangas	Δ Alluvial – Mudstone	Δ Mudstone – Sandstone	Δ Sandstone – Kerangas			
$A_{\text{sat_mass}}$	–	–	–	–	–	–	0.02	0.000	0.393
$A_{\text{sat_area}}$	1.24 \pm 1.27	-1.91 \pm 0.91*	-0.88 \pm 0.87	–	–	–	3.02	0.051	0.548
$V_{\text{cmax_mass}}$	130.74 \pm 159.88	-272.69 \pm 116.82*	-314.61 \pm 123.86*	–	–	–	0.16	0.166	0.290
$V_{\text{cmax_area}}$	14.28 \pm 16.75	-39.16 \pm 11.97**	-19.92 \pm 12.74	–	–	–	27.38	0.159	0.439
$R_{\text{leaf_mass}}$	–	–	–	–	–	–	0.00	0.000	0.141
$R_{\text{leaf_area}}$	–	–	–	–	–	–	0.11	0.000	0.108
LMA	5.09 \pm 12.91	12.37 \pm 6.53*	-32.97 \pm 10.30**	-0.54 \pm 0.36	-0.41 \pm 0.19*	2.29 \pm 0.47***	22.41	0.301	0.741
Leaf thickness	–	–	–	–	–	–	0.07	0.000	0.722
g_{dark}	–	–	–	–	–	–	0.01	0.000	0.097
$[N]_{\text{leaf}}$	-0.64 \pm 0.61	-1.06 \pm 0.42*	-0.60 \pm 0.42	–	–	–	0.57	0.186	0.298
$[P]_{\text{leaf}}$	-0.13 \pm 0.07*	-0.35 \pm 0.05***	-0.05 \pm 0.05	–	–	–	0.07	0.565	0.642
$[Ca]_{\text{leaf}}$	0.56 \pm 0.81	-2.87 \pm 0.57***	-0.10 \pm 0.55	–	–	–	1.52	0.234	0.548
$[K]_{\text{leaf}}$	-0.83 \pm 0.58	-0.82 \pm 0.41*	0.45 \pm 0.39	–	–	–	1.33	0.073	0.551
$[Mg]_{\text{leaf}}$	–	–	–	–	–	–	0.65	0.000	0.738

FIGURE 5 Intraspecific differences in leaf traits for generalist species between (a) alluvial and mudstone forests (b) mudstone and sandstone forests and (c) sandstone and kerangas forests. Points represent the standardised estimate of the mean with horizontal whiskers representing the 95% confidence interval. Positive values represent higher trait values in the more nutrient-poor forest. For non-standardised parameter estimates, see Table 4. No significant differences in $A_{\text{sat_mass}}$, $R_{\text{leaf_mass}}$, $R_{\text{leaf_area}}$, leaf thickness, g_{dark} and $[\text{Mg}]_{\text{leaf}}$ were found between forests in generalist species so these traits are not presented here (see Table S4).



scale more closely with $[\text{N}]_{\text{leaf}}$ when $[\text{P}]_{\text{leaf}}$ is high (Walker et al., 2014), although it should be noted that $[\text{N}]_{\text{leaf}}$ and $[\text{P}]_{\text{leaf}}$ were highly correlated in this study ($r = 0.74$; Figure S8). However, leaf cation concentrations were not strongly correlated with $[\text{N}]_{\text{leaf}}$ or $[\text{P}]_{\text{leaf}}$ ($r < 0.7$) but were significantly related to photosynthetic rates, suggesting cation availability can also be an important control on photosynthetic rates in tropical forests. The lower pH of kerangas forest soils may be indicative of higher rates of Ca and Mg leaching (Katagiri et al., 1991), which results in a switch to limitation of photosynthesis by the low availability of these cations in these forests. Our results support the emerging perspective from studies across the tropics that multiple nutrients may limit productivity (Wright, 2019; Sayer & Banin, 2016). We also observed shifts in the intercept of photosynthetic-nutrient and respiratory-nutrient relationships, with greater nutrient-use efficiency

in the nutrient-poorer forests (Figure 2; Table 2). Higher LMA is likely to represent an important adaptation to maintain high photosynthetic and respiratory efficiency in nutrient-poorer environments (Hidaka & Kitayama, 2011). The high niche specificity with respect to nutrient availability may allow many different dipterocarp species to coexist across heterogeneous edaphic environments, supporting high species richness (John et al., 2007).

Height-related variation in leaf traits in Bornean forests

In addition to edaphic conditions, we found tree height to be an important driver of leaf trait variation in dipterocarps (Figure 3).

Our findings further support evidence that relationships between area-based photosynthesis and respiration and tree height exist in tropical forest trees (Kenzo et al., 2015; Meir et al., 2002; Cavaleri et al., 2010; Kenzo et al., 2006; Asao et al., 2015), including in Bornean dipterocarps (Kenzo et al., 2006), but that height-related increases in photosynthetic capacity and leaf dark respiration per unit area are largely explained by changes in leaf morphology, particularly LMA (Kenzo et al., 2006; Asao et al., 2015; Kenzo et al., 2015). Thicker leaves with higher LMA may allow leaves of taller trees to absorb more high-intensity light and increase light-use efficiency (Hanba et al., 2002). Higher temperatures, lower relative humidity and higher vapour pressure deficits in the upper canopy may also select for higher LMA that confers greater thermal tolerance (Sastry & Barua, 2017; Fauset et al., 2018) and greater water-use efficiency (Poorter et al., 2009) to reduce the risk of hydraulic failure. Lower measured g_{dark} in taller trees is indicative of greater hydraulic stress as g_{dark} is important in regulating evapotranspiration (Duursma et al., 2019). While increases in leaf thickness and LMA with tree height may allow greater rates of photosynthesis and respiration per unit area under equivalent investment per unit mass, this may not equate to greater overall photosynthetic assimilation if there are concurrent reductions in total leaf area (Mencuccini et al., 2019). Indeed, thicker leaves in tall trees may not be an adaptation, but may simply result from greater hydraulic limitations that reduce leaf water potential, turgor pressure and therefore limit leaf expansion (Woodruff & Meinzer, 2011). Longer hydraulic path lengths increase hydraulic resistance (Koch et al., 2004), which combined with elevated effects of gravity impose physical limits on leaf size (Jensen & Zwieniecki, 2013). These hydraulic constraints are likely to be particularly important to Bornean dipterocarps, which include the tallest tropical trees (Shenkin et al., 2019) that regularly reach heights of 60–80 m (Banin et al., 2012).

Not all dipterocarp forests exceed 60 m height, especially those occupying less nutrient-rich soils (Jucker, Asner, et al., 2018) that have greater light penetration to lower canopy levels (Russo et al., 2011). Given this, we might expect relationships between leaf traits and tree height to vary among forests that vary in soil nutrient supply and canopy structure, if light acts as a key control on leaf trait expression (Figure 4; Table 3). However, we only found significant forest type–height interactions for $A_{\text{sat_mass}}$, $A_{\text{sat_area}}$, $[N]_{\text{leaf}}$, $[P]_{\text{leaf}}$ and $[K]_{\text{leaf}}$ with steeper slopes in nutrient-richer soils. While this finding is likely to be explained by differences in canopy light penetration, logistical challenges associated with accurately measuring and quantifying light availability across the wide vertical gradients encountered in this study meant that direct measures of light gradients were not possible.

Leaf trait variation in generalist species

Some dipterocarp species within the Sepilok reserve and other lowland dipterocarp forests are able to persist across more than

one forest type despite differences in edaphic conditions and canopy structure (Baltzer et al., 2005; Dent & Burslem, 2016; Margrove et al., 2015). Intraspecific variation in several leaf traits was found between forest types, but depended on the forest types the species occupied (Figure 5; Table 4). No traits differed significantly between alluvial and mudstone forests except $[P]_{\text{leaf}}$ (Figure 5a), suggesting differences in nutrient availability may not act as an environmental filter here but other filters, such as sporadic flooding, may be more important (Born et al., 2015; Born et al., 2014; Margrove et al., 2015; Margrove, 2018). Intraspecific trait differences were greatest in mudstone–sandstone generalists (Figure 5b), which may be driven by larger differences in nutrient availability between the soils of these forests (Figure 1; Figure S1). Our results reveal intraspecific trait differences between these forests are not restricted to saplings (Baltzer et al., 2005; Dent & Burslem, 2016), but persist in adult trees. While photosynthetic rates were lower in sandstone forests, they were still equivalent or greater in generalist species compared with other species (Table 1), which may allow them to remain competitive across both forest types.

Unlike mudstone–sandstone generalists, species found across both sandstone and kerangas forests were able to maintain area-based rates of photosynthesis despite reductions in mass-based photosynthesis (Figure 5c). Increases in LMA can help to increase photosynthetic phosphorus-use efficiency as phosphorus availability declines (Hidaka & Kitayama, 2009) and was identified as a key trait to maintain photosynthetic P-use efficiency in upper montane Bornean forests (1,560–1,860 m a.s.l.; Hidaka & Kitayama, 2011). Our results suggest intraspecific variation in LMA may also be a key trait to allow some species to compete across different edaphic conditions in lowland Bornean forests.

CONCLUSIONS

Leaf trait variation in Bornean dipterocarps is driven by both edaphic conditions and tree height. Our results support evidence that leaf traits in dipterocarps change across edaphic gradients (Katabuchi et al., 2012), and reveal how leaf nutrient concentrations constrain photosynthetic capacity and respiratory rates. Intraspecific variation in leaf morphology appears to be an important driver of height-related variation in photosynthetic rates and may allow a few generalist species to survive across a wider range of edaphic conditions. Lower intraspecific trait variation was identified in specialist species that may prevent them from inhabiting a wider range of edaphic conditions. This has important implications for the conservation and restoration of Bornean dipterocarp forests as variation in edaphic conditions needs careful consideration when planting these highly specialised species. Our results also have important implications for the modelling of carbon fluxes in tropical forests as we show how different nutrients can constrain photosynthetic capacity and respiration between forest types and also how these gas exchange metrics

vary with tree height. Our results contrast long-held theories of nitrogen and phosphorus limitation in tropical forests (Vitousek & Farrington, 1997; Vitousek, 1984) as we find cations are also related to saturating photosynthesis and photosynthetic capacity. We find the scaling relationships between leaf nutrients and gas exchange traits are not universal across forests and can be modified by local conditions, such as nutrient stoichiometry, water availability and micro-topography. Overall, our findings highlight that both nutrient limitation and height-related variation in leaf physiology can support environmental niche partitioning among dipterocarp species.

AUTHORS' CONTRIBUTIONS

D.C.B., L.F.B., D.F.R.P.B. and L.R.R. conceived the ideas and designed the methodology; D.C.B. and P.R.L.B. collected the data; D.C.B. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.w6m905qrs> (Bartholomew et al., 2022).

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