Tree Function and Habitat Niche Partitioning in Tropical Forests:

Implications for Responses to Environmental Change

Submitted by **David Clive BARTHOLOMEW**, to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Geography, August 2021.

I certify that all material in this thesis which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

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Abstract

Tropical forests possess exceptional levels of tree species richness but explaining this diversity has presented a long existing challenge. Habitat niche partitioning provides a hypothesis for species co-existence, whereby species avoid competitive exclusion by partitioning demands on multiple resources within an environment. However, limited understanding concerning how tree function is influenced by multiple environmental variables has limited the support for this hypothesis. This knowledge gap also limits our ability to predict how tropical forest tree communities will respond to environmental change, given multiple dimensions of a species' niche are likely to be affected.

In this thesis, I investigate the role of niche partitioning in supporting co-existence of species and the turnover of species across edaphic gradients, as well as how long-term changes to the environment from selective logging and drought affect niche space of tropical tree species. I use species distribution models and measurements of leaf physiological traits to determine the key dimensions of tree species' niches in primary forests.

In chapter 2 I demonstrate niche partitioning is strong within tropical forests with at least 60-86% of abundant species occupying their own unique niche. Species partition a wide range of abiotic environments, including soil nutrient, topographic and light environments, with greater environmental heterogeneity enhancing the scope for niche partitioning. Building on this, in chapter 3 I find that variation in nutrient availability explains more variation in leaf physiology and habitat preferences than light availability of species from the Dipterocarpaceae family that dominates South-East Asian forests. This highlights the importance of edaphic environments in structuring tropical forest communities. I also find different leaf nutrients are related to photosynthetic capacity in different forest types, revealing that multiple different nutrients may limit productivity and affect species distributions in tropical forests.

Many tropical forest tree species are highly specialised with limited ability to adjust their traits between environments, underlining their potential vulnerability to environmental change. In chapter 4 I show seedlings from selectively logged Bornean forests have different community weighted mean trait values, with greater belowground investment in logged forests. These adaptations are sufficient to

overcome soil stress and to maintain foliar nutrient concentrations. However, I show seedlings of species that dominate old-growth forests are less able to adapt their traits and experience elevated mortality rates in logged forests. I attribute this to greater soil nutrient limitation as they are unable to maintain leaf nutrient concentrations. Selective logging will therefore likely drive shifts in species composition towards greater dominance of earlier-successional species that have traits capable of surviving in disturbed environments. This could result in local-scale reductions in species diversity and functional diversity, which could reduce long-term resilience to environmental change. In contrast, in Chapter 5 I demonstrate small trees in Amazonian forests are able to respond to changes in their environment following long-term drought conditions. Following mortality of large canopy trees, small trees can respond to increased light availability even under reduced water availability by adjusting resource allocation and by increasing nutrient use efficiency. Despite evidence of resilience to long-term drought conditions, hyper-dominant species show a greater capacity to respond, which may further enhance the dominance of these species under future climates.

In conclusion my results highlight the importance of habitat niche partitioning in structuring tropical forest tree communities and identify key environmental variables that determine species distribution and tree function. My results have important implications for the conservation and restoration of tropical forests under environmental change. Avoidance of environmental homogenisation and changes to as few environmental conditions as possible is likely to be important in maintaining high species diversity in tropical forests and to avoid increased dominance by few generalist species. Many current conservation and restoration projects focus on recovering vegetation, but my research highlights the additional need to maintain and restore soil environments, especially for the long-term persistence of highly specialist species.

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A close representation of my feelings towards nature from someone who inspired my love for it:

> *"An understanding of the natural world is a source of not only great curiosity, but great fulfilment."*
>
> **Sir David Attenborough**

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Abbreviations

A	Net photosynthetic assimilation
A-C_i	Response of net photosynthetic assimilation to leaf internal carbon dioxide concentration
AIC	Akaike information criterion
AICc	Akaike information criterion corrected for small sample sizes
Al	Aluminium
AM	Arbuscular mycorrhizae
AmazonFACE	Amazon free air carbon dioxide enrichment experiment
A_{sat}	Rate of photosynthesis under saturating light conditions and atmospheric carbon dioxide concentrations
ATP	Adenosine triphosphate
B	Boron
BCI	Barro Colorado Island
Ca	Calcium
Ca_{leaf} / $[Ca]_{leaf}$	Leaf calcium concentration
CHM	Canopy height model
C_i	Carbon dioxide concentration inside the leaf
Cl	Chlorine
CNDD	Conspecific negative density dependence
Co	Cobalt
CO_2	Carbon dioxide
Cr	Chromium
Cu	Copper
CWD	Climatological water deficit
CWM	Community weighted mean
DBH	Diameter at breast height
DEM	Digital elevation model
DNA	Deoxyribonucleic acid
DVCA	Danum Valley conservation area
ECM	Ectomycorrhiza
ENSO	El Niño Southern Oscillation
Fe	Iron
g_{dark}	Stomatal conductance of dark-adapted leaves
GF	Gap fraction
GPP	Gross Primary Production
g_s	Stomatal conductance
HCl	Hydrochloric acid
HSM	Hydraulic safety margin
INDFORSUS	Indicators of Forest Sustainability
INFAPRO	Innoprise-FACE Foundation Rainforest Rehabilitation Project
INLA	Integrated Nested Laplace Approximation
IPCC	Intergovernmental Panel on Climate Change

IUCN	International Union for the Conservation of Nature
J_{max}	Maximum rate of the electron transfer chain
K	Potassium
K_{leaf} / $[K]_{leaf}$	Leaf potassium concentration
LA:SA	Leaf area to shoot area ratio
LAI	Leaf area index
LFP	Leaf force to punch
LiDAR	Light detection and ranging
LMA	Leaf mass per area
LMF	Leaf mass fraction
log	Natural logarithm
log_{10}	Logarithm with base 10
MAP	Mean annual precipitation
MAT	Mean annual temperature
Mb	Molybdenum
Mg	Magnesium
Mg_{leaf} / $[Mg]_{leaf}$	Leaf magnesium concentration
Mn	Manganese
N	Nitrogen
NA	Not applicable
Na	Sodium
NADP+	Nicotinamide adenine dinucleotide phosphate
NH_4	Ammonium
Ni	Nickel
N_{leaf} / $[N]_{leaf}$	Leaf nitrogen concentration
NO_3	Nitrate
ns	Non-significant
NSC	Non-structural carbohydrates
NUE	Nutrient use efficiency
P	Phosphorus
PAR	Photosynthetic active radiation
PC	Principal component
PCA	Principal component analysis
PLC	Percentage loss of conductivity
P_{leaf} / $[P]_{leaf}$	Leaf phosphorus concentration
PO_4	Phosphate
pPCA	Phylogenetic principal component analysis
Q10	Temperature sensitivity co-efficient
R^2_C	Conditional R^2
R^2_m	Marginal R^2
RCP	Representative concentration pathway
RIL	Reduced impact logging
R_{leaf}	Leaf respiration in the dark
RMF	Root mass fraction

RNA	Ribonucleic acid
RS	Root length to shoot length ratio
RuBisCO	Ribulose-1,5-bisphosphate carboxylase-oxygenase
S	Sulphur
sd	Standard deviation
SE	Standard error
Si	Silicon
SMA	Standardised major axis regression
sqrt	Square-root
SRAI	Solar-radiation aspect index
SRL	Specific root length
TCA	Tricarboxylic acid
TFE	Through-fall exclusion
TPI	Topographic position index
TRI	Terrain ruggedness index
TWI	Topographic wetness index
UK	United Kingdom
USA	United States of America
USFR	Ulu Segama Forest Reserve
V_{cmax}	Maximum rate of carboxylation
VPD	Vapour pressure deficit
VWC	Volumetric water content
Zn	Zinc

Chapter 1: General Introduction

1.1 Tropical Forests

Tropical forests represent the most biodiverse biome globally, containing more than half of Earth's known species (Terborgh, 1992). Despite only covering c. 10% of the Earth's surface, more than 43,000 tree species are known to inhabit tropical forests, comprising 96% of the global total (Fine & Ree, 2006). The Amazon forest represents the largest and most biodiverse of global tropical forests, spanning c. 6 million km^2 and containing an estimated 3.9×10^{11} trees (ter Steege *et al.*, 2013; Draper *et al.*, 2021). However, large disparities in species abundance exist within tropical forests, with a small proportion of species dominating: ter Steege *et al.* (2013) estimated just 227 'hyperdominant' species (1.4% of all species) account for half of the Amazon's trees, whilst >10,000 species are exceptionally rare constituting just 0.12% of trees. Meanwhile, the Dipterocarpaceae family dominates in South-East Asian forests, accounting for >20 % of trees (Slik *et al.*, 2003) and >40 % of basal area despite only representing c. 7 % of the species (Lee *et al.*, 2002). Understanding the mechanisms that support exceptional species richness and large disparities in species dominance in tropical forests remain some of the greatest challenges in modern ecology.

In addition to supporting high biodiversity, tropical forests play a critical role in controlling the global carbon cycle (Pan *et al.*, 2011; Grace *et al.*, 2014), storing up to 55% of global forest carbon stocks (Pan *et al.*, 2011). Tropical forests contribute 34% of global terrestrial gross primary production (GPP) (Beer *et al.*, 2010), with rates of GPP exceeding 2000 g C m^{-2} yr^{-1} (Chen *et al.*, 2017). Most of the carbon cycling is also concentrated in a few hyper-dominant and large statured tree species (Fauset *et al.*, 2015). However, the capacity of tropical forests to store and sequester carbon is declining because of climate change, land conversion and other anthropogenic threats (Harris *et al.*, 2012; Pearson *et al.*, 2014; Brienen *et al.*, 2015; Pearson *et al.*, 2017; Hubau *et al.*, 2020). Tropical forests also have a major influence on global climate patterns, driven by evapotranspiration of vast quantities of water emitted to the atmosphere. For example, an east Amazonian forest transpires 1,389 ± 279 mm yr^{-1}, recycling 75% of incoming throughfall (da Costa *et al.*, 2018). The loss of tropical forests is predicted to have climatic impacts well beyond the tropics as a consequence of reduced transpiration rates (Lawrence & Vandecar, 2014). In order to predict how tropical forests will change and thus their future contribution to local and global climates, an improved understanding of the controls on tropical tree physiology and their physiological responses to environmental change is needed.

1.2 South-East Asian and Neotropical rainforests

Globally, there are four major tropical rainforest eco-regions – the Neotropics, comprising Amazonia and central American forests, the Afrotropics, Indo-Malaysia and Australasia (Olson *et al.*, 2001). Each region contributes considerably to the global carbon cycle and possesses exceptional levels of biodiversity (Gentry, 1992; Chen *et al.*, 2017; Sullivan *et al.*, 2020). However, considerable differences between the regions exist both abiotically and biotically. These differences generate contrasting environmental conditions, such as water, nutrient and light availability, that are key determinants of species niches. Here, I present important contrasts with respect to environmental conditions, forest structure and dynamics, and species composition, concentrating on Neotropical and South-East Asian forests, particularly Amazonia and Borneo, as they represent the focal regions of this thesis.

Both Amazonia and Borneo have hot and wet climates, with mean annual precipitation exceeding 2000 mm yr^{-1} and mean annual temperatures reaching 25 ˚C. However, despite these similarities, some climatic differences exist between the regions. Borneo is an island in the tropical Indo-Pacific, meaning it receives a maritime climate, whilst much of the Amazon forest lies distant from the ocean, meaning it has a more seasonal, continental climate. The Amazon rainforest has a distinct dry season, lasting 3 - 5 months, whilst the dry season in Borneo is usually short, lasting only 1 month. Overall, during the three driest months, Borneo has greater precipitation, meaning it does not experience such an extreme climatological water deficit, with precipitation exceeding 100 mm each month across most of Borneo (Figure 1.1). Meanwhile, the maritime climate of Borneo also drives differences in cloud cover between the regions with more night-time rainfall and less daytime cloud cover than the Amazon (Richards, 1996). Greater seasonality is hypothesised to explain why rainfall is an important determinant of spatial patterns of Neotropical and African diversity (Ter Steege *et al.*, 2003; Parmentier *et al.*, 2007; Punyasena *et al.*, 2007), but cannot explain patterns of diversity in Borneo (Slik *et al.*, 2009). A less seasonal environment in Borneo may have facilitated greater specialisation to other environmental resources, such as nutrient availability.

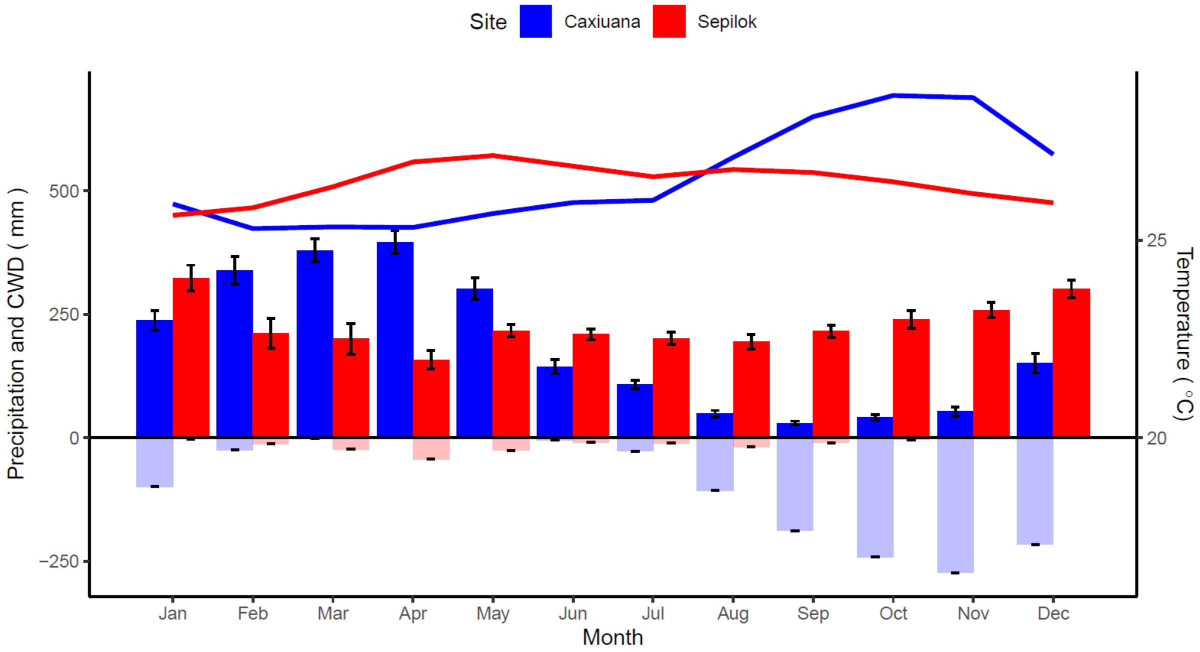

Figure 1.1 – Annual variation in mean monthly precipitation, mean monthly climatological water deficit (CWD) and mean monthly temperature for Caxiuanã, Brazilian Amazon (blue) and Sepilok, Malaysian Borneo (red). CWD is calculated from the cumulative difference between total evapotranspiration and total precipitation. Precipitation is presented by solid bars above the x-axis, with CWD presented by semi-transparent bars below the x-axis. Error bars represent mean ± standard error. Temperature is presented by the line. Data presented are mean averages for 2003-2019 from the ERA5 global re-analysis (Hersbach *et al.*, 2020).

Many of the soils in tropical forest ecosystems are old and highly weathered (Vitousek, 1984). The Amazon is dominated by old oxisols and ultisols that are poor in phosphorus and cations, especially in Central and Eastern Amazonia (Vitousek, 1984; Quesada *et al.*, 2010). Recent Andean uplift in the Western Amazon has resulted in more fertile soils here (Quesada *et al.*, 2010), creating a gradient in nutrient availability and a shift in nutrient limitation from nitrogen in the west, to phosphorus and cations in East Amazonia (Quesada *et al.*, 2012). Gradients in soil nutrient availability also exist across Borneo, but typically at much finer spatial scales. In contrast to the relatively flat, low-lying Eastern Amazon, Borneo is topographically complex with underlying volcanic and oceanic bedrocks that generate a wide range of soil conditions at proximity. Alluvial, mudstone, sandstone, podzol, arenosol, limestone, freshwater swamp, peat swamp and ultramafic formations, amongst others, exist on Borneo, supporting heterogenous forest landscapes (Ghazoul, 2016), with strong nutrient availability gradients existing at several locations, including Sepilok, Bako, Brunei and Lambir Hills (Davies & Becker, 1996; Moran *et al.*, 2000; Nilus, 2004; Russo *et al.*, 2011). Borneo has high beta diversity (high species differentiation between habitats) that is attributed to edaphic and topographic variation, as species composition can change rapidly over short spatial scales (Nilus, 2004; Paoli *et al.*, 2006; Slik *et al.*, 2009). Whilst edaphic conditions are also important determinants of Neotropical diversity, these conditions tend to change over much larger spatial scales with co-variation in climatic conditions (ter Steege *et al.*, 2006). Variation in edaphic properties does not just affect diversity patterns but can also influence forest structure and function (Jucker *et al.*, 2018b).

Tropical rainforests characteristically have dense, multi-layered canopies. Historically, the forest has been stratified into three distinct strata: understory, canopy and emergent (Brown, 1919). However, the canopy structure of a tropical forest is considerably more complex, as it is composed of a mosaic of trees and canopy gaps of different heights and sizes, giving rise to a strong vertical gradient of light availability (Richards, 1996). Under intact canopies, the understory typically possesses low photosynthetic active radiation and vegetation relies predominantly on diffuse light and sunflecks for photosynthesis (Chazdon & Pearcy, 1991; Leakey *et al.*, 2003). Amazonian and Bornean forests however have contrasting forest structures that likely result in different vertical light profiles. Borneo possesses the world's tallest tropical trees, with a record 100.8 m yellow meranti, *Shorea faguetiana,* found in Danum Valley (Shenkin *et al.*, 2019). Meanwhile, the tallest tree recorded in the Amazon is >10 m shorter, an 88.5 m *Dinizia excelsa* located in Eastern Amazonia (Gorgens *et al.*, 2019). These giant Amazonian trees however are restricted to a very, small isolated region, whereas tall trees are widespread across much of Borneo. Consequently, the vertical light profiles of Neotropical rainforests are typically much shorter than those of South-East Asian rainforests. As a result of differences in canopy structure, we may expect the importance of light availability on determining species niches and function to vary between regions. Forest structure is also influenced by edaphic conditions, influencing canopy height, complexity and understory light availability (Russo *et al.*, 2011; Jucker *et al.*, 2018b). Shorter, more open canopies are typical of nutrient poor forests, whilst taller, more dynamic forests are characteristic of nutrient-rich soils (Coomes *et al.*, 2009; Jucker *et al.*, 2018b). Greater fine-scale variation in edaphic conditions on

Borneo may therefore also support greater variation in forest structure and light availability, with important consequences for productivity and species niches. Despite this, much of our understanding of how forest structure affects tree function comes from the Neotropics.

Differences in forest structure and maximum canopy height between Neotropical and South-East Asian forests have largely been attributed to the dominance of the Dipterocarpaceae family across South-East Asia (Corlett & Primack, 2005). Dipterocarp trees have tall, straight trunks and shallow, streamlined “cauliforous” crowns (Ghazoul, 2016), allowing them to grow tall without toppling (Shenkin *et al.*, 2019; Jackson *et al.*, 2020). Species of non-dipterocarps also grow taller in Bornean forests, possibly driven by light competition within dipterocarp-dominated landscapes (Banin *et al.*, 2012). The dominance of a single family is unique to the rainforests of South-East Asia with Amazonian flora dominated by many different families (Draper *et al.*, 2021). Why dipterocarps are so dominant across South-East Asia remains largely unknown, but one hypothesis is that dipterocarps may be able to outcompete other species by overcoming phosphorus limitation through the formation of ectomycorrhizal (ECM) associations (Liu *et al.*, 2018; Liang *et al.*, 2020). Most tropical forest species are unable to form associations with ECM, instead forming symbioses with arbuscular mycorrhiza (AM) (Brearley, 2012). Partitioning of phosphorus resources between ECM and AM fungi may facilitate dipterocarp species to access a unique pool of phosphorus (Liu *et al.*, 2018), allowing them to thrive in soils that are predominantly phosphorus limited. In contrast, nitrogen-fixing Fabaceae represent the most dominant family of Neotropical forests, with >30% of large-hyperdominant tree species coming from this family (Draper *et al.*, 2021). Differences in species composition between the regions can be attributed to differences in biogeographic evolutionary history (Slik *et al.*, 2018) but will have implications for forest function. However, the role of this phylogenetic history in affecting niche dynamics and forest function within tropical forests remains largely unknown.

Forest dynamics differ considerably between Bornean and Amazonian forests because of their contrasting reproductive phenology. The ever-wet forests of South-East Asia are unique amongst tropical forests for displaying supra-annual mass flowering and fruiting (Sakai, 2002), whilst Neotropical forests do not display patterns of simultaneous reproductive phenology. The cycle of mass flowering in South-East

Asian forests is largely related to El Niño Southern Oscillation (ENSO) events, with mast events frequently triggered by cumulative climatic effects associated with El Niño anomalies such as precipitation, cloud cover and minimum temperature (Chechina & Hamann, 2019). The evolutionary driver of mass flowering and fruiting remains to be fully elucidated, but seed predator satiation and density-dependent pollen limitation are likely to be important (Janzen, 1974; Curran & Leighton, 2000; Blundell & Peart, 2004; Maycock *et al.*, 2005). Why South-East Asian rainforests display mass flowering, whilst Amazonian forests do not is probably associated with differences in species composition and climate between the regions (Sakai, 2002). The importance of an ever-wet climate for the evolution of mass flowering is likely to be high because this phenomenon is absent in seasonally dry South-East Asian forests (Chechina & Hamann, 2019).

Despite distinct differences between Neotropical and South-East Asian forests, much of our understanding of how environmental conditions determine species niches comes from Amazonian and other Central American forests. Large forest plot networks exist across the Amazon rainforest (Malhi *et al.*, 2002; Peacock *et al.*, 2007) and Central America (Condit *et al.*, 2016), giving numerous insights into the functioning of tropical forest ecosystems. Phosphorus and precipitation gradients have been widely studied across Panama revealing their respective roles in determining species distributions, forest functioning and tree physiology in Neotropical forests (Condit *et al.*, 2004; Engelbrecht *et al.*, 2007; Baldeck *et al.*, 2013; Condit *et al.*, 2013; Turner *et al.*, 2018; Umaña *et al.*, 2020b). Despite similar gradients existing across Bornean landscapes, studies here have been more limited to date. Furthermore, several large-scale experiments have been established in Neotropical forests, including throughfall exclusion experiments in Caxiuanã and Tapajos (Meir *et al.*, 2015), soil fertilisation experiments including on Barro Colorado Island, Panama, and the Amazon Fertilisation Experiment in Manaus, Brazil (Wright *et al.*, 2011; Wright, 2019; Lugli *et al.*, 2021), and the recently established AmazonFACE, a CO_2 fertilisation experiment in Manaus (Fleischer *et al.*, 2019). Many of these manipulative experiments are missing from South-East Asian forests or have only taken place at much smaller scales (e.g. Moser *et al.*, 2014; Sellan, 2019; Wright, 2019). Consequently, we still lack an understanding of the controls on species niches and the mechanisms that support high tree diversity in Bornean rainforests.

1.3 Environmental Niches of Tropical Forest Trees

Trees exist within a multi-dimensional environmental space. Partitioning of this environmental space is hypothesised to be an important phenomenon that supports high species richness in tropical forests, whereby different species partition key limiting resources and avoid competitive exclusion (Ricklefs, 1977; Brokaw & Busing, 2000; Paoli *et al.*, 2006; Queenborough *et al.*, 2007; Kitajima & Poorter, 2008). Light, water and nutrients are all critical to support tree physiology because of their direct role in supporting carbon metabolism and are suggested to be key environmental axes that are partitioned (Paoli *et al.*, 2006; Kitajima & Poorter, 2008; Esquivel-Muelbert *et al.*, 2017b; D'Andrea *et al.*, 2020). Meanwhile, biomechanical constraints limit certain species to topographic environments, providing another possible axis for niche partitioning. Physiological adaptations allow trees to compete for key resources, overcome resource limitation in impoverished environments or tolerate harmful environments when resources are in excess, thereby allowing gradients in resource availability to be partitioned. Differences in niche width exist between species, with some generalist species able to survive across a wider range of environmental conditions than specialist species, likely owing to greater plasticity of physiological traits (Baltzer *et al.*, 2007; Esquivel-Muelbert *et al.*, 2017a). Evidence for niche partitioning in tropical forests largely comes from habitat association studies (Harms *et al.*, 2001; Gunatilleke *et al.*, 2006; Paoli *et al.*, 2006). These studies use habitat randomisation tests that compare the spatial structure of populations to that of habitat types, estimating whether a species distribution is more closely related to a habitat than by statistical chance. Whilst these tests can understand associations to distinct habitats, they cannot separate out individual environmental co-variates or the physiological mechanisms driving them. Consequently, the relative importance of different environmental variables in driving niche partitioning remains largely unquantified in tropical forests. Moreover, we lack an understanding of what determines the width of a species niche, making it difficult to predict responses to changing conditions under environmental change. In this section, I introduce our current understanding of how availability of nutrients, water and light control the niche of tropical forest trees.

1.3.1 Nutrient availability

Edaphic conditions are increasingly recognised as important controls on species distribution and physiological functioning (John *et al.*, 2007; Quesada *et al.*, 2012; Condit *et al.*, 2013; Bunyavejchewin *et al.*, 2019). Species have been identified to turnover across edaphic gradients in Borneo (Nilus, 2004), Panama (Umaña *et al.*, 2020b) and Amazonia (John *et al.*, 2007; Baldeck *et al.*, 2013; Oliveira *et al.*, 2019), whilst also altering functional composition (Umaña *et al.*, 2020b). Nutrient availability is a key limiting factor on photosynthetic capacity and gross primary productivity in tropical forests (Mercado *et al.*, 2011). On old, weathered soils characteristic of many tropical forests, phosphorus availability often limits species-level productivity and reproduction (Turner *et al.*, 2018; Fortier & Wright, 2021), but evidence of nitrogen, phosphorus and cation co-limitation also exists for a range of forests (Wright, 2019). Trees can respond to nutrient limitation by altering their leaf morphology (Wright *et al.*, 2004; Onoda *et al.*, 2017). Nutrient limited environments tend to promote more conservative leaf traits, including high leaf mass per area (LMA), high herbivory resistance and long leaf lifespans (Coomes *et al.*, 2009; Ordoñez *et al.*, 2009; Reich & Cornelissen, 2014; Dent & Burslem, 2016; Weemstra *et al.*, 2020), as trees prioritise the retention of nutrients over investment in mechanisms to increase supply. Some species can increase supply though by forming mutualistic symbioses with N-fixing bacteria or mycorrhizal fungi, or by releasing carboxylates into the environment (Lambers *et al.*, 2021). Additional micro-nutrients are also critical to tree physiology (Table 1.1), but their role in structuring tree communities in tropical forests is largely unquantified (although see John *et al.*, 2007). Other elements, such as nickel, chromium and iron can be found in toxic quantities in some tropical soils, such as the ultramafic soils of South-East Asia (Galey *et al.*, 2017). Specialised adaptations are needed to tolerate these soils, such as hyperaccumulation and hyper-tolerance (Manara *et al.*, 2020), excluding species lacking these adaptations. Within tropical forest ecosystems, most nutrients are stored within biomass (Vitousek & Sanford Jr, 1986), making availability dependent on litterfall and tree mortality events. Adaptations that increase nutrient use efficiency or supply can provide a competitive advantage for some species and provide key opportunities for niche partitioning in tropical forests.

Table 1.1: Many different elements are essential for plant growth, each playing a unique role in maintaining the health of an individual plant. When nutrients are limiting, plants can suffer from deficiency diseases, resulting in lower productivity and growth and leaving them vulnerable to herbivory and mortality. Adapted from Taiz and Zeiger (2010).

Element		**Micro-/Macro-nutrient**	**Function**	**Details**	**Deficiency Disease**
Nitrogen	N	Macro	Organic compounds with carbon	Required for proteins & nucleic acids	Growth Inhibition Yellowing of (older) leaves
Phosphorus	P	Macro	Energy storage (ATP) Structural integrity	Required for ATP, DNA & RNA	Disruption of respiration & photosynthesis Stunted growth Dark green leaves Necrotic spots
Calcium	Ca	Macro	Ion-cofactor Secondary messenger	New cell wall synthesis Mitotic spindle Plant membrane function Regulates transcription & cell survival	Necrosis of meristems Young leaf deformation Short, brown branched roots Severe stunting
Magnesium	Mg	Macro	P transfer Chlorophyll	Photosynthesis & respiration DNA & RNA synthesis Enzyme activation Chlorophyll	Chlorosis between leaf veins Premature foliar abscission
Potassium	K	Macro	Ion-Cofactor Cell turgor & electro-neutrality	Plant cell osmoregulation Respiration & photosynthesis enzyme activation	Leaf tip & margin necrosis
Silicon	Si	Macro	Structure of cell walls	Reinforces cell walls – alternative to lignin	Reduced growth, fertility & stress resistance

				Reduces metal toxicity (e.g. Al & Mn)	
Sulphur	S	Macro	Organic compounds containing carbon	Required for proteins	Growth Inhibition Yellowing of leaves (mature & young)
Boron	B	Micro	Cell wall structure Metabolism	Cell elongation Nucleic acid synthesis Hormone responses Membrane function Cell cycle regulation	Young leaf & terminal bud necrosis Stiff & brittle stems High degree of branching (loss of apical dominance) Fruit, fleshy root & tuber necrosis/abnormalities
Chlorine	Cl	Micro	Oxidative photosynthetic reactions	Required for water splitting in photosynthesis and cell division	Wilting leaf tips Leaf chlorosis & necrosis
Copper	Cu	Micro	Electron transfer	Redox reactions (e.g. photosynthetic light reactions)	Premature leaf abscission
Iron	Fe	Micro	Electron transfer	Electron transfer proteins (e.g. cytochromes) Synthesis of chlorophyll protein complexes	Leaf chlorosis
Manganese	Mn	Micro	Ion-enzyme activity Oxidative photosynthesis	Tricarboxylic acid (TCA) cycle activation	Necrotic spots
Molybdenum	Mb	Micro	Electron transfer		
Nickel	Ni	Micro	Electron transfer	Urea breakdown	Leaf tip necrosis
Sodium	Na	Micro	K substitute		
Zinc	Zn	Micro	Electron transfer	Enzyme activity (e.g. chlorophyll biosynthesis)	Rosette habit No auxin production

1.3.2 Water availability

Water availability is a major determinant of tropical forest function at large scales, controlling the distribution of biomes and species (Hirota *et al.*, 2011; Esquivel-Muelbert *et al.*, 2017b; Trueba *et al.*, 2017; Dexter *et al.*, 2018; Oliveira *et al.*, 2019). Plant water availability is determined by both climatic and soil conditions, such as soil depth and texture (Pollacco *et al.*, 2020). The inextricable link between carbon acquisition and water loss that results from stomatal gas exchange (Sperry & Love, 2015) makes water an important component of any plant's niche. If water becomes limiting, excessive tension on the water column driven by excessive evapotranspiration can lead to failure of the water transport system – a major cause of death in tropical forests (Rowland *et al.*, 2015a; Brodribb, 2017; McDowell *et al.*, 2018). Drought tolerance is known to be an important determinant of species distributions across Neotropical forests (Engelbrecht *et al.*, 2007; Esquivel-Muelbert *et al.*, 2017a; Umaña *et al.*, 2020b). Variability in hydraulic traits and rooting depth provides an axis for hydraulic niche segregation in Amazonian forests (Brum *et al.*, 2018; Oliveira *et al.*, 2019) and can determine responses to drought events (Rowland *et al.*, 2015a; Barros *et al.*, 2019; Bittencourt *et al.*, 2020).

1.3.3 Light availability

Light is another important component of a tree's environmental niche because of its direct role in photosynthesis. Light is required by plants to provide energy for adenosine triphosphate (ATP) synthesis and the reduction of nicotinamide adenine dinucleotide phosphate (NADP+) that provide the energy and oxidising power to drive the reactions of the Calvin-Benson cycle and carbohydrate synthesis (Farquhar *et al.*, 1980). Light is therefore a key determinant of growth rates and leaf physiology. LMA, a key functional trait that determines a plant's position along the fast-slow leaf economic spectrum (Wright *et al.*, 2004), has been shown to be highly responsive to light in tropical forests (Poorter *et al.*, 2009). The high leaf area index (LAI) typical of tropical forests only allows 1-2% of light to penetrate to the forest floor under clear skies, with most of the understory frequently under diffuse radiation conditions (Chazdon & Fetcher, 1984). Understory plants in these forests obtain 10-90% of their light from sunflecks, accounting for 65% of their carbon gain (Chazdon & Pearcy, 1991, Leakey et al., 2003, Richards, 1996). Shade tolerance is consequently an important control on species distribution (Poorter & Markesteijn, 2008; Denslow *et al.*,

2019) and can dictate whether a species can recruit under the shade of the canopy or requires a canopy gap. Many canopy trees recruit in the understory, meaning they must adapt to changing light availability through their life. In the Amazon, acclimation to light has been shown (Meir *et al.*, 2002), but similar studies have yet to identify changes in physiology with tree height in Bornean forests.

Whilst light availability is inextricably linked to forest structure, this in turn is related to both water availability and soil fertility. Water availability can set limits on tree physiology (Brodribb *et al.*, 2017), architecture (West *et al.*, 1999; Sperry *et al.*, 2008) and height (Koch *et al.*, 2004), with feedbacks on both the amount and type of light that penetrates through the canopy (Montgomery & Chazdon, 2001). As a tree grows taller, more tension is imposed on the hydraulic column by gravity, meaning hydraulic failure is increasingly likely in taller trees when water availability is reduced (Rowland *et al.*, 2015a). Consequently, across both local and large-scales, taller trees are found on wetter and less-drained soils (Feldpausch *et al.*, 2011). Meanwhile, nutrient availability, also often closely correlated with soil texture (Quesada *et al.*, 2010), can alter forest structure, with shorter and more open canopies found on nutrient-poor soils (Quesada *et al.*, 2010; Russo *et al.*, 2011; Jucker *et al.*, 2018b). At fine spatial scales, micro-topographic features can provide opportunities to segregate niches by changing water and nutrient availability (Oliveira *et al.*, 2019). Many species are known to associate to either ridges or valleys (Harms *et al.*, 2001; Itoh *et al.*, 2003; Gunatilleke *et al.*, 2006) and change their function with topography (Jucker *et al.*, 2018b), but it remains unknown whether these differences are a consequence of the physical properties of micro-topographic features or the associated variation in nutrient, water and light availability.

1.4 Responses to changing niche space caused by environmental change

Tropical forests are currently experiencing unprecedented rates of environmental change driven by global climate and land use changes (Lewis, 2006; Laurance, 2015). Direct effects such as logging, landscape fragmentation and deforestation have reduced canopy cover (Pfeifer *et al.*, 2016), removed nutrients (Swinfield *et al.*, 2020) and altered micro-climates of tropical forests (Hardwick *et al.*, 2015; Blonder *et al.*, 2018), changing important components of a species niche, such as water, light and nutrient availability. Meanwhile emission of greenhouse gases since the industrial revolution have changed the global climate, including that of tropical forests. Drought events are becoming longer, more frequent and more extreme across tropical forests alongside increased precipitation seasonality (Figure 1.2; Dai, 2012; Trenberth *et al.*, 2013; Hilker *et al.*, 2014; Chadwick *et al.*, 2015; Gloor *et al.*, 2015; Feng *et al.*, 2018). Combined, these events are increasing in frequency, as well as intensity, leading to elevated rates of mortality, especially of large trees (Phillips *et al.*, 2010; Rowland *et al.*, 2015a; Feldpausch *et al.*, 2016), with consequent effects on nutrient and light availability from changes to nutrient inputs and canopy structure (Saatchi *et al.*, 2013). Moreover, temperatures are rising in tropical forests (Figure 1.1), having direct and indirect consequences on tree physiology (Malhi *et al.*, 2009; Slot & Winter, 2016; Mercado *et al.*, 2018; Smith *et al.*, 2020). In the Amazon, for example, average temperatures have risen by 0.25˚C per decade since the 1970s (Malhi & Wright, 2004), with a further 3-6˚C increase predicted by 2100 (Zelazowski *et al.*, 2011). Combined, these environmental changes could have impacts on the composition and dynamics of tropical forests as climatic niches change and may no longer overlap with species niches.

As the environment becomes unfavourable, a given species has three options: migrate, adapt, or die (Aitken *et al.*, 2008; Dawson *et al.*, 2011). A species can avoid changes to its environment by altering its distribution to follow the migration of its climatic envelope. In response to recent warming, some non-tropical forest species have shifted their species distribution poleward (Parmesan & Yohe, 2003). The potential for tropical forest species to migrate, however, is considerably lower as they may have to migrate thousands of kilometres to keep pace with climatic shifts (Colwell *et al.*, 2008). Some species can shift to higher elevations to avoid climatic changes but may be restricted due to low dispersal ability and other environmental factors (Feeley *et al.*, 2011). Increasing habitat destruction and fragmentation will reduce the potential for migration to suitable climates (Pearson & Dawson, 2005; Pang *et al.*, 2021). Tropical forest trees typically have highly specialised environmental niches, such as specific soil nutrient (John *et al.*, 2007; Dalling *et al.*, 2016) or soil moisture requirements (Esquivel-Muelbert *et al.*, 2017a), which will restrict their potential to shift their distribution. In Amazonia, under more intense dry seasons the abundance of dry-affiliated species and mortality of wet-affiliated species has already been found to increase (Esquivel-Muelbert *et al.*, 2019). The long lifespans, limited dispersal ability and high species interdependency of tropical forest species is likely to further restrict migration as an effective response strategy to climate change.

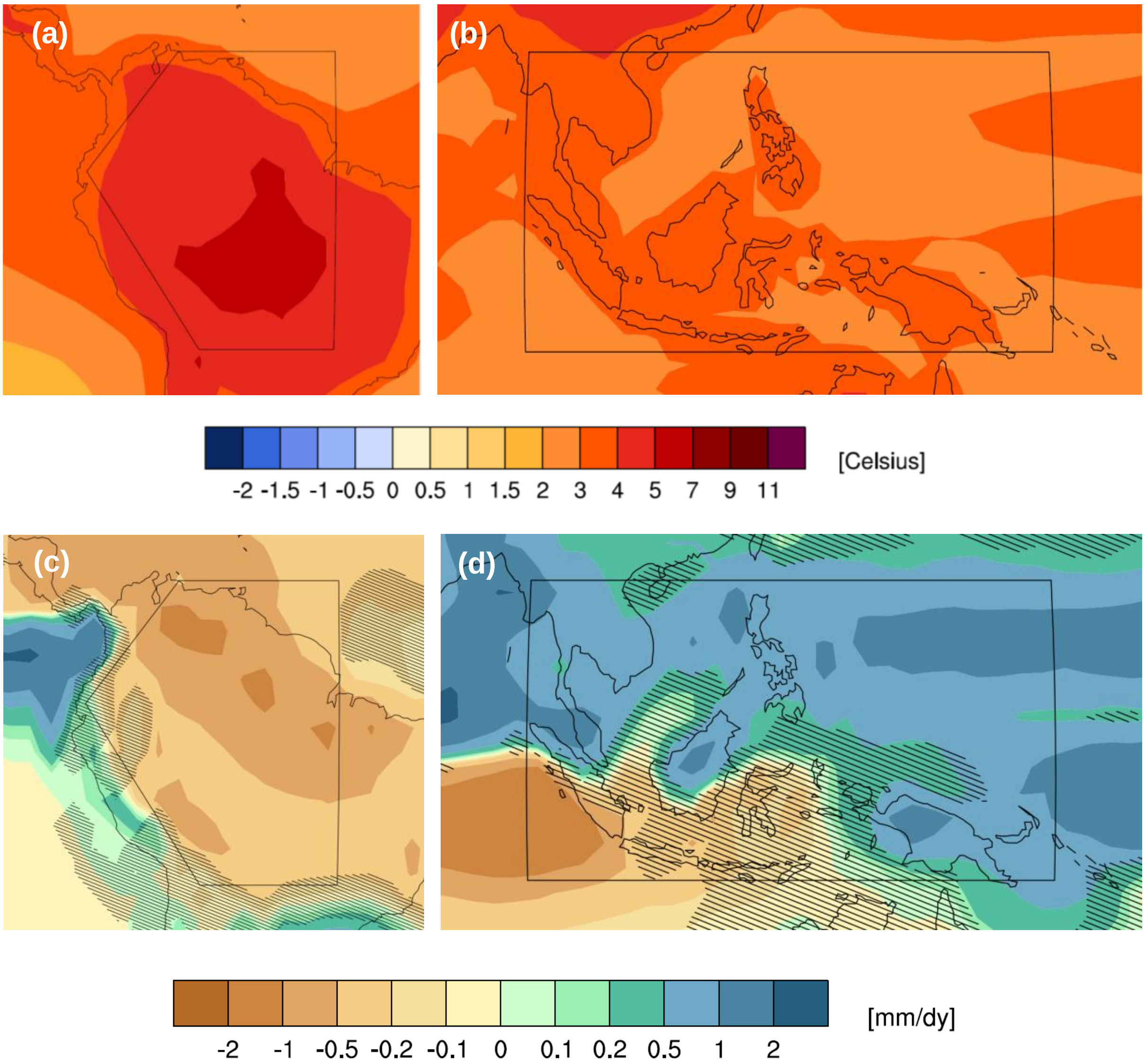

Figure 1.2 – Climate change is predicted to cause shifts in temperature and precipitation patterns in regions supporting wet tropical forest ecosystems. Based on the most extreme non-mitigation RCP 8.5 scenario from the IPCC AR5 climate model simulations, mean annual temperature is predicted to increase across Amazonia **(a)** and south-east Asia **(b)**, whilst mean dry season (August-November) precipitation is predicted to decline across much of Amazonia **(c)**, but have more variable changes in south-east Asia **(d)**. Maps plot the difference in mean annual temperature/precipitation for the period 2081-2100 compared to 1986-2005 as predicted by global climate models. Hatching represents areas where the signal is less than one standard deviation of natural variability using a pre-industrial control. Maps were generated based on the IPCC AR5 Climate Change Atlas using the KNMI Climate Explorer tool (Taylor *et al.*, 2012).

Some species can survive environmental change by adapting to new environmental conditions. Adaptations manifest in two different forms: inter-generational and intra-generational. Inter-generational adaptations result from evolutionary changes to the genetic material, including changes in allele frequency from selection and drift (Fisher, 1999), new allele combinations deriving from recombination events (Stebbins, 1950; Griffiths, 1981), and new alleles from mutations to the genetic code (Stebbins, 1950). Intra-generational adaptation, involves changes to the phenotype and/or gene expression within an individual in response to environmental changes (Nicotra *et al.*, 2010). Climate change is predicted to have a particularly large impact on tropical forests as historically they have experienced a relatively stable climate which has led them to be adapted to narrower environmental conditions relative to other biomes (Wiens & Graham, 2005; Donoghue, 2008; Wiens *et al.*, 2010; Brown, 2014). The potential for evolutionary changes in tropical forests is predicted to be low, because of the long generation times and slow molecular evolution of tropical trees (Smith & Donoghue, 2008), suggesting genetic evolution is likely to be insufficient for trees to adapt to the current rate of climate change. In contrast, acclimation, or phenotypic plasticity, allows individuals to respond positively to environmental conditions via changes to their morphology, physiology and behaviour within the time-scale of one generation (Price *et al.*, 2003). Many functional traits are not fixed, including eco-physiological traits (Cai *et al.*, 2009; Albert *et al.*, 2018). Some traits and organs are likely to be more plastic than others, allowing them to respond more easily to changes in the environment. Leaves have a relatively fast turnover compared with other organs, meaning responses of key leaf traits, such as LMA, leaf lifespan and leaf metabolism, are likely to be key in promoting resilience under climate change and for the persistence of tropical forest species. Leaves are able to acclimate to natural environmental changes, such as increasing light availability as they grow through the canopy (Montgomery & Chazdon, 2001; Meir *et al.*, 2002), but their ability to respond to human-induced environmental changes, such as climate change or logging, remains to be fully elucidated.

Not all species are predicted to have equivalent potential to respond to changing environmental conditions. Species with a wider environmental niche, commonly known as generalist species, are predicted to have a greater chance of adapting to environmental change because novel conditions are more likely to overlap with their current niche. Tropical rainforests are composed of species with highly variable degrees of specialism (Baltzer *et al.*, 2007; Esquivel-Muelbert *et al.*, 2017a). The role of phenotypic plasticity in supporting the wider environmental niche of generalist species is largely unknown and consequently, the hypothesis of lower vulnerability of generalist species to environmental change remains unanswered. Understanding which functional traits are plastic and help habitat generalists to survive across a wide range of environments and the specific environmental conditions required by specialists will help improve predictions of extinction risk, guide conservation priorities and enhance restoration efforts.

Phenotypic plasticity is also predicted to change through an individual's lifetime, affecting the likelihood of different ontogenetic stages to survive environmental change. As trees develop, their physiology becomes increasingly integrated because of structural constraints, reducing the potential for phenotypic plasticity. Small trees may consequently have the greatest potential to acclimate to changing environments as trait trade-offs may be less limiting at this life history stage. However, small trees could potentially experience the greatest changes in abiotic environmental conditions as events such as drought will not just reduce water availability, but simultaneously change light and nutrient availability as a consequence of changes to canopy structure following drought-induced mortality of large trees (Rowland *et al.*, 2015a; Rowland *et al.*, 2020). In order to predict if species will be able to persist under global change, understanding the potential for responses to multiple, interacting environmental changes is needed.

Failure to migrate or adapt in the face of environmental change could leave tropical forests vulnerable to elevated mortality. For long-term persistence, species need to be able to survive across their whole life span in order to reach reproductive maturity and propagate. An inability to survive at any ontogenetic life history stage could ultimately lead to local or even global extinctions. This thesis aims to improve our understanding of the environmental niches of tropical forest trees and identify the potential of different species to respond to future environmental changes.

1.5 Outline of thesis

The overall aim of this thesis is to identify how niche partitioning can support high species richness in tropical forests and how environmental change may affect niche dynamics. I use species distribution models and measurements of tree physiology to understand how different environments are partitioned in intact tropical forests. I then use long-term logging and drought experiments to understand how seedlings and small trees respond to environmental change.

Overall, this thesis is divided into 6 chapters (Figure 1.3). This chapter, **chapter 1**, outlines our current understanding of species environmental niches in tropical forests, comparing and contrasting Neotropical and South-East Asian forests, as well as outlining the major environmental changes facing tropical forests and their potential impacts on species persistence.

Chapters 2-5 present the main results from my empirical research. In **chapter 2**, I aim to understand the potential for niche partitioning as a mechanism for species co-existence in tropical forests. In this chapter, I model the fine-scale species distribution of 444 species from three sites across two continents (Barro Colorado Island, Panama, and Pasoh and Danum Valley, Malaysia), utilising data from the ForestGEO forest plot network. I use these models to assess the role of soil nutrient availability, topography and canopy structure on determining species distributions and niche partitioning, whilst assessing the importance of environmental heterogeneity for supporting species-rich tree communities.

In **chapter 3**, I aim to disentangle the different components of a species' abiotic environmental niche. By measuring leaf traits across an edaphic gradient and across trees of different height, I identify the relative importance of nutrient and light availability on determining leaf physiology and provide a mechanistic understanding of niche partitioning. In this chapter, I also compare traits of more generalist dipterocarp species between forest types to understand the potential for species to adjust their physiology in response to their environment.

Chapters 4 and 5 focus on understanding how trees respond to environmental change in tropical forests. In **chapter 4**, I aim to understand how forest function and dynamics are affected by selective logging in Bornean forests. I measure a range of functional traits to understand the major stresses facing seedlings in logged forests and use seedling mortality data to reveal the potential for natural regeneration of logged forests. I use a mixed approach, measuring both community weighted mean traits and intraspecific adjustment of traits in species common to both primary and logged forests to understand whether species that dominate primary forests are more vulnerable to logging and whether shifts in species composition are likely to occur in logged forests.

My final empirical research chapter, **chapter 5**, presents results from a long-term drought experiment located in Caxiuanã, Brazil. The aim of this chapter is to understand the resilience of Amazonian forests to long-term drought by measuring how small trees respond to multiple interacting environmental changes. More specifically, I investigate whether small trees can capitalise on increased light availability following mortality of large trees despite reduced water availability. I also investigate whether genera have different capacities to respond, identifying whether resilience to environmental change is equal across tree communities.

Finally, **chapter 6** synthesises the findings of this thesis and draws overall conclusions from this compendium of research. A summary of key findings from additional research conducted as a co-author during my PhD is also presented here (These publications, my contribution and their abstracts are presented in Appendix 1). I conclude by presenting the important implications of my research for the conservation and restoration of tropical forests.

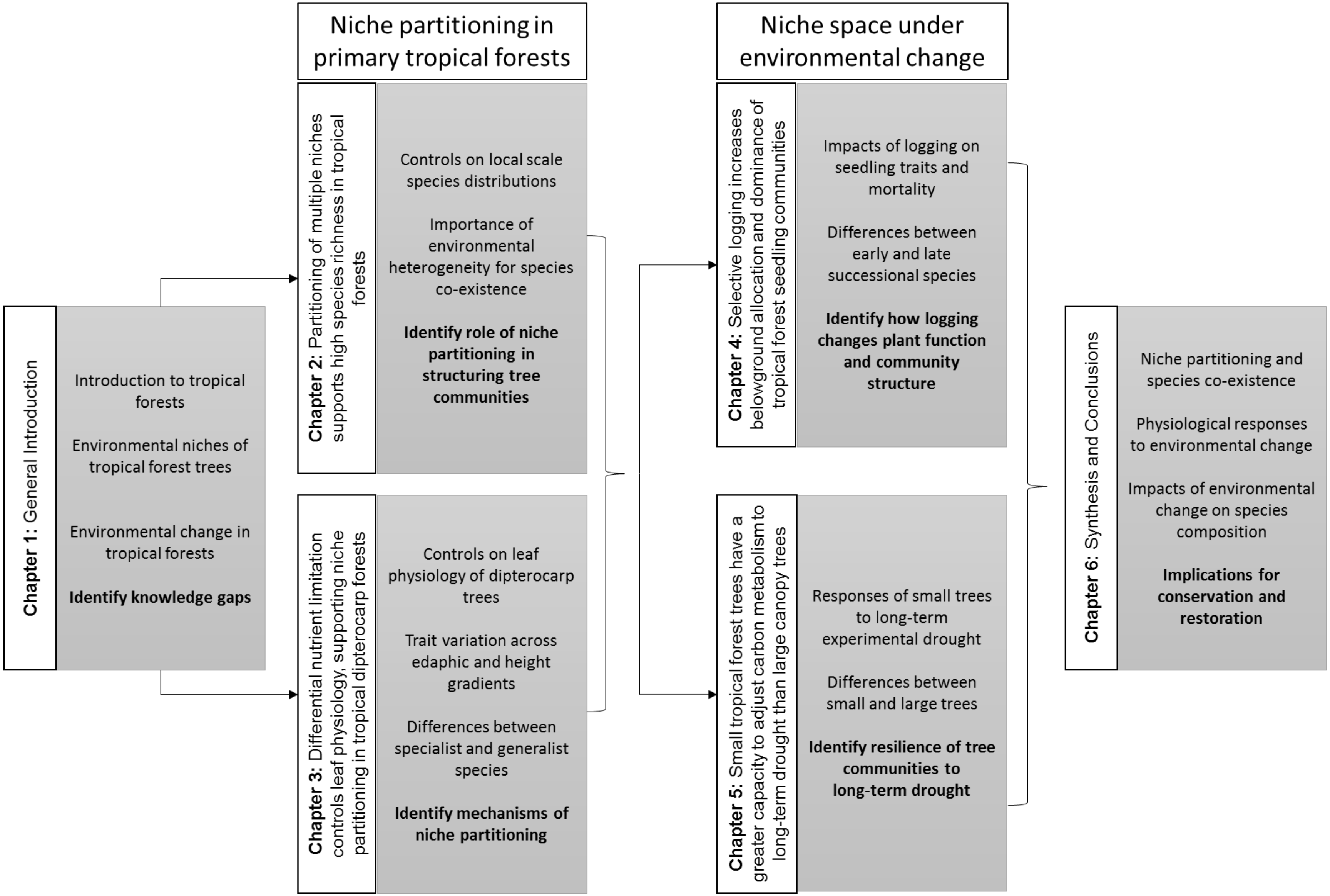

Figure 1.3 – Conceptual diagram of the specific aims of each chapter of this thesis. Each box represents a separate chapter as shown in the figure.

Chapter 2: Partitioning of multiple niches supports high species richness in tropical forests

An edited version of this chapter with additional study sites is in preparation for submission to Nature.

I express thanks to David Burslem, Lindsay Banin and Lucy Rowland who helped design the study, gave input on data analysis and reviewed the manuscript. I am grateful for support from Janine Illian regarding the INLA statistical methodology and to Isabel Price for providing R code. I also thank Paulo Bittencourt for helping conceive the idea for this study, Tommaso Jucker for input on processing the LiDAR data, Kyle Dexter for advice on phylogenetic analysis and Liu Xubing for help with geo-spatial kriging of soil nutrients data. Thank you to all collaborators for providing datasets, including David Coomes, Stuart Davies, Yao Tze Leong, Helene Muller-Landau, Michael O’Brien, Hamdan Omar, Tan Sek Aun, Glen Reynolds and Ben Turner. Lastly, thank you to the ForestGEO network for supporting this work.

2.1 Abstract

Richness of tree communities in tropical forests can exceed one thousand in less than a square kilometre, but the mechanisms that support the co-existence of these species remains contested. Classical theory proposes that species partition multi-dimensional niche space to avoid competitive exclusion. Partitioning of light, soil nutrient and topographic niches among coexisting tropical trees has been identified previously, but studies have not measured their combined effect because of difficulties in distinguishing between niche and dispersal-based drivers of local scale (<1 km^2) distributions. Here, we model the local-scale distribution of over 650,000 trees from 444 species at three tropical forest sites on two continents (Barro Colorado Island, Panama, and Pasoh and Danum Valley in Malaysia). We test associations to 31 soil nutrient and airborne LiDAR-derived canopy structure and micro-topography metrics using novel point-pattern statistical models that account for dispersal-limited spatial aggregations. We find that a substantial majority (60-86%) of species occupy a unique environmental niche shared by no other species at a single site. The relationship between the proportion of species with a unique niche and the number of niche dimensions remains unsaturated suggesting further scope for niche partitioning beyond the studied variables. Species were associated to all 31 measured canopy, soil nutrient and topographic environments, but the relative importance of these dimensions varied between sites. Greater site-level environmental heterogeneity enhanced niche partitioning but the number of associations to individual resources could not always be explained by its variability; site and species-specific resource limitation likely also plays a role. We find evidence of species specialisation on various forms of N and P and both phylogenetic niche conservatism and niche divergence, highlighting how local conditions interact in complex ways to affect species' distributions. Overall, we conclude that niche partitioning is a key mechanism for species coexistence in highly diverse tropical forests.

2.2 Main

Understanding the mechanisms that support species co-existence remains a fundamental challenge in community ecology (Wright, 2002). Niche partitioning theories propose that species co-exist by avoiding resource competition through division of multi-dimensional niche space (Whittaker, 1965; Hutchinson, 1978). Evidence for niche partitioning to explain co-existence of heterotrophic species is strong (Schoener, 1974). In contrast, a long-held paradigm that green plants have essentially four key requirements - solar radiation, water, carbon dioxide and a basic set of mineral nutrients (Harper, 1969) - is often used to cast doubt on the scope for niche partitioning among autotrophic species. This conceptual problem has led research to focus on other mechanisms, such as conspecific negative density dependence (Janzen, 1970; Connell *et al.*, 1971; Harms *et al.*, 2000; Comita & Hubbell, 2009; Bagchi *et al.*, 2010; Terborgh, 2012; Bagchi *et al.*, 2014), or on neutral theories that suggest niche mechanisms are entirely unimportant (Bell, 2001; Hubbell, 2001; Volkov *et al.*, 2003). Explaining the exceptional species richness of tropical forests has posed a particular challenge, though, because any mechanism needs to account for the local (<1 km^2) coexistence of up to ~ 1000 tree species (Davies *et al.*, 2021).

Contrasts between the plant communities of forest gaps and shaded understories provided early evidence for niche partitioning among tropical forest tree species (Denslow, 1980). The formation of forest gaps offers the opportunity for fast-growing, light demanding species to coexist alongside shade tolerant species via spatial segregation according to light availability (Dalling *et al.*, 2001; Wright *et al.*, 2003; Sterck *et al.*, 2006; Velazquez & Wiegand, 2020). Gap formation, however, is not the sole determinant of light availability in tropical forests, as variation in light regimes has both horizontal and vertical dimensions (Fetcher, 1984; Raich, 1989). The importance of the three-dimensional structure of forests is rarely considered, but derives from variation in canopy height, foliar density and topographic aspect, which change both absolute irradiance and the proportion of direct and diffuse light (Parker *et al.*, 2019). Partitioning of light availability gradients has been observed even in the absence of gaps (Montgomery & Chazdon, 2002), suggesting that heterogeneity in multiple dimensions of canopy structure variables must be considered for understanding of niche partitioning with respect to light availability.

Multiple nutrient elements and ions are critical to the function of all plants, supporting metabolism and growth. The biogeochemical niche hypothesis suggests species can co-exist by avoiding nutritional competition from having the same specific needs and uses for each element (Sardans *et al.*, 2021). Soil nutrient availability is an important determinant of tropical tree species distributions at local (<1 km^2), mesoscale (1-100 km^2) and landscape (>100 km^2) scales, providing important axes for niche partitioning

(Clark *et al.*, 1998; Russo *et al.*, 2005; Paoli *et al.*, 2006; John *et al.*, 2007; Condit *et al.*, 2013; Jucker *et al.*, 2018b). Typically, studies have focused on a small subset of nutrients, such as N, P and macro-nutrient cations, despite the existence of at least 17 essential elements for plant growth (Epstein, 1972). Furthermore, nutrients may manifest in various forms, such as P, which can be found in simple or complex forms (Liu *et al.*, 2018), they can vary in availability with pH (John *et al.*, 2007), can act as toxins (Manara *et al.*, 2020), and can modify trophic interactions (Kaspari, 2020), providing further potential axes for niche partitioning.

Gradients in precipitation across tropical forest landscapes are an important determinant of tropical tree species distributions (Engelbrecht *et al.*, 2007; Condit *et al.*, 2013; Esquivel-Muelbert *et al.*, 2017b). At local scales, however, variation in water availability will be determined by fine-scale variation in drainage caused by micro-topography and soil texture. Several studies have identified micro-topography as a key driver of species distributions at local scales (Harms *et al.*, 2001; Itoh *et al.*, 2003; Gunatilleke *et al.*, 2006), but these studies failed to separate variation in micro-topography from co-varying nutrient availability. Incorporation of micro-topographic features alongside soil nutrient availability is therefore necessary for understanding the role of topography in facilitating niche partitioning in tropical forests (Baldeck *et al.*, 2013).

Niche specialisation is predicted to be highest close to the equator, helping support the latitudinal gradient in species richness via tighter species packing and greater species turnover across environmental gradients (Cao *et al.*, 2021). Greater abiotic environmental heterogeneity may facilitate enhanced niche differentiation because of greater available niche space (Brown *et al.*, 2013). However, most studies investigating the role of environmental heterogeneity on niche partitioning have focused on topographic variation (Brown *et al.*, 2013; Cao *et al.*, 2021) and fail to account for this in terms of specific resources such as soil nutrients and canopy structure.

In this paper we test the relative contribution of canopy structure, soil nutrient availability and micro-topography to niche partitioning in tropical forests by modelling the drivers of local-scale species distribution patterns of all abundant species (≥ 6 individuals ha^{-1}, n = 444 species) from three tropical forest sites. We fit Latent Gaussian models using Integrated Nested Laplace Approximation that allow the point patterns of individuals belonging to species to be modelled at fine scales with complex model structures whilst accounting for spatial aggregation from limited dispersal (Illian *et al.*, 2012; Lindgren & Rue, 2015; Sørbye *et al.*, 2018). The data were derived from spatially explicit maps of species' presences of all trees >1 cm diameter at breast height from the three large permanent lowland forest dynamics plots in Barro Colorado Island (BCI), Panama, Pasoh in Peninsular Malaysia and Danum Valley in Malaysian Borneo (Davies *et al.*, 2021). At each site, canopy structure and micro-topography were measured using airborne laser scanning and up to 19 soil variables were measured and geospatially modelled to the 20 x 20 m grid scale (see Methods & Table 2.1) (John *et al.*, 2007). By comparing sites varying in environmental heterogeneity, we show that niche partitioning increases with topographic, edaphic and canopy variation and can explain spatial patterns for up to 86% of the locally abundant species.

At all three sites, all measured soil nutrient, canopy structure and topographic environmental co-variates were associated with the distribution of one or more species (median = 11.5% of species, range = 3.2 - 39.5%; Figure 2.1, SI Figure 2.1), although the relative importance of each co-variate varied among sites. Most co-variates had more associations than the type I error rate of 7.22% (see Methods). Species varied widely in the number and type of associations at all sites, with significant associations with up to nine different environmental co-variates (Figure 2.2). More species were significantly associated to multiple co-variates at Danum Valley (77.5% of species) than at Pasoh (63.8%) and BCI (46.8%; SI Figure 2.2). Conversely, more species at BCI and Pasoh were associated to none or only one co-variate than at Danum Valley. Whilst these differences may be explained by different model structures between sites, equivalent patterns held when models were re-run with the same model structure at all sites (Figure 2.2). In these reduced models with 15 fixed co-variates, species from Danum Valley had significantly more environmental associations (2.82 ± 0.15) than at Pasoh (2.25 ± 0.12) and BCI (1.59 ± 0.14; $p < 0.001$; Figure 2.2a). Partitioning of multiple environmental resources can provide the opportunity for a high number of unique niches. At our sites 59.6 - 86.0% of species had a unique combination of environmental associations (BCI: 59.6%; Danum Valley: 86.0%; Pasoh: 73.8%) and thus a unique niche shared by no other species. We found no evidence of a saturating relationship between the proportion of species with unique niches and the number of niche dimensions, suggesting there is further scope for niche partitioning beyond that studied here (Figure 2.3). By occupying a unique niche space, species can avoid competition and competitive exclusion, facilitating species coexistence (Whittaker, 1965; Hutchinson, 1978).

Whilst interpreting cross-site patterns based on just three sites is challenging, we found the number of species-environment associations to increase with environmental heterogeneity ($p = 0.018$; Figure 2.2b; see Methods). Niche partitioning is likely to be stronger in more heterogeneous environments as there is greater niche space for species to partition (Brown *et al.*, 2013). When investigating each environmental co-variate separately, the number of associations increased with the plot-level variation of eight of the fourteen co-variates (Figure 2.4). This indicates that variation in some environmental variables is sufficient to provide an axis for niche partitioning, but other environmental variables may only become important under certain conditions or thresholds. Some soil nutrients, for example, may only be important in driving species distributions if they are limiting (Turner *et al.*, 2018), or if they reach certain concentrations that they become toxic (Manara *et al.*, 2020).

Table 2.1: Information about the sites included in this study including number of species and trees, soil order following US soil taxonomy (Staff, 1999), elevational range, mean annual temperature (MAT) and mean annual precipitation (MAP) (Davies *et al.*, 2021).

Site	Region	Country	Area (ha)	Census date	Species	Species modelled	Trees	Trees modelled	Soil order	Soil variables used	Elevation (m asl)	MAT (˚C)	MAP (mm yr^{-1})
Barro Colorado Island	Central America	Panama	50	2010	299	94	221,580	207,000	Oxisol	Al, B, Ca, Co, Cu, Fe, K, Mg, Mn, N, NH_4, NO_3, Na, P, PO_4, Zn, pH	137 - 166	27.1	2551
Danum Valley	South-East Asia	Malaysia	50	2019	694	129	263,911	194,931	Inceptisol	Al, B, Ca, Co, Cr, Cu, Fe, K, Mg, Mn, NH_4, NO_3, Na, Ni, P, PO_4, Zn, pH	209 - 317	26.7	2822
Pasoh	South-East Asia	Malaysia	50	2011	921	221	300,211	252,186	Ultisol/ entisol	Al, Ca, Fe, K, Mg, Mn, NH_4, NO_3, Na, P, PO_4, pH	94 - 121	27.9	1788

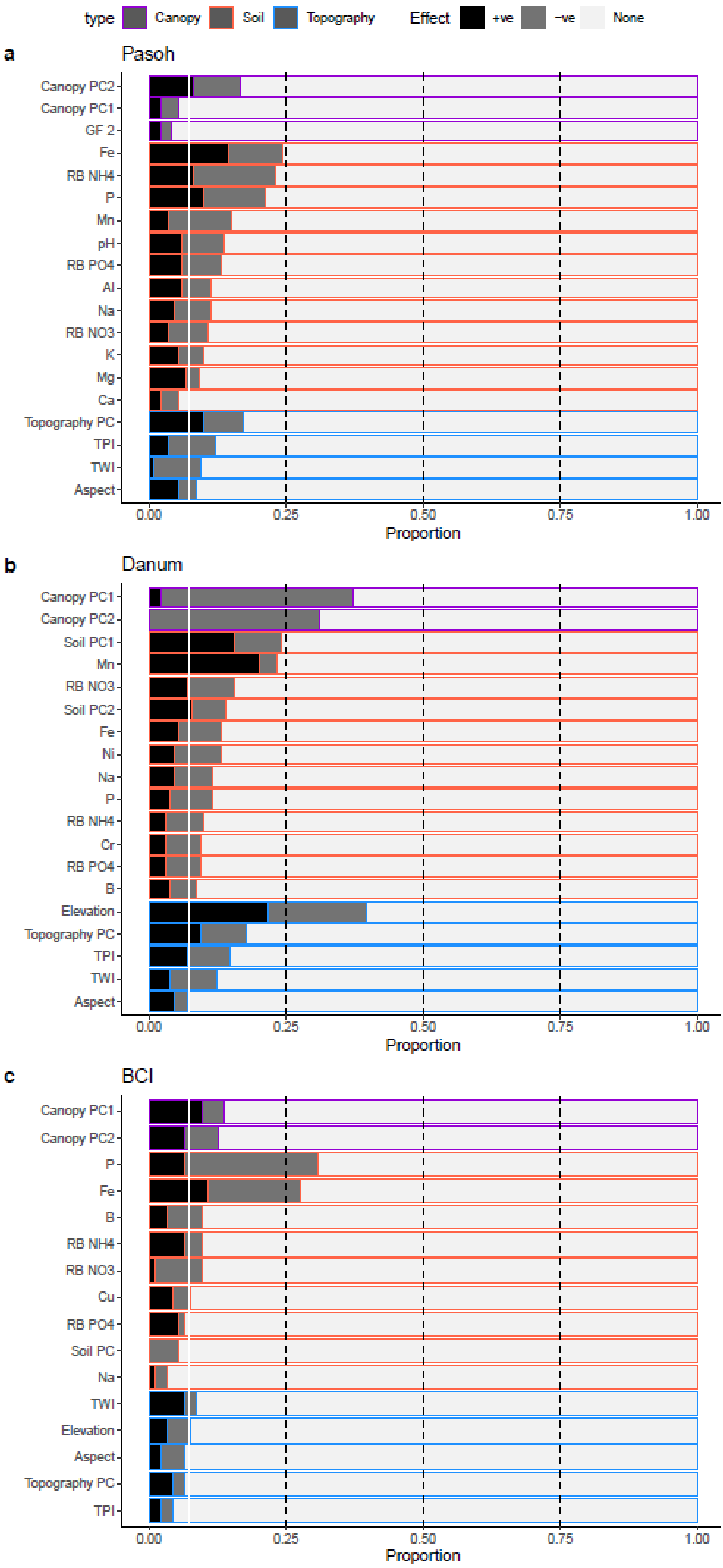

Figure 2.1: The proportion of species with a significant positive (black) or negative (grey) association to a range of environmental co-variates at each of the three study sites: (a) Pasoh (n = 221), (b) Danum Valley (n = 129), (c) Barro Colorado Island (n = 94). Co-variates are ranked according to the proportion of associations within each type of environmental co-variate: canopy (purple), soil nutrient (red), topographic (blue). The white dotted line represents the proportion of species expected to be associated with each co-variate under a type I error rate of 0.0722 (see Methods). Bars below this threshold indicate the co-variate does not significantly control species distributions. Some co-variates were condensed into principal components because of autocorrelation between co-variates (see SI Figures 2.7, 2.8 & 2.10), whilst not all soil co-variates were measured at each site (see Table 2.1).

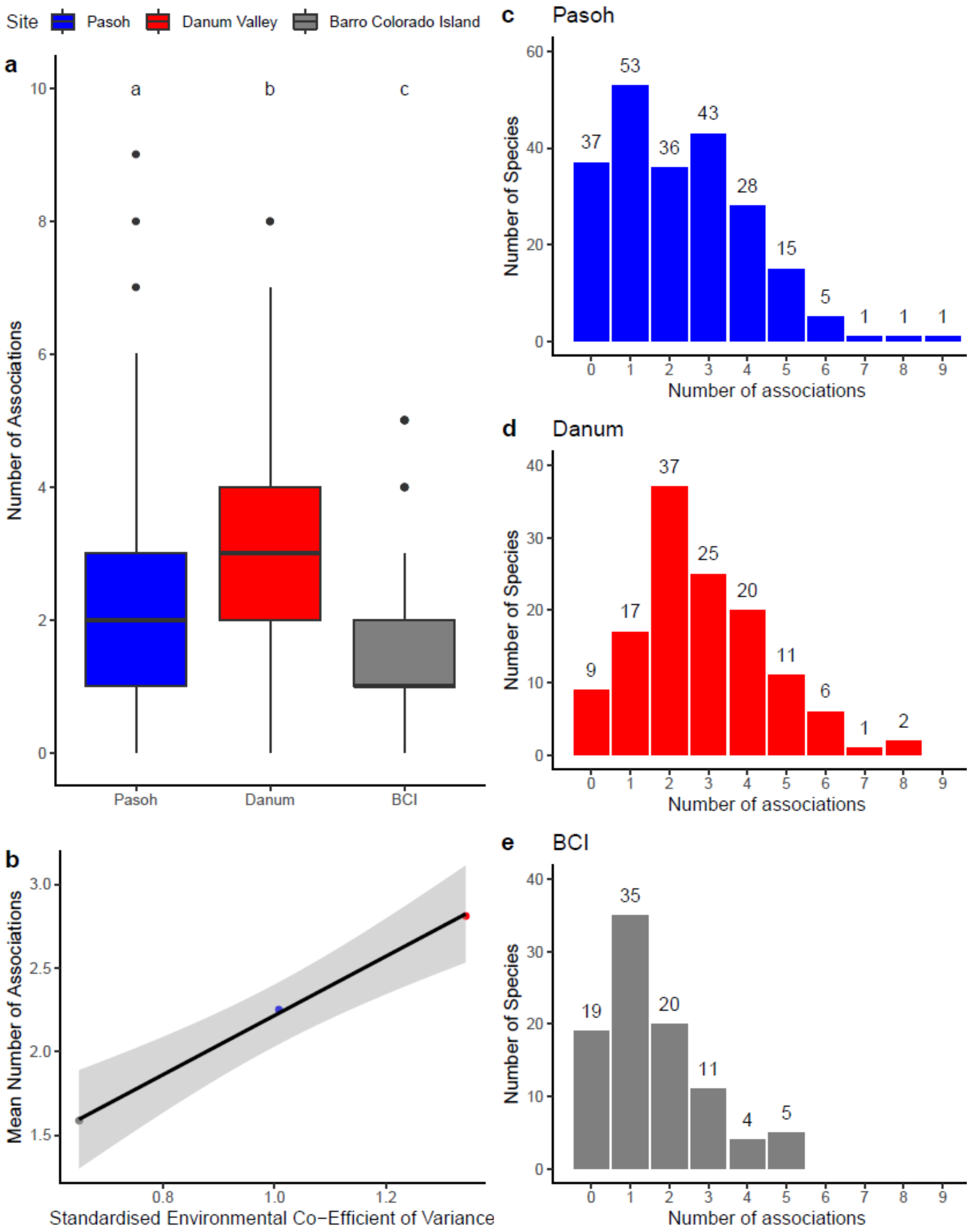

Figure 2.2: Number of measured environmental co-variates (associations) that contributed to the distribution of each species at each site (a). A significant relationship between the mean number of associations and the standardised environmental co-efficient of variance was found ($p = 0.018$; b). Histograms for the number of environmental co-variates that explained species distributions at each site are presented: (c) Pasoh, (d) Danum Valley, (e) Barro Colorado Island. All species were modelled by the same 15 environmental co-variates at all sites allowing direct comparisons among sites to be made (see Methods & SI Methods). Letters in (a) represent significant differences among sites from a general linear model ($p < 0.05$; see Methods).

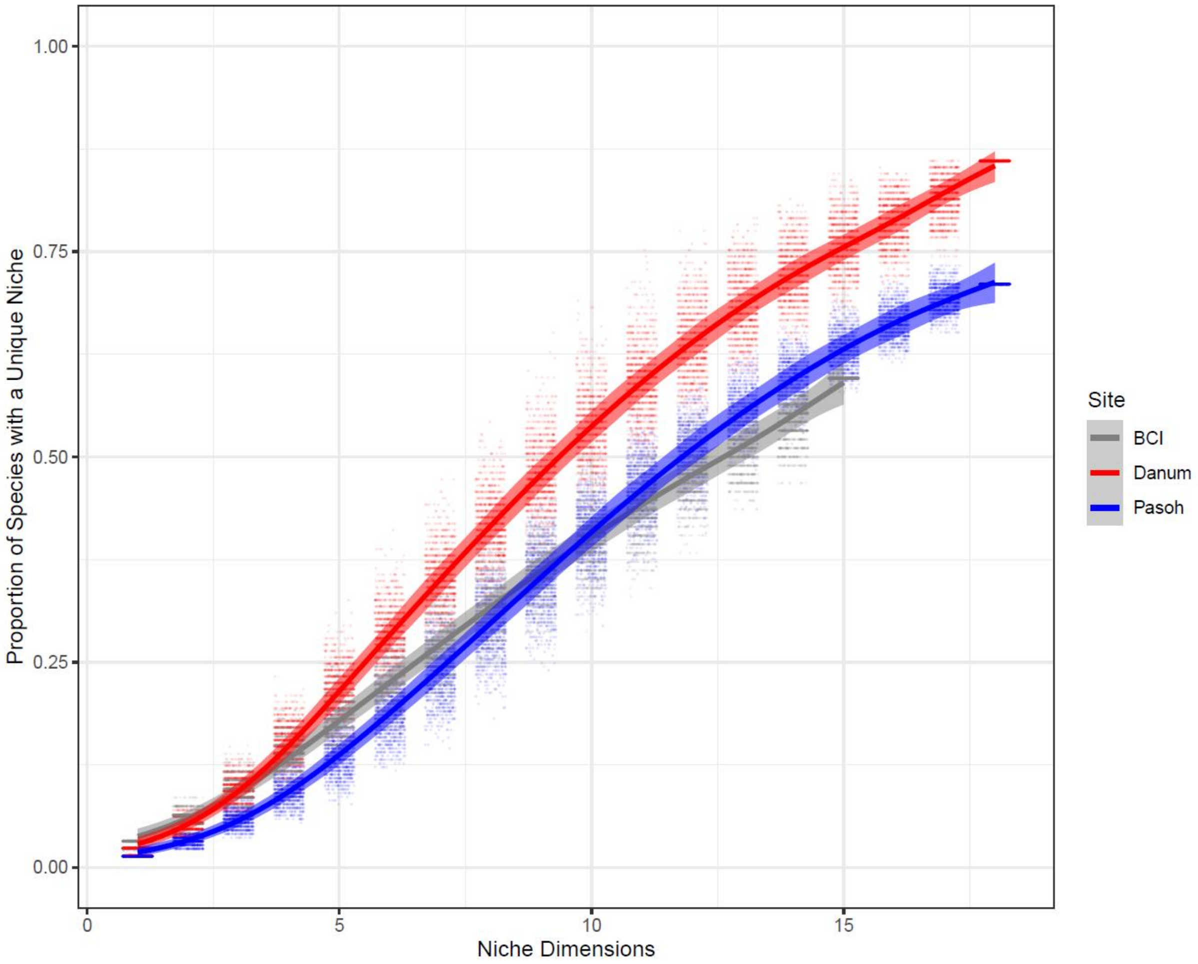

Figure 2.3: Accumulation curve of the proportion of species with a unique niche (a unique set of significant environmental associations) shared by no other species with increasing number of niche dimensions for each site. Data points represent 1000 bootstrap estimates for each number of niche dimensions for each site (see Methods). Generalised additive model curves are fitted through the mean with a 95% confidence interval. Data are horizontally jittered for visualisation purposes.

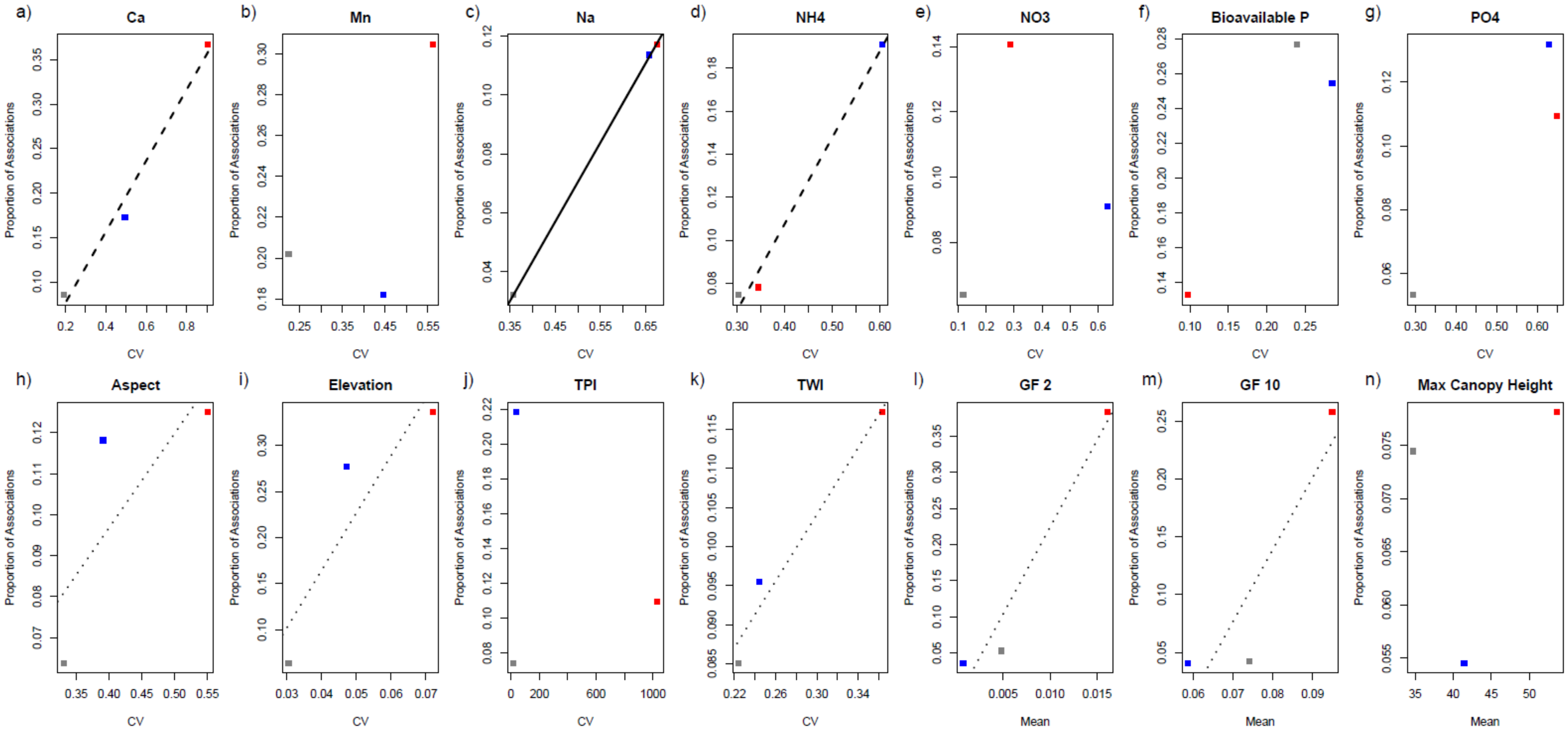

Figure 2.4: Relationships between the proportion of species associated to each environmental co-variate and the plot level co-efficient of variation for seven soil nutrient variables and four topographic variables and plot level means for three canopy structure variables: (a) calcium, (b) manganese, (c) sodium, (d) ammonium, (e) nitrate, (f) bioavailable phosphorus, (g) dissolved phosphate, (h) topographic aspect, (i) elevation, (j) topographic position index, (k) topographic wetness index, (l) canopy gap fraction at 2 m, (m) canopy gap fraction at 10 m and (n) maximum canopy height. Iron was additionally included in our models, but different extraction methods between sites meant direct comparisons of plot-level coefficient of variation could not be made. Significant Pearson's correlations are presented with solid ($p < 0.05$) and dashed lines ($p < 0.1$), with additional non-significant relationships with a spearman's correlation of $\rho = 1$ presented with dotted lines. Sites are represented by separate colours: BCI – grey, Danum Valley – red, Pasoh – blue.

Topography has long been identified as a key driver of local-scale species distributions and elevation was an important driver at Danum Valley (21.7% positively and 17.8% negatively associated) but explained the distribution of fewer species at Pasoh and BCI (Figures 2.1 & 2.4). Danum Valley is more topographically complex than the other study sites with steeper slopes, greater terrain ruggedness and >100 m elevational range (Table 2.1; Figure 2.4). The proportion of species associated with elevation and TWI increased with variation in these variables (Figure 2.4), suggesting an important role of topographic variation in strengthening niche partitioning. Topography can determine local water availability via changes in soil texture, drainage and proximity to the water table, promoting hydrological niche segregation among species with different hydraulic strategies (Brum *et al.*, 2018; Oliveira *et al.*, 2019; Esteban *et al.*, 2021; Bittencourt et al. in review). Greater topographic complexity may therefore facilitate the co-existence of species with different hydraulic strategies and enhance species richness in tropical forests.

Soil nutrient availability was identified as an important driver of local-scale species distributions at all sites, although the specific nutrients explaining distributions varied among sites (Figure 2.1). At Pasoh and BCI, a high proportion of species was found to be associated with bioavailable P (Pasoh: 21.3%, BCI: 30.8% of species) and Fe (Pasoh: 24.4%, BCI: 27.7%). Bioavailable P and Fe also explained the distribution of more species than expected by the type one error rate at Danum Valley (see Methods), but they were not the most important soil nutrient co-variates, with soil PC1 (cations and pH; Table 2.2) and Mn explaining the distribution of more species at this site than any other soil nutrient co-variates. Our findings support increasing evidence that P acts as an important driver of species distributions in tropical forests both at local and landscape scales, including previous studies at BCI (John *et al.*, 2007; Condit *et al.*, 2013), and supports the notion that phosphorus may be more limiting that nitrogen in tropical forests (Turner *et al.*, 2018). We found a significant negative relationship between the effect sizes of species' associations to dissolved PO_4 and bioavailable P in BCI ($p = 0.008$), but not at either Asian forest site (Figure 2.5a). Of the studied sites, bioavailable P concentrations are lowest at BCI, which might favour a trade-off between species that efficiently scavenge for dissolved inorganic PO_4 and those that mobilise adsorbed inorganic P (Lambers *et al.*, 2008). However, identifying trade-offs in associations to different P pools were challenging because dissolved PO_4

represents a component of bioavailable P and is thus nested within bioavailable P. At Pasoh, dissolved PO_4 concentrations were highest, meaning the positive relationship between the effect sizes of species' associations with dissolved PO_4 and bioavailable P ($p < 0.001$; Figure 2.5a) may be a statistical consequence of greater nestedness. Whilst we identify potential niche partitioning of different P pools, we focus on bioavailable forms of inorganic P in this study. Some species, such as those that form ectomycorrhizal associations, are able to additionally access organic P pools (Liu *et al.*, 2018). Differential access to various P pools may thus provide multiple possibilities for niche partitioning and species co-existence.

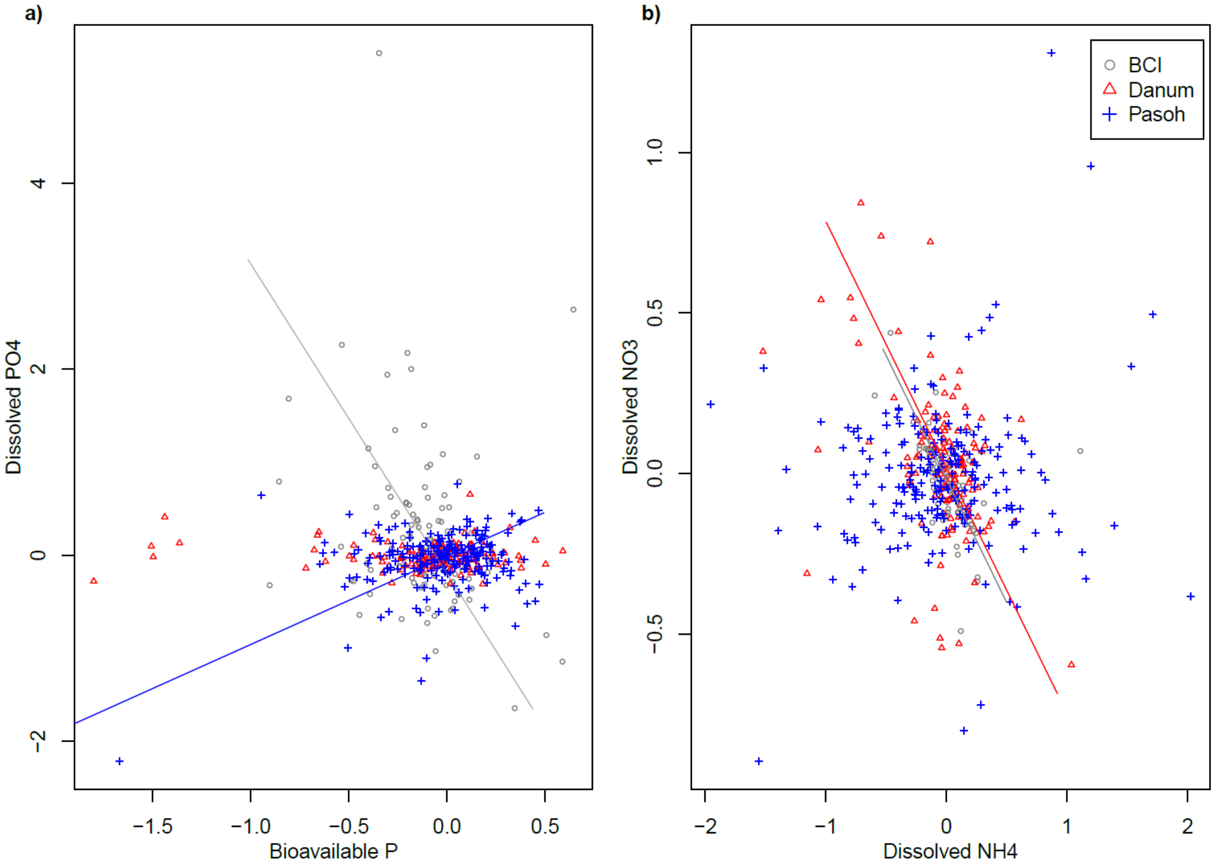

Figure 2.5: Standardised major axis regression between effect sizes of species associations to (a) bioavailable P and dissolved PO_4 and (b) dissolved NH_4 and dissolved NO_3 for each site: BCI – grey circles, Danum Valley – red triangles, Pasoh – blue crosses. Lines of significant regressions ($p < 0.05$) are presented. Effect sizes are taken from the models with the same 15 environmental co-variates shared by all sites.

Table 2.2: Variable loadings to the canopy, soil and topography principal components at each site. The percentage of the total variance explained by each principal component is expressed.

	Barro Colorado Island		Danum Valley		Pasoh	
	Canopy PC1 (61.6%)	**Canopy PC2 (22.1%)**	**Canopy PC1 (67.1%)**	**Canopy PC2 (19.0%)**	**Canopy PC1 (63.5%)**	**Canopy PC2 (22.2%)**
GF at 2 m	0.616	0.667	0.706	0.611	-	-
GF at 5 m	0.808	0.514	0.838	0.496	0.649	0.658
GF at 10 m	0.877	0.156	0.896	0.158	0.828	0.454
GF at 20 m	0.859	-0.313	0.851	-0.321	0.898	-0.134
Mean Canopy Height	-0.893	0.381	-0.842	0.465	-0.907	0.319
Maximum Canopy Height	-0.600	0.590	-0.769	0.422	-0.663	0.594
	Soil PC (53.7%)		**Soil PC1 (52.9%)**	**Soil PC2 (15.1%)**		
pH	0.847		0.871	-0.248		
Al	-		-0.803	0.331		
Ca	0.909		0.873	0.331		
Co	-		0.273	-0.688		
Cu	-		0.762	0.416		
K	0.535		0.578	0.225		
Mg	0.773		0.775	-0.343		
Mn	-0.683		-	-		
N	0.726		-	-		
Zn	0.583		0.690	0.407		
	Topography PC (99.9%)		**Topography PC (98.1%)**		**Topography PC (88.8%)**	
Elevation	**-**		**-**		0.873	
Slope	0.999		0.990		0.975	
TRI	0.999		0.990		0.975	
TRI: Terrain ruggedness index; GF: Canopy gap fraction						

The important role of Fe at all sites was surprising as it contrasts previous evidence that suggests Fe does not control local scale distributions of tropical tree species, including at BCI (John *et al.*, 2007; Condit *et al.*, 2013). These conflicting results may be because we only study the drivers of abundant species or because we included individual soil variables directly in this study rather than within ordination axes as done previously (John *et al.*, 2007). Iron can geologically fix phosphorus by forming crystalline and occluded forms that are sparingly soluble and reduce the biological availability of P in highly weathered soils (Cross & Schlesinger, 1995; Dieter *et al.*, 2010). A significant negative relationship between associations to Fe and dissolved PO_4 at BCI ($p = 0.043$) and Fe and bioavailable P at Pasoh ($p < 0.001$) were found (SI Figure 2.3). Adaptations that allow some species to overcome intense phosphorus limitation in iron-rich soils may allow them to outcompete other species that are confined to iron-poor soils and provide an additional dimension for partitioning of soil phosphorus pools (Turner, 2008).

Despite an important role of phosphorus, we found nitrogen in the form of dissolved NH_4 at Pasoh and dissolved NO_3 at Danum Valley to be of equivalent or greater importance at explaining species distributions than bioavailable P at both Asian sites (Figure 2.1). This suggests phosphorus limitation may not be universal across the tropics but could vary locally (Sayer & Banin, 2016; Wright, 2019; Bartholomew et al. in review). When comparing associations to the different forms of nitrogen, we found a significant negative relationship between the effect size of species' associations to NO_3 and NH_4 at BCI ($p < 0.001$) and Danum Valley ($p < 0.001$), but not Pasoh ($p = 0.988$; Figure 2.5b). Whilst the effect size of association to NO_3 and NH_4 was low at all sites for the majority of species, some species did exhibit a strong preference for one nitrogen form over the other. Our results support growing evidence that suggests most species can plastically adjust uptake of different nitrogen forms according to supply (Houlton *et al.*, 2007; Andersen *et al.*, 2013; Russo *et al.*, 2013; Andersen *et al.*, 2017), but some species specialise to use one form over the other (Andersen *et al.*, 2017). This nitrogen niche differentiation may provide a mechanism to promote co-existence between nitrate-specialist and ammonium-specialist species at local scales.

In Danum Valley, we found an additional role for nutrients associated with ultramafic soils in determining species distributions, such as cation imbalances (soil PC1 – 24.0% of species) and potentially phytotoxic elements (Mn – 23.3%, Ni – 13.2%, soil PC 2 –

14.0%) (Galey *et al.*, 2017). Specialised adaptations are needed to survive on ultramafic soils, such as metal hyperaccumulation and hypertolerance (Galey *et al.*, 2017; Manara *et al.*, 2020) and may provide a further dimension for niche differentiation between species. Meanwhile, associations with sodium were found at both Asian sites, increasing in importance with variation in soil Na ($p = 0.009$; Figure 2.4c). Whilst sodium is not an essential element for most plants, recent research has suggested that it has an important role in regulating herbivore abundance (Kaspari *et al.*, 2008; Kaspari, 2020). Greater variation in sodium may therefore provide variation in herbivory intensity that may act as an important environmental filter for some species.

Canopy structure was found to explain species distributions at all sites but was of greatest importance at Danum Valley (Figures 2.1 & 2.5). Here, 37.2% of species were associated to canopy PC1 and 31.0% to canopy PC2, with most of these associations negative. Both canopy principal components were positively related to the size and number of canopy gaps (Table 2.2), suggesting many species at Danum Valley have a low preference for open canopies. In contrast, both positive and negative associations to canopy gaps were found at BCI and Pasoh. This may indicate that a higher proportion of the species present at Danum Valley are shade tolerant, whereas a mix of shade tolerance strategies may exist at Pasoh and BCI. Both BCI and Pasoh have experienced historic and recent anthropogenic and natural disturbances that may support more pioneer species (Condit *et al.*, 1999; Ickes, 2001; Ickes *et al.*, 2001; Sheil & Burslem, 2003; Luskin *et al.*, 2019; Luskin *et al.*, 2021), whilst the low disturbance regime at Danum Valley may have excluded these shade intolerant species (Kennedy *et al.*, 1997). Conversely, our results may be a statistical relic because of a large canopy gap that is found in one corner of the Danum Valley plot where few trees are located, and mean canopy height is below 5 m. The low abundance of trees here may explain why we predominantly detect negative associations to these gaps in our models, whereas positive associations are detected at the other sites where one single canopy gap does not dominate the signal.

We found limited phylogenetic clustering or over-dispersion in species-environment associations at all three sites (Table 2.3; SI Figures 2.4-2.5), suggesting species-environment associations are predominantly evolutionarily labile. However, we found positive phylogenetic autocorrelation in associations to PO_4 ($p < 0.001$) at Pasoh and to canopy PC2 ($p = 0.009$) and Fe ($p = 0.041$) at Danum Valley. Associations to these co-variates may require adaptations that are not evolutionarily labile but instead are phylogenetically conserved. Whilst adaptations to the canopy structure may be phylogenetically conserved, this result should be interpreted with caution as canopy structure is ultimately determined by canopy tree species. The upper canopy of Asian forests is dominated by species from the Dipterocarpaceae family (Banin *et al.*, 2012) and may explain the stronger phylogenetic autocorrelation we observe in associations to both of the canopy principal component axes at the Asian forest sites compared with BCI (Table 2.3; SI Figure 2.5). When comparing the fifteen species found at both Pasoh and Danum Valley, the strength of the species-environment association at one site did not correlate with that from the other site for any variables, except for those with the strongest associations (NH_4 and bioavailable P; SI Figure 2.6). This indicates that the most important drivers of species distributions are conserved between sites, but less important drivers are affected by the local abiotic and biotic environments. At Pasoh, we found a significant negative phylogenetic autocorrelation in associations to pH ($p = 0.019$) and to NO_3 ($p = 0.023$; Table 2.3; SI Figure 2.5a), indicating that closely related species are spatially over-dispersed according to these co-variates. Pasoh has the lowest NO_3 availability and the lowest pH of our study sites and these may act as strong selection pressures for local coexistence of closely related species. Niche differentiation of closely related species may provide a mechanism of sympatric speciation and species coexistence (Brown & Wilson, 1956; Schluter, 2000b; Schluter, 2000a; Debski *et al.*, 2002), and could be one of the drivers for greater species richness in Pasoh than the other sites studied here.

Table 2.3: Phylogenetic autocorrelation as calculated by Abouheif Moran’s I from a phylogenetic principal component analysis for environmental co-variates at each site. Positive values of I represent phylogenetic conservatism, whilst negative values represent phylogenetic dispersion. An I value of zero represents expectations under Brownian motion (see Methods; Abouheif, 1999). Significant effects are highlighted in bold.

Site	BCI			Danum Valley			Pasoh		
Variable	Abouheif Moran’s I	p	Adjusted p	Abouheif Moran’s I	p	Adjusted p	Abouheif Moran’s I	p	Adjusted p
Al	-	-	-	-	-	-	-0.002	0.943	1.000
Aspect	-0.007	0.962	1.000	-0.024	0.779	1.000	0.005	0.771	1.000
B	0.002	0.846	1.000	-0.124	0.038	0.726	-	-	-
Ca	-	-	-	-	-		-0.030	0.480	1.000
Canopy PC1	0.042	0.456	1.000	0.112	0.020	0.374	0.056	0.151	1.000
Canopy PC2	0.061	0.304	1.000	**0.198**	**<0.001**	**0.009**	0.051	0.183	1.000
Cr	-	-	-	-0.028	0.716	1.000	-	-	-
Cu	0.110	0.081	1.000	-	-	-	-	-	-
Elevation	0.086	0.152	1.000	0.001	0.875	1.000	-	-	-
Fe	0.014	0.721	1.000	**0.168**	**0.002**	**0.041**	0.031	0.393	1.000
GF 2	-	-	-	-	-	-	-0.038	0.196	1.000
K	-	-	-	-	-	-	0.115	0.009	0.179
Mg	-	-	-	-	-	-	0.047	0.180	1.000
Mn	-	-	-	0.056	0.249	1.000	0.019	0.569	1.000
Na	-0.058	0.494	1.000	-0.114	0.057	1.000	-0.000	0.913	1.000
Ni	-	-	-	0.006	0.803	1.000	-	-	-
P	0.109	0.085	1.000	0.053	0.265	1.000	0.024	0.422	1.000
pH	-	-	-	-	-	-	**-0.151**	**<0.001**	**0.019**
NH_4	0.058	0.287	1.000	-0.064	0.286	1.000	0.042	0.270	1.000
NO_3	0.089	0.150	1.000	0.066	0.179	1.000	**-0.165**	**0.001**	**0.023**
PO_4	0.076	0.179	1.000	-0.024	0.763	1.000	**0.249**	**<0.001**	**<0.001**
Soil PC1	-0.049	0.567	1.000	0.093	0.063	1.000	-	-	-
Soil PC2	-	-	-	0.045	0.314	1.000	-	-	-
Topography PC	-0.021	0.883	1.000	0.029	0.516	1.000	-0.055	0.155	1.000
TPI	0.075	0.210	1.000	0.056	0.235	1.000	0.012	0.679	1.000
TWI	0.028	0.576	1.000	-0.022	0.791	1.000	0.043	0.242	1.000

The results presented in this study highlight the large multi-dimensional niche space of tropical forests and the importance of niche partitioning for species coexistence. Although niche partitioning with respect to topography, soil nutrient availability and canopy light environments has long been recognised (Denslow, 1980; Clark *et al.*, 1998; Dalling *et al.*, 2001; Harms *et al.*, 2001; Montgomery & Chazdon, 2002; Itoh *et al.*, 2003; Wright *et al.*, 2003; Russo *et al.*, 2005; Gunatilleke *et al.*, 2006; Paoli *et al.*, 2006; Sterck *et al.*, 2006; John *et al.*, 2007; Condit *et al.*, 2013; Jucker *et al.*, 2018b; Velazquez & Wiegand, 2020), studies investigating their combined importance are rare. Greater environmental heterogeneity was found to enhance niche partitioning but was insufficient to explain all species-environment associations, suggesting that other mechanisms including conspecific negative density dependence and neutral theories are also likely to be important in explaining the exceptional diversity of tropical forests (Janzen, 1970; Connell *et al.*, 1971; Harms *et al.*, 2000; Bell, 2001; Hubbell, 2001; Volkov *et al.*, 2003; Comita & Hubbell, 2009; Bagchi *et al.*, 2010; Terborgh, 2012; Bagchi *et al.*, 2014). Nonetheless, we reveal the high frequency of specialisation among tropical tree species and the importance of maintaining complex environments and habitat niche diversity in tropical forests. Minimising anthropogenic disturbance that increases environmental homogenisation (Edwards *et al.*, 2019) is therefore likely to be critical if tropical forests are to continue to support high species richness and the services they provide under environmental change.

2.3 Methods

2.3.1 Study sites

This study draws on data collected in three lowland primary tropical forests sites by the Smithsonian Tropical Research Institute’s ForestGEO plot network: Barro Colorado Island, Panama (BCI), Danum Valley, Malaysia and Pasoh, Malaysia (Table 2.1; Anderson-Teixeira *et al.*, 2015; Davies *et al.*, 2021). At each site, a long-term 50 ha forest dynamics research plot has been established. All trees >1 cm diameter at breast height (measured at 1.3 m; DBH) within each plot have been measured, identified to species level and mapped to the nearest 10 cm (Condit *et al.*, 2019; Davies *et al.*, 2021). Tree censuses were undertaken between 2010 and 2019 (Table 2.1).

For the purpose of this study, we divided each 50 ha plot into 1250 20 x 20 m square quadrats, and the abundance of each species in each quadrat was calculated. All environmental variables described subsequently were calculated at 20 x 20 m pixel resolution to allow raster layers to be incorporated in our species distribution models.

2.3.2 Topography and Canopy Structure

Topographic and canopy structure metrics were extracted from canopy height models (CHM) and digital elevation models (DEM; SI Table 2.1). Both CHMs and DEMs were derived from airborne light detecting and ranging (LiDAR) datasets, which are described in detail elsewhere (Fricker *et al.*, 2015; Jucker *et al.*, 2018a; Omar *et al.*, 2020). We used the DEM aggregated to 5 x 5 m pixels to extract slope angle, aspect and terrain ruggedness index (TRI) using the *terrain* function in the *raster* R package (Hijmans, 2019) and topographic position index using the *tpi* function in the *spatialEco* package (Evans, 2020). We transformed aspect into the solar-radiation aspect index (SRAI) following the equations of Roberts and Cooper (1989). SRAI transforms aspect into a continuous variable bounded by zero and one, with hotter, dryer south-westerly slopes having the maximum value and the cooler, wetter north-eastern slopes having the minimum value in the northern hemisphere. A DEM aggregated to 10 x 10 m was used to estimate the topographic wetness index (TWI) using the *upslope.area* function from the package *dynatopmodel* (Metcalfe *et al.*, 2018). We used the CHM to estimate maximum and mean canopy height, as well as canopy gap fraction at 2 m, 5 m, 10 m and 20 m height using the *raster* package (Hijmans, 2019). Auto-correlation ($r > 0.7$) amongst topographic variables and amongst canopy variables was identified (SI Figures 2.7-2.8), with all variables with auto-correlation issues centred, scaled and condensed into principal components using the R package *factoextra* (Kassambara & Mundt, 2017). Principal components that explained more variation than the total variation divided by the number of co-variates were used in our models (Table 2.2).

2.3.3 Soil nutrient availability

Soils samples were collected across each plot using a regular grid, with additional samples collected in a random compass direction at 2, 8 or 20m from the base point to capture soil variation at finer spatial scales (see SI Figure 2.9). 50 g of topsoil (0 – 10 cm depth) was collected and samples were analysed at the Smithsonian Tropical Research Institute, Panama, following Wolf *et al.* (2015) for various nutrient concentrations and pH (Table 2.1). Al, Ca, Fe (Pasoh only), K, Mg, Mn, N and Na were extracted from soils using 0.1 M $BaCl_2$ (2 h, 1:30 soil to solution ratio) and B, Co, Cr, Fe (BCI and Danum Valley), Ni, bioavailable P (BCI and Danum Valley) and Zn were extracted using Mehlich III extractant solution. Bioavailable P was extracted using a Bray extractant for Pasoh. Nutrient concentrations were analysed using inductively-coupled plasma optical-emission spectrometry (Optima 7300 DV ICP-OES, Perkin-Elmer Ltd, Shelton, CT, USA). In addition, the pH of the soil was measured 30 minutes after stirring 10 g of soil in 20 ml of distilled water using a pH probe. Resin bags were inserted into the soil for 15 days and NO_3, NH_4 and PO_4 were extracted with 75 ml of 0.5 M HCl and analysed using flow injection analysis (LACHAT Instruments, Milwaukee, WI, USA). Not all nutrients were recorded at each site - see Table 2.1 for a summary of available data.

Soil nutrient concentrations frequently correlate (SI Figure 2.10). In order to avoid including auto-correlated co-variates in our models, all elements that displayed a Pearson's correlation coefficient > 0.7 when matched with any other element were converted into principal components following the same method as for topographic and canopy co-variates (Table 2.2). Nutrients with no auto-correlation issues and principal component eigenvalues were subsequently geo-spatially kriged following John *et al.* (2007) and the resultant maps were used to derive predicted values for each of the 20 x 20 m quadrats.

2.3.4 Species distribution models

To understand the local-scale drivers of species distribution patterns, we fitted environmental covariates to the species abundance matrix using Integrated Nested Laplace Approximation (INLA) models using the R *INLA* package (Rue *et al.*, 2009; Lindgren & Rue, 2015). Biotic mechanisms, such as limited dispersal, can cause local scale conspecific spatial aggregations that cannot be explained by environmental variation (Baldeck *et al.*, 2013). INLA uses a spatially structured random field that can account for these spatial aggregations at various scales using a hyperprior U and a penalised complexity prior φ that determines the proportion of the spatial random effect that is accounted for by the structured spatial field (Sørbye *et al.*, 2018). As U increases, the proportion of the spatial point pattern that is explained by the environmental co-variates in the model is reduced. Here, we fitted an INLA model with a range of standardised topographic, canopy and soil nutrient environmental co-variates, a spatially structured effect on a grid and a spatially unstructured random-error term for all species with an abundance of > 6 trees ha^{-1} at each site with three intermediate values of U (0.1, 0.5, 1.0) with an alpha of 0.01, following Sørbye *et al.*

(2018) (see Supplementary methods for full model equations). We set φ as $\mathrm{P}(\varphi < 0.5) = \frac{2}{3}$, as it is assumed *a priori* that the spatially structured effect accounts for less variability than the unstructured random effect (Sørbye *et al.*, 2018). Environmental co-variates were log or square-root transformed prior to standardisation, where transformations improved the normality of the data (see SI Table 2.2). For each environmental co-variate, a 95% credible interval was generated at each U value and the mean of the three medians was taken as the species-environment association effect size. Species were assessed as significantly associated to an environmental co-variate if the interval of the 2.5% and 97.5% posterior estimates for all three models did not overlap zero, representing a conservative prediction of species-environment associations.

2.3.5 Estimation of the Type I error rate

We modelled the distribution of 444 species with a complex fixed co-variate structure (up to 19 co-variates). These models are likely to produce a high number of type one errors (i.e. false positives) where a significant association to an environmental variable is found despite not existing in reality. In order to quantify the rate of type one errors, we ran null models using the Danum Valley tree map and the BCI environment map. Models were fitted for 129 species using 15 fixed co-variates following equation 1. A total of 149 out of a possible 2064 associations were found to be significant in these null models, giving an estimated type I error rate of 0.0722. Any variables with less than 7.22% of species associated with it are therefore interpreted as not significantly affecting species distributions because fewer species are associated than from null expectations.

2.3.6 Data analysis

The proportion of species associated to each environmental co-variate was calculated from models run with the full co-variate structure (SI Methods equations 1-3). To allow for comparisons between sites, models were re-run with a reduced set of 15 co-variates that was available for all sites (SI Methods equation 4). We tested for differences in the mean number of associations between sites by fitting a general linear model with a Poisson error structure with site included as a fixed effect and compared to a null model with no fixed effects using a log-likelihood χ test (Thomas, 2015).

To test the role of environmental heterogeneity in supporting niche partitioning, we calculated the coefficient of variation for each environmental co-variate using the 20 x 20 m pixel values. Co-efficient of variation is a measure of the standard deviation standardised to the mean (Millard, 2013). As canopy gap fraction and maximum canopy height already represent the horizontal and vertical variation in light environments respectively, the mean was used instead for these co-variates. A mean standardised co-efficient of variation for each plot was calculated to estimate overall environmental heterogeneity at the plot level. We used a linear model to test whether environmental heterogeneity was related to the mean number of associations at each site. We additionally tested whether the proportion of associations to each environmental co-variate was correlated with the co-efficient of variation of the co-variate using a two-sided Pearson's correlation test. Pearson's correlation tests were also used to compare effect sizes for the 15 species found at both Pasoh and Danum Valley. Trade-offs between the associations with two measured forms of soil nitrogen (NO_3 and NH_4) and soil P (bioavailable P and PO_4) were tested using standardised major axis regression in the R package *smatr* (Warton *et al.*, 2012), with p-values adjusted using a Bonferroni correction to account for multiple comparisons between sites. Trade-offs between associations to Fe and soil P (bioavailable P and PO_4) were also tested to understand the role of Fe in affecting P associations.

To understand whether the scope for niche partitioning was saturated, we tested the relationship between the proportion of species with a unique combination of significant associations (unique niches) and the number of environmental co-variates (niche dimensions). For each site, we took 1000 randomly sampled co-variate combinations with replacement for each number of niche dimensions and calculated the proportion of species with a unique niche for each bootstrap. A generalised additive model with binomial error structure was fitted to the bootstrap estimates for each site with a loess smoother of 0.75.

In order to test for a phylogenetic signal, we built a phylogeny for each site using the *S.Phylomaker* tool that prunes the global mega-phylogeny for vascular plants (Qian & Jin, 2016). We use scenario 3 to prune the tree, which leaves unresolved nodes as polytomies. We performed a phylogenetic principal components analysis (pPCA) of our species-environment association effect sizes in the R package *adephylo* to test for a multivariate phylogenetic autocorrelation effect at each site (Jombart & Dray, 2010;

Jombart *et al.*, 2010). We centred and scaled our data and computed phylogenetic proximities using Abouheif's proximity (Abouheif, 1999). Phylogenetic auto-correlation was tested for each environmental co-variate using a two-sided Abouheif's test based on Moran's I using the *abouheif.moran* function from the *adephylo* R package. One million random permutations per site were used to test for a significant phylogenetic signal, with p-values adjusted for multiple testing using a Bonferroni correction. Significant positive values of I represent phylogenetic conservatism, significant negative values represent phylogenetic dispersion and non-significant values represent expectations under Brownian motion (Abouheif, 1999).

Chapter 3: Differential nutrient limitation controls leaf physiology, supporting niche partitioning in tropical dipterocarp forests

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3.1 Abstract

1) Revealing 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, we still lack an understanding of how edaphic conditions affect tree physiology and whether these relationships drive niche partitioning within Bornean forests.
2) This study evaluates how leaf physiological function changes with nutrient availability across a fine-scale edaphic gradient and whether these relationships vary according to tree size. Furthermore, we test whether adjustment of leaf traits allows more generalist species to populate a wider range of environments.
3) We measured 12 leaf traits, including maximum photosynthetic capacity (V_{cmax}), leaf dark respiration (R_{leaf}), leaf mass per area (LMA), minimum stomatal conductance (g_{dark}) and leaf nutrient concentrations, of 218 trees ranging in height from 4.4 to 66.1 m from 13 dipterocarp species within four tropical forest types (alluvial, mudstone, sandstone, kerangas) occurring along an edaphic gradient within plots separated by < 5km in North Borneo.
4) When combining all species, all leaf traits varied consistently in response to soil nutrient availability across forest types except R_{leaf}, $[Mg]_{\mathrm{leaf}}$ and $[Ca]_{\mathrm{leaf}}$. Within species, V_{cmax}, R_{leaf} and LMA were more related to leaf nutrients than tree height, suggesting responses to light availability within these forests are constrained by nutrient availability. Contrasting trait-nutrient relationships were found between forest types, suggesting adaptations to different edaphic environments accommodate different nutrient limitations. Finally, five generalist species found across two forest types displayed limited adjustment in their leaf traits to a shift in forest type, implying low trait plasticity in these species.
5) Our results show dipterocarp species are specialised to narrow edaphic conditions, but the extent of specialisation varies among species and appears unrelated to leaf trait plasticity. Multiple nutrients appear to partition niches and could drive species distributions and high biodiversity within Bornean forest landscapes.

3.2 Introduction

Environmental niche partitioning across species has been suggested as one of the drivers of high biodiversity in tropical forests, based on the hypothesis that competitive exclusion of species is reduced when coexisting species partition key limiting resources (Ricklefs, 1977; Brokaw & Busing, 2000; Paoli *et al.*, 2006; Queenborough *et al.*, 2007; Kitajima & Poorter, 2008). There is significant evidence in support of environmental niche partitioning as an important process determining the assembly of tropical forest communities (Davis & Richards, 1933; Paoli *et al.*, 2006; Queenborough *et al.*, 2007; Chuyong *et al.*, 2011; Katabuchi *et al.*, 2012; Baldeck *et al.*, 2013; Johnson *et al.*, 2017). 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 and/or if they have evolved genetically distinct ecotypes in different habitats. 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 (Paoli *et al.*, 2006; Kitajima & Poorter, 2008; Katabuchi *et al.*, 2012; Esquivel-Muelbert *et al.*, 2017b; D'Andrea *et al.*, 2020). 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 forests of South-East Asia are dominated by the Dipterocarpaceae family, typically comprising at least 20% of stems in a forest (Slik *et al.*, 2003; Brearley *et al.*, 2017). Borneo contains 267 known dipterocarp species, with many species specialised to specific habitats (Nilus, 2004; Paoli *et al.*, 2006; Sukri *et al.*, 2012; Brearley *et al.*, 2017), and with rapid species turnover across fine-scale environmental gradients (Slik *et al.*, 2003; Jucker *et al.*, 2018b; Bongalov *et al.*, 2019). 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 *et al.*, 2018b). Moreover, dipterocarps are dispersed by gravity and gyration, implying that dispersal is not reliant on other taxa and should not limit a species' distribution over the small spatial scales represented by site-level environmental gradients. 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; Vleminckx *et al.*, 2018; Oliveira *et al.*, 2019; Fontes *et al.*, 2020), while the few studies conducted in Asian tropical forests focus on seedlings or small tree size classes, or a more limited subset of performance or leaf traits (e.g. Palmiotto *et al.*, 2004; Baltzer *et al.*, 2005; Russo *et al.*, 2005; Russo *et al.*, 2010; Dent & Burslem, 2016). 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. Fyllas *et al.*, 2009; Patiño *et al.*, 2012; Esquivel-Muelbert *et al.*, 2017a; 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.

In order 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). Under this framework, more acquisitive traits, such as high photosynthetic capacity and low leaf mass per area, are optimal in resource-rich environments, at the cost of higher mortality and tissue turnover, and more conservative traits in resource-poor environments, leading to greater tissue longevity and higher survival at the cost of slower growth rates (Russo *et al.*, 2021). The ability to modify traits in response to resource availability - trait plasticity - has been identified as a key mechanism that allows some species to compete across a wider range of environmental conditions without evolving genetically distinct ecotypes (Whitlock, 1996; Russo & Kitajima, 2016). However, costs associated with achieving trait plasticity may prevent it from being a universal evolutionarily stable strategy within a community (Dewitt *et al.*, 1998; Van Kleunen & Fischer, 2007). Few studies have explored intraspecific trait variation across edaphic gradients in tropical forests and thus the role of trait plasticity in determining plant species ranges is unknown.

Within wet tropical forests, nutrient and light availability are likely to pose the greatest limits to tree growth because of their fundamental role in photosynthesis and carbon gain. Across large nutrient availability 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). Fertile soil conditions support more acquisitive, faster leaf strategies because nutrients are critical to important leaf functions, including photosynthesis, respiration and osmotic control (Evans & Sorger, 1966; Evans, 1989; Reich *et al.*, 1998; Xu *et al.*, 2012). Phosphorus is traditionally considered the predominant limiting nutrient in tropical forests located on old soils (Vitousek, 1984; Vitousek & Farrington, 1997). However, more recent evidence suggests phosphorus limitation may not be universal across tropical forests, with evidence of nitrogen-phosphorus co-limitation (and other important nutrients) found (Wright *et al.*, 2011; Santiago, 2015; Sayer & Banin, 2016; Wright, 2019). In addition to nitrogen and phosphorus, cations are required in several photosynthetic reactions (Evans & Sorger, 1966), but the importance of cation limitation in determining species niches remains largely unknown. The high turnover of dipterocarp species along edaphic gradients in Borneo may be associated with specialised nutrient requirements, in addition to other edaphic factors affecting nutrient uptake such as pH, soil particle size (Sellan *et al.*, 2019) and mycorrhizal associations (Liu *et al.*, 2018). In Bornean lowland forests, leaf nutrient concentrations correlate with soil nutrient availability (Dent & Burslem, 2016), with likely implications for physiological and metabolic processes in these forests. However, previous research on leaf trait variation in Borneo has largely focused on seedlings, saplings or integrative structural and chemical traits, owing to difficulties in canopy access, leaving a large gap in our knowledge of how the response to soil fertility varies with vertical niche space and how trait coordination changes with nutrient availability.

Light is another fundamental control on leaf traits affecting carbon assimilation, with greater light availability selecting for higher photosynthetic capacity, leaf dark respiration and leaf mass per area (LMA) to maximise rates of carbon assimilation and growth (Meir *et al.*, 2002; Poorter *et al.*, 2009; Atkin *et al.*, 2015; Hasper *et al.*, 2017). As trees grow taller, the ability to respond to changing light availability will be driven by the capacity for ontogenetic plasticity in leaf physiology. Studies from the Neotropics and dry deciduous Southeast Asian forests have shown that leaves adjust their physiology, including photosynthetic capacity, to vertical gradients in light availability (Chazdon & Pearcy, 1991; Meir *et al.*, 2002; Leakey *et al.*, 2003; Domingues *et al.*, 2007; Cavaleri *et al.*, 2010; Lloyd *et al.*, 2010; Kenzo *et al.*, 2015). These adaptations to vertical light profiles even persist as the main factor controlling leaf function when other strong environmental stresses, such as drought, are imposed (Bartholomew *et al.*, 2020). Average maximum canopy height of lowland dipterocarp forests generally lies in the range 60 – 80 m, which exceeds the typical height of Neotropical and African forests by 20 - 30 m (Banin *et al.*, 2012). The taller canopy of Southeast Asian forests results in greater vertical stratification with the canopy (Banin *et al.*, 2012; Banin *et al.*, 2014; Jucker *et al.*, 2018b; Shenkin *et al.*, 2019) and may increase the extent and frequency of light limitation in lower canopy strata in these forests. However, 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 *et al.*, 2018b). 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 of steeper gradients in light availability arising from greater height and leaf area index of these forests. However, to date no studies have measured how photosynthetic capacity changes with tree height in Bornean forests and how these vertical gradients in plant function change across forest types with different soil nutrient availabilities and maximum canopy heights, so our understanding of whole-plant responses to environmental conditions is limited.

The Kabili-Sepilok Forest Reserve (herein Sepilok) in Northern Borneo represents an ideal system to study the role of soil nutrients and forest structure on expression of functional traits. This forest is composed of four distinct lowland forest types within the same climatic space due to their close proximity (<5km): alluvial floodplain forests with adjacent mudstone hills (Born *et al.*, 2014), sandstone forests and kerangas heath forest (Nilus, 2004; Jucker *et al.*, 2018b). Differences in soil nutrients, water availability, leaf area index, topography, canopy height and gap fraction, species distribution, biomass and above-ground wood production have all been observed along this gradient in Sepilok (Banin *et al.*, 2014; Dent & Burslem, 2016; Coomes *et al.*, 2017; Jucker *et al.*, 2018b). Most dipterocarp species are only common in one forest type, while a few are more widely distributed generalist species that are relatively common in two forest types, allowing direct comparisons of leaf function to be made across species with wider and narrower environmental niches. Whilst some dipterocarp species are more generalist than others, it should be noted that these generalist species are considerably more specialised than some of the hyperdominant species found in the Neotropics (e.g. ter Steege *et al.*, 2013).

Here we evaluate how edaphic conditions and light availability control leaf-level eco-physiological strategies of 218 trees from 13 species of Dipterocarpaceae (8 highly specialist species and 5 more generalist species) in the Sepilok Forest Reserve. We investigate how plasticity in leaf traits varies with tree height and the degree of edaphic specialism. We tested the following hypotheses:

1) Trees growing in habitats richer in soil nutrient availability will possess more acquisitive leaf traits (higher V_{cmax}, higher R_{leaf}, lower LMA, higher g_{dark}).
2) Photosynthetic capacity and respiration will scale with foliar nutrient concentrations within and across forest types.
3) Leaf traits will scale with tree height and species specialised to nutrient-rich soils will have greater changes in leaf traits with tree height, because of steeper gradients in light availability in nutrient-rich forests.
4) Species found across more than one forest type will modify their leaf traits in response to the different soil nutrient availability across environments and thus have greater intraspecific variability in traits than specialist species.

3.3 Methods

3.3.1 Study site

This study was carried out in Sepilok, Sabah, Malaysia (5°10' N 117°56' E). This 4500 ha 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 3098 mm, 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 dominated by podzols with associated 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, aboveground carbon density and forest structure (Greig-Smith *et al.*, 1967; Dent *et al.*, 2006; Dent & Burslem, 2016; Coomes *et al.*, 2017; Jucker *et al.*, 2018b). Differences in soil nutrient availability exist between forest types (SI Figure 3.1). 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, whilst the kerangas has the shortest canopy of the forest types (Jucker *et al.*, 2018b). Nine permanent 4 ha plots (3 alluvial/mudstone, 3 sandstone, 3 kerangas) were established in 2000 across the distinct forest types and have been intensively monitored since. For more details, see Jucker *et al.* (2018b) and Nilus (2004).

3.3.2 Tree selection

From June to October 2018, we sampled 218 trees (5-160 cm diameter at breast height (DBH), measured at 1.3m; 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. 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*, *Vatica micrantha*; SI Table 3.1). 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. Species were assigned a habitat association (alluvial, mudstone, sandstone, 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) (SI Table 3.2). Our habitat associations match previous studies that have classified habitat associations for dipterocarp species in Sepilok (Baltzer *et al.*, 2005; Baltzer & Thomas, 2007; Dent

& Burslem, 2009; Eichhorn *et al.*, 2010; Born *et al.*, 2014; Born *et al.*, 2015; Margrove *et al.*, 2015; Dent & Burslem, 2016), 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 *et al.*, 2018b): 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. 73m a.s.l.; see SI Figure 3.2). Species associated to two forest types were called generalists for the purpose of this analysis, whilst species associated to just one forest type were classified as specialists. No single species was associated with three or all four forest types (SI Table 3.2); 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 *et al.*, 2017a), 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, Tokyo, Japan) 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). The crown exposure of each tree was assessed following Keeling and Phillips (2007), identifying whether trees were shaded (light scores 1-3) or sunlit (light scores 4-5; SI Figure 3.3).

3.3.3 Leaf traits

Leaves were sampled from a sunlit branch, or a branch from the top of the crown for understory trees, using rope-climbing canopy access. Leaves from cut branches were used to measure twelve leaf traits: maximum photosynthetic capacity (V_{cmax}) and leaf dark respiration (R_{leaf}) standardised to 25 ˚C, abaxial leaf conductance after 30 minutes of dark adaptation (g_{dark}), leaf mass per area (LMA), leaf thickness and leaf nutrient concentrations ($[N]_{\mathrm{leaf}}$, $[P]_{\mathrm{leaf}}$, $[Ca]_{\mathrm{leaf}}$, $[K]_{\mathrm{leaf}}$, $[Mg]_{\mathrm{leaf}}$) (Table 3.1). We present both mass-based and area-based measures of V_{cmax} and R_{leaf} but focus primarily on mass-based traits because our questions focus on resource investment. Full details of trait measurements can be found in the supplementary methods.

Table 3.1: Leaf traits measured in this study and their units

Trait	Unit
$V_{\mathrm{cmax\_mass}}$	μ mol g^{-1} s^{-1}
$V_{\mathrm{cmax\_area}}$	μ mol m^{-2} s^{-1}
$R_{\mathrm{leaf\_mass}}$	μ mol g^{-1} s^{-1}
$R_{\mathrm{leaf\_area}}$	μ mol m^{-2} s^{-1}
LMA	g m^{-2}
Leaf thickness	mm
g_{dark}	mol m^{-2} s^{-1}
$[N]_{\mathrm{leaf}}$	g kg^{-1}
$[P]_{\mathrm{leaf}}$	g kg^{-1}
$[Ca]_{\mathrm{leaf}}$	g kg^{-1}
$[K]_{\mathrm{leaf}}$	g kg^{-1}
$[Mg]_{\mathrm{leaf}}$	g kg^{-1}

3.3.4 Data Analysis

To test hypothesis 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 (V_{cmax}, R_{leaf}, LMA, leaf thickness, g_{dark}, $[N]_{\mathrm{leaf}}$, $[P]_{\mathrm{leaf}}$, $[Ca]_{\mathrm{leaf}}$, $[K]_{\mathrm{leaf}}$ and $[Mg]_{\mathrm{leaf}}$; 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 it improved model quality using AIC scores (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 hypothesis 2, we used standardised major axis regression (SMA), using the package *smatr* (Warton *et al.*, 2012), to test for relationships between V_{cmax} and R_{leaf} 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. 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_{cmax}, R_{leaf} and LMA within each forest.

To test hypothesis 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 test (Bolker *et al.*, 2009; Harrison *et al.*, 2018) by comparing the full linear mixed effects model to a generalised 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. Intraspecific relationships between V_{cmax}, R_{leaf} and LMA 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, 2020).

To test hypothesis 4, we tested for intraspecific differences in V_{cmax}, R_{leaf}, LMA and g_{dark} between forest types for each of the five generalist species (SI Table 3.2) using Mann-Whitney tests. Species were only ever found in two forest types, and never at opposite ends of the fertility gradient. Consequently, tests were always across only two habitat types, comparing a relatively more fertile to a less fertile habitat. In order to account for differences in traits because of differences in canopy exposure, we additionally ran the analysis separately for shaded and sunlit trees. 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 an analysis of variance, we compared models with a constant variance structure to models where the variance structure was allowed to change according to the generalist or specialist classification (Pinheiro *et al.*, 2012). *Shorea johorensis* was removed for this analysis because only large trees were measured for this species.

3.4 Results

3.4.1 Variation in soil conditions and leaf traits across the edaphic gradient in nutrient availability

Soil nutrient availability differed between forest types (SI Figure 3.1). 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 in the concentrations of most nutrients, except for higher exchangeable Mg at 0-5 cm, exchangeable Ca and K at 5-15 cm and 15-30 cm in mudstone forest. The most notable difference between alluvial and mudstone forest was in soil texture, with greater clay and lower sand content in mudstone soils. 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.

All the photosynthetic and morphological leaf traits measured (V_{cmax}, R_{leaf}, LMA, leaf thickness, g_{dark}) varied significantly between all forest types (Figure 3.1f-j). Values of V_{cmax} 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 3.1h). In contrast, mean R_{leaf} was significantly lower in the mudstone forest compared to all other forest types (Figure 3.1g). We found no significant bivariate trait-trait relationships between V_{cmax}, R_{leaf} and LMA in any of the four forests, except a positive relationship between R_{leaf} and LMA in the sandstone forest (SI Figure 3.4).

Leaf nutrient concentrations differed between forest types (Figure 3.1a-e). $[N]_{\mathrm{leaf}}$, $[P]_{\mathrm{leaf}}$ and $[K]_{\mathrm{leaf}}$ followed the same gradient across the forest types: alluvial > mudstone > sandstone > kerangas. Mean $[Ca]_{\mathrm{leaf}}$, was highest in the mudstone forest and lowest in the sandstone forest (Figure 3.1c), whereas mean $[Mg]_{\mathrm{leaf}}$ was greatest in the sandstone and lowest in the mudstone forest (Figure 3.1e). Gradients in leaf nutrient

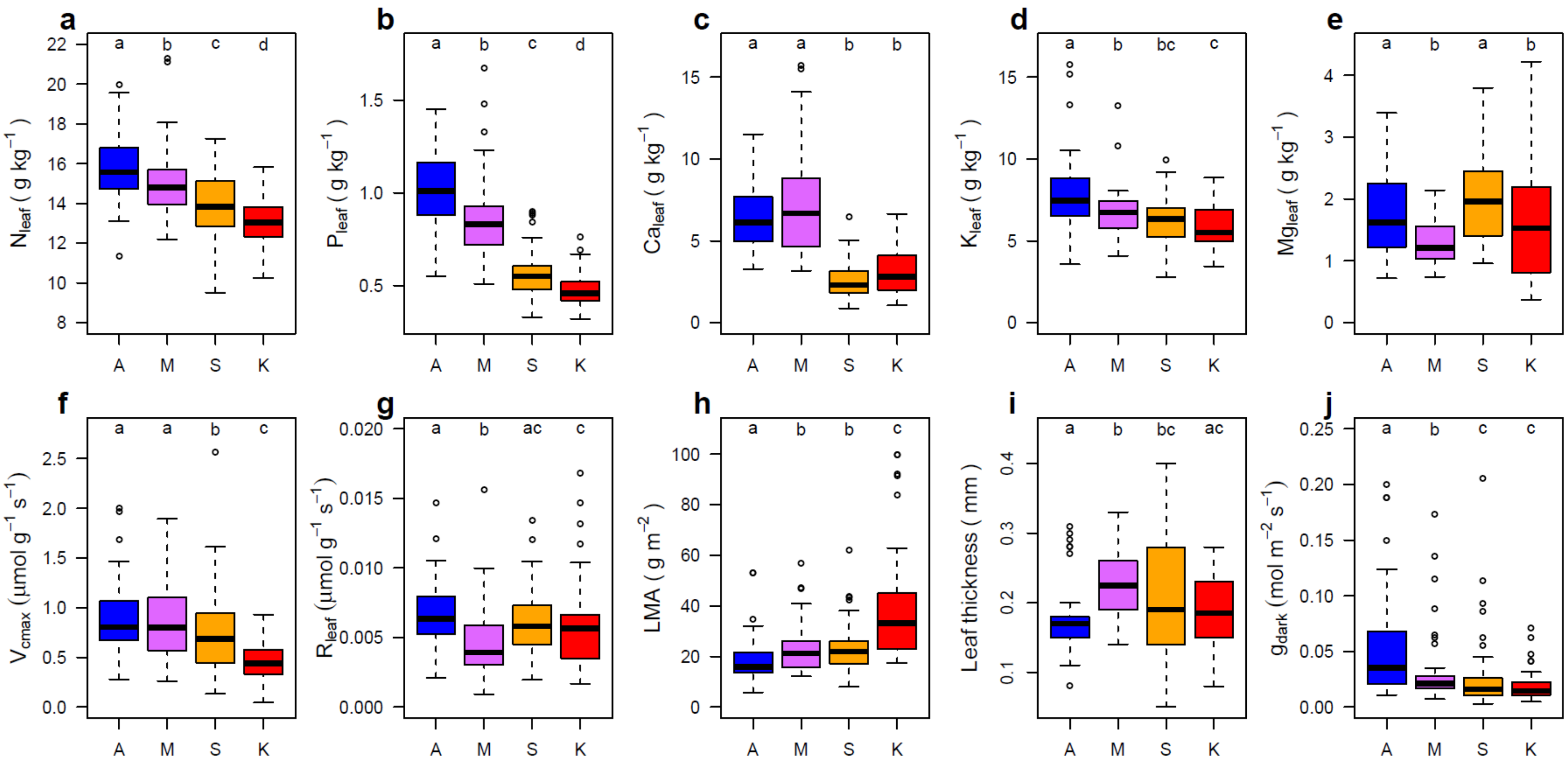

Figure 3.1: Boxplots showing how leaf nutrient concentrations (a-e), V_{cmax} (f), R_{leaf} (g), leaf mass per area (LMA; h), leaf thickness (i) and dark-adapted stomatal conductance (g_{dark}; j) change between the four forests (alluvial (A) – blue, mudstone (M) – purple, sandstone (S) – orange, kerangas (K) – red). Data presented represent individual-level traits (see SI Figure 3.12 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 1.5*interquartile range.

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 $[Mg]_{\mathrm{leaf}}$. Despite no significant differences in soil total N, total P, soluble P, exchangeable K and exchangeable Mg concentrations between alluvial and mudstone soils (except in deeper (15-30 cm) horizons (SI Figure 3.1)), we did find significant differences in $[N]_{\mathrm{leaf}}$, $[P]_{\mathrm{leaf}}$, $[K]_{\mathrm{leaf}}$ and $[Mg]_{\mathrm{leaf}}$ between these forests. Moreover, we found significantly lower $[Mg]_{\mathrm{leaf}}$ in kerangas compared to sandstone forest trees, despite no significant differences in soil exchangeable Mg concentrations at any sampled depth.

3.4.2 Scaling of photosynthetic capacity and respiration with foliar nutrient concentrations

Using standardised major axis regression (SMA), we found V_{cmax} and R_{leaf} were significantly related to leaf nutrient concentrations (Table 3.2; Figure 3.2), but the physiological measures showed significant relationships with different leaf nutrients depending on the forest type. V_{cmax} showed significant positive relationships with $[N]_{\mathrm{leaf}}$ in the alluvial forest, with $[N]_{\mathrm{leaf}}$ and $[P]_{\mathrm{leaf}}$ in the mudstone forest, with $[N]_{\mathrm{leaf}}$, $[P]_{\mathrm{leaf}}$, $[Ca]_{\mathrm{leaf}}$ and $[K]_{\mathrm{leaf}}$ in the sandstone forest and with $[Ca]_{\mathrm{leaf}}$ and $[Mg]_{\mathrm{leaf}}$ in the kerangas forest (Table 3.2; Figure 3.2a-e). Differences in photosynthetic nutrient use efficiency between forests were observed by significant shifts in the intercept of the V_{cmax}-nutrient SMA relationships. Shifts in the intercept of V_{cmax}-$[N]_{\mathrm{leaf}}$ relationships between forests were observed for alluvial vs sandstone ($p = 0.01$), but not between mudstone and sandstone ($p = 0.485$) or mudstone and alluvial ($p = 0.593$). The intercept of the relationship shifted for V_{cmax} and $[P]_{\mathrm{leaf}}$ between sandstone and mudstone ($p < 0.001$) and for V_{cmax} and $[Ca]_{\mathrm{leaf}}$ between sandstone and kerangas ($p < 0.001$). R_{leaf} displayed less consistent relationships with leaf nutrients across forest types; it was positively related to $[N]_{\mathrm{leaf}}$ in the alluvial and kerangas forests and to $[P]_{\mathrm{leaf}}$ in the mudstone, sandstone and kerangas forests. R_{leaf} also showed a negative relationship with $[Mg]_{\mathrm{leaf}}$ in the sandstone forest (Table 3.2; Figure 3.2f-j). We found a significant shift in the intercept of SMA relationships between R_{leaf} and leaf nutrient concentrations showing differences in respiratory nutrient use efficiency between forests. The intercept of the R_{leaf}-$[N]_{\mathrm{leaf}}$ relationship differed significantly between alluvial and kerangas forests ($p < 0.001$) and the R_{leaf}-$[P]_{\mathrm{leaf}}$ relationship differed significantly between mudstone and sandstone ($p < 0.001$) and kerangas ($p < 0.001$), but not for the contrast between sandstone and kerangas forests ($p = 0.051$).

Table 3.2: Summary of standardised major axis regressions between natural log transformed V_{cmax} and R_{leaf} 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
V_{cmax}	$[N]_{\mathrm{leaf}}$	Alluvial	-10.67	**3.77**	**0.151**	**0.010**
		Mudstone	-15.46	**5.63**	**0.203**	**0.006**
		Sandstone	-12.27	**4.50**	**0.244**	**<0.001**
		Kerangas	-14.00	5.15	0.043	0.164
	$[P]_{\mathrm{leaf}}$	Alluvial	-0.22	2.25	0.067	0.095
		Mudstone	0.11	**2.33**	**0.311**	**<0.001**
		Sandstone	1.21	**2.71**	**0.249**	**<0.001**
		Kerangas	0.99	2.44	0.053	0.120
	$[Ca]_{\mathrm{leaf}}$	Alluvial	-2.58	1.29	0.017	0.398
		Mudstone	2.11	-1.25	0.000	0.996
		Sandstone	-1.67	**1.42**	**0.134**	**<0.001**
		Kerangas	-1.75	**0.90**	**0.129**	**0.013**
	$[K]_{\mathrm{leaf}}$	Alluvial	-3.69	1.75	0.012	0.488
		Mudstone	-5.33	2.71	0.072	0.114
		Sandstone	-4.14	**2.05**	**0.109**	**0.003**
		Kerangas	-4.36	1.98	0.000	0.983
	$[Mg]_{\mathrm{leaf}}$	Alluvial	0.38	-1.20	0.003	0.739
		Mudstone	-0.67	2.02	0.003	0.750
		Sandstone	-1.46	1.55	0.001	0.824
		Kerangas	-1.06	**0.81**	**0.224**	**<0.001**
R_{leaf}	$[N]_{\mathrm{leaf}}$	Alluvial	-12.48	**2.69**	**0.122**	**0.023**
		Mudstone	22.09	6.13	0.093	0.059
		Sandstone	-14.09	3.39	0.034	0.101
		Kerangas	-18.53	**5.20**	**0.087**	**0.037**
	$[P]_{\mathrm{leaf}}$	Alluvial	-5.04	1.62	0.008	0.569
		Mudstone	-5.13	**2.20**	**0.202**	**0.004**
		Sandstone	-3.95	**1.99**	**0.140**	**<0.001**
		Kerangas	-3.09	**2.84**	**0.166**	**0.003**
	$[Ca]_{\mathrm{leaf}}$	Alluvial	-3.33	-0.92	0.020	0.374
		Mudstone	-7.88	1.29	0.000	0.973
		Sandstone	-4.33	-0.97	0.024	0.164
		Kerangas	-6.31	1.08	0.039	0.170
	$[K]_{\mathrm{leaf}}$	Alluvial	-7.58	1.27	0.033	0.247
		Mudstone	-10.70	2.77	0.023	0.362
		Sandstone	-7.86	1.50	0.012	0.329
		Kerangas	-8.86	2.09	0.005	0.637
	$[Mg]_{\mathrm{leaf}}$	Alluvial	-5.41	0.82	0.001	0.815
		Mudstone	-5.93	1.97	0.014	0.466
		Sandstone	-4.46	**-1.09**	**0.087**	**0.008**
		Kerangas	-5.50	0.91	0.071	0.062

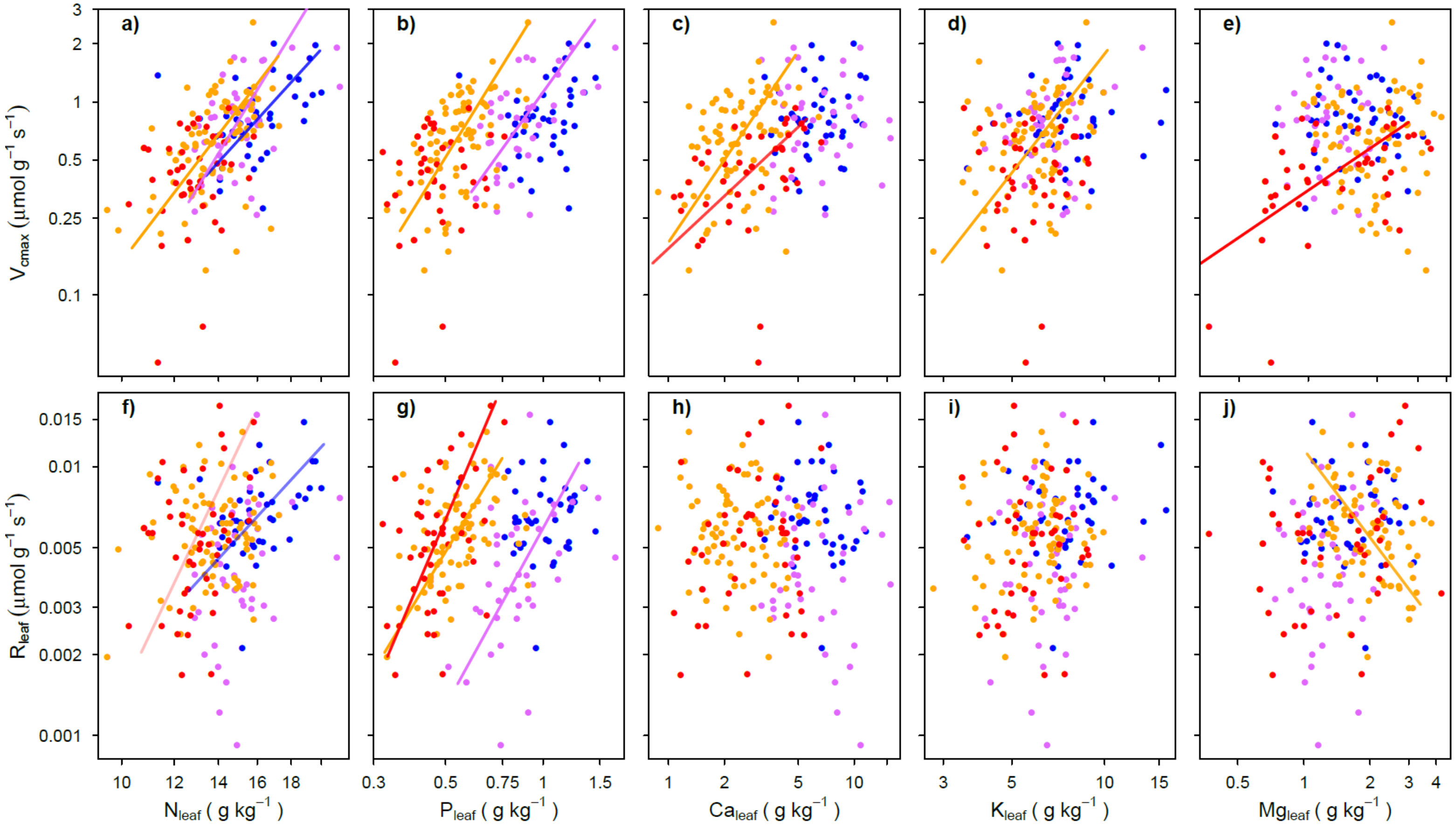

Figure 3.2: Standardised major axis regressions (SMAs) for V_{cmax} (a-e) and R_{leaf} (f-j) with leaf nutrient concentrations ($[N]_{leaf}$ – a & f; $[P]_{leaf}$ – b & g; $[Ca]_{leaf}$ – c & h; $[K]_{leaf}$ – d & i; and $[Mg]_{leaf}$ – e & j). Colours represent the four different forests (blue – alluvial, 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 R_{leaf} –$[N]_{leaf}$ relationship that was weakly significant (see Table 3.2). Note data and axes have been natural log transformed.

3.4.3 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 (R_{leaf}, LMA, leaf thickness, g_{dark}, $[N]_{\mathrm{leaf}}$, $[P]_{\mathrm{leaf}}$, $[Ca]_{\mathrm{leaf}}$, $[K]_{\mathrm{leaf}}$ and $[Mg]_{\mathrm{leaf}}$), except V_{cmax} (Table 3.3; Figure 3.3 & SI Figure 3.5). However, the between-forest differences explained greater variation in leaf traits than tree height (Table 3.3; Figure 3.4). Significant variation was explained through the inclusion of a species random effect term in models for most leaf traits (V_{cmax}, R_{leaf}, leaf thickness, $[N]_{\mathrm{leaf}}$, $[P]_{\mathrm{leaf}}$, $[Ca]_{\mathrm{leaf}}$, $[K]_{\mathrm{leaf}}$ and $[Mg]_{\mathrm{leaf}}$), with the exception of LMA and g_{dark} (Table 3.3). Despite these significant species effects, we also observed large intraspecific variation in leaf traits (SI Figure 3.6). This intraspecific variation was largely not determined by height; when the 12 species were considered individually, no species showed a significant relationship between tree height and V_{cmax} (SI Figure 3.7a), and only five and four showed significant relationships between tree height and R_{leaf} and LMA respectively (SI Figure 3.7b-c). In *D. acutangulus* (sandstone), *D. caudiferus* (alluvial) and *P. tomentella* (alluvial/mudstone), R_{leaf} and LMA both increased with tree height, whilst *C. melanoxylon* (kerangas) only elevated R_{leaf}, but not LMA with height and *S. smithiana* (mudstone/sandstone) only increased LMA with height, but not R_{leaf}. *H. beccariana* (sandstone/kerangas) was the only species to show a negative relationship between R_{leaf} and tree height. This indicates that the significant height effect on leaf traits is driven by strong relationships in a few species rather than a common response across all species.

Table 3.3: Model summaries 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, whilst 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 variance ± standard deviation of the random intercept slope. Dashes are given 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			
$V_{\mathrm{cmax\_mass}}$	log	-0.21 ± 0.14	-0.21 ± 0.15	-0.50 ± 0.16	-0.96 ± 0.19	-				0.08 ± 0.27	0.2125	0.4113
$V_{\mathrm{cmax\_area}}$	log	4.11 **± 0.15**	4.21 **± 0.15**	3.99 **± 0.16**	3.72 **± 0.19**	0.01 **± 0.003**				0.08 ± 0.28	0.1343	0.3589
$R_{\mathrm{leaf\_mass}}$	sqrt	0.99 ± 0.21	0.81 ± 0.21	0.76 ± 0.21	0.84 ± 0.24	0.05 ± 0.06				0.02 ± 0.01	0.1033	0.1953
$R_{\mathrm{leaf\_area}}$	log	-1.02 ± 0.12	-1.28 ± 0.13	-0.91 ± 0.13	-0.77 ± 0.14	0.02 ± 0.002				0.03 ± 0.17	0.2265	0.3245
LMA	1/log	0.39 ± 0.01	0.36 ± 0.01	0.35 ± 0.01	0.31 ± 0.01	-0.001 ± 0.0002				-	0.3570	-
Leaf thickness	-	0.14 ± 0.02	0.14 ± 0.01	0.18 ± 0.02	0.21 ± 0.02	0.001 ± 0.00002				0.003 ± 0.06	0.1793	0.7657
g_{dark}	log	-2.97 ± 0.14	-3.47 ± 0.15	-3.87 ± 0.13	-4.00 ± 0.15	-0.01 ± 0.004				-	0.2360	-
$[N]_{\mathrm{leaf}}$	-	14.85 ± 0.61	15.89 ± 0.76	13.19 ± 0.71	12.65 ± 0.87	0.03 ± 0.01	-0.02 ± 0.02	0.02 ± 0.02	0.02 ± 0.03	1.12 ± 1.06	0.2979	0.5829
$[P]_{\mathrm{leaf}}$	log	-0.08 ± 0.08	-0.08 ± 0.1	-0.76 ± 0.1	-0.77 ± 0.12	0.0005 ± 0.002	0.003 ± 0.003	0.01 ± 0.002	0.004 ± 0.004	0.02 ± 0.13	0.6085	0.749
$[Ca]_{\mathrm{leaf}}$	log	1.89 ± 0.13	1.97 ± 0.11	1.17 ± 0.13	1.08 ± 0.14	-0.01 ± 0.002				0.08 ± 0.29	0.4561	0.7151
$[K]_{\mathrm{leaf}}$	log	2.15 ± 0.10	2.00 ± 0.12	1.68 ± 0.12	1.70 ± 0.14	-0.005 ± 0.002	-0.004 ± 0.003	0.005 ± 0.003	0.005 ± 0.004	0.03 ± 0.17	0.154	0.4854
$[Mg]_{\mathrm{leaf}}$	log	0.56 ± 0.11				-0.01 ± 0.001				0.14 ± 0.37	0.0272	0.7041

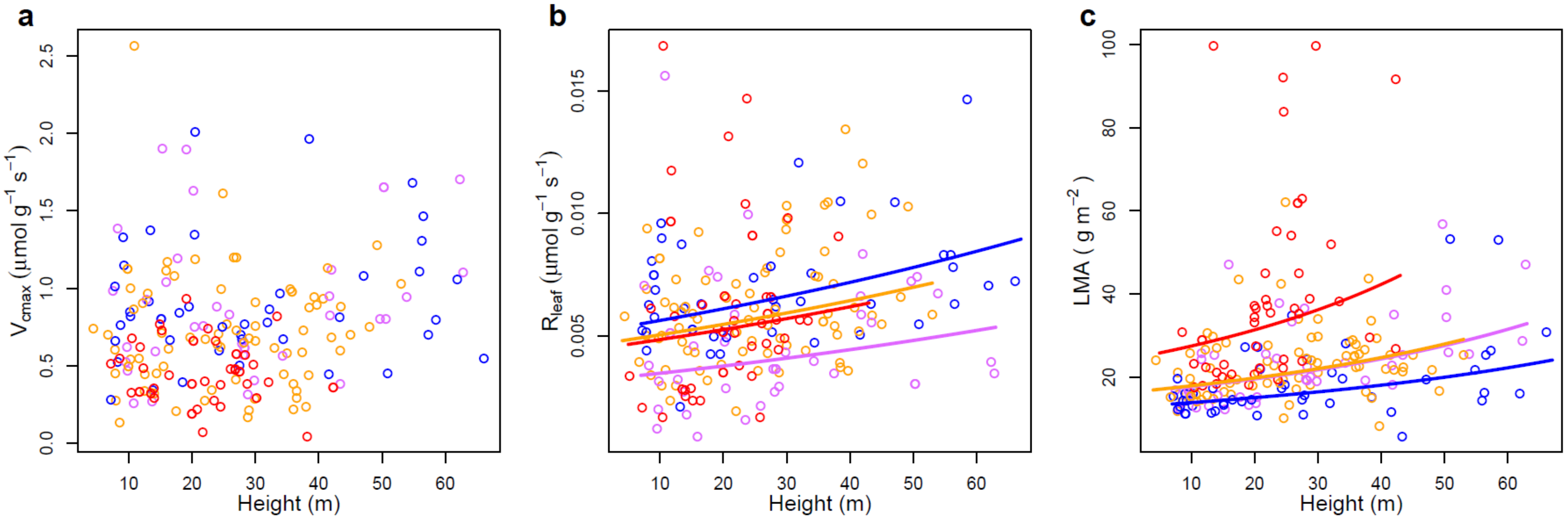

Figure 3.3: Scatterplots showing how V_{cmax} (a), R_{leaf} (b) and leaf mass per area (c) change with tree height. Colours represent the four different forests (blue – alluvial, purple – mudstone, orange – sandstone, red – kerangas). Lines represent predicted fits from the minimal adequate general linear model for each trait (see Table 3.3).

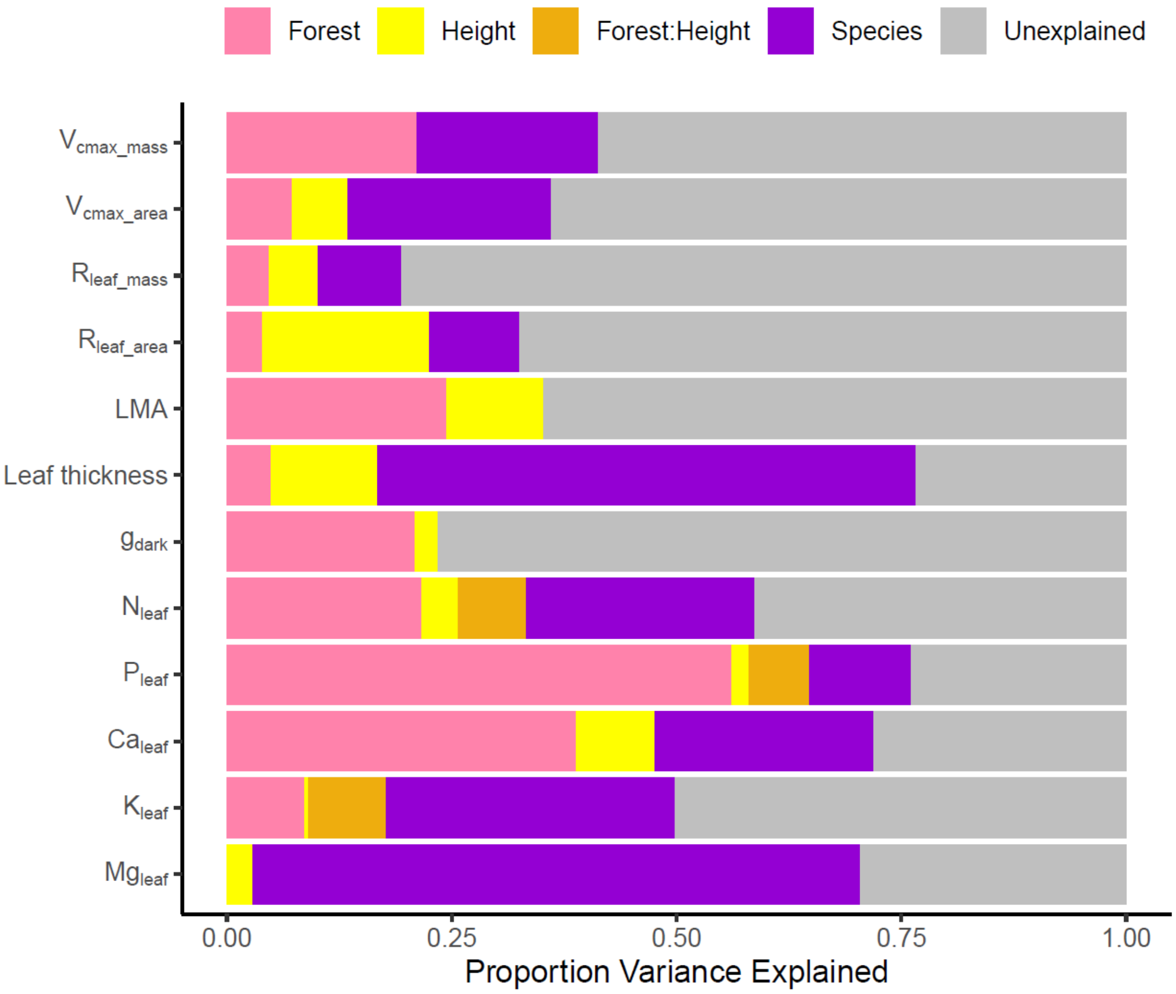

Figure 3.4: Proportion of variance in leaf traits explained by the minimal adequate linear mixed effect model for each trait (see Table 3.3). Forest type (pink), tree height (yellow) and the interaction between them (orange) were included in the models as fixed effects, whilst species (purple) was included as a random effect. Unexplained variance is presented in grey.

After accounting for interspecific trait variation and height in our models, we found significant forest type effects on all traits except $[Mg]_{leaf}$ in our models (Table 3.3). Moreover, we found a significant interaction suggesting that the effect of tree height on $[N]_{leaf}$, $[P]_{leaf}$ and $[K]_{leaf}$ varied according to forest type (Table 3.3). $[N]_{leaf}$ and $[K]_{leaf}$ both increased with tree height, except for $[K]_{leaf}$ in the alluvial forest and $[N]_{leaf}$ and $[K]_{leaf}$ in the mudstone forest where leaf nutrient concentrations declined with tree height. $[P]_{leaf}$ 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 19.5-76.6% of the variation in leaf traits, depending on the trait (Table 3.3), with larger amounts of variation attributable to species identity or forest type than height (Figure 3.4).

3.4.4 Trait modification in generalist species between forest types

Using Mann-Whitney tests, we tested for significant shifts in trait values for each of the five generalist species across the forest types. Across the generalist species we found only three instances (out of 20 tests conducted) of significant differences in V_{cmax}, R_{leaf}, LMA or g_{dark} between the two forest types they occupied (Figure 3.5). The only exceptions were reductions in V_{cmax} in *S. smithiana* (Mudstone: 1.49 ± 0.14, Sandstone: 0.92 ± 0.07, $p = 0.005$) and *H. beccariana* (Sandstone: 0.86 ± 0.05, Kerangas: 0.53 ± 0.05, $p = 0.002$), and an increase in LMA in *H. beccariana* (Sandstone: 20.42 ± 2.39, Kerangas: 46.02 ± 7.50, $p < 0.001$) from the forests with greater rather than lower soil nutrient concentrations (Figure 3.5). These adjustments were driven by variation in traits of shaded trees, except for shifts in LMA in *H. beccariana* that occurred in both sunlit and shaded trees (SI Figures 3.8-3.9).

Compared to specialist species, generalist species had 1.74 times greater standard deviation in V_{cmax} ($p < 0.001$; SI Figure 3.6) and 1.37 times greater standard deviation in leaf thickness ($p = 0.002$). Standard deviation in leaf nutrients was also greater in generalists for $[N]_{leaf}$ (x 1.24, $p = 0.031$), $[P]_{leaf}$ (x 1.41, $p < 0.001$) and $[Ca]_{leaf}$ (x 1.36, $p = 0.003$) than specialists, whilst standard deviation in $[K]_{leaf}$ was 1.07 times greater in specialists ($p = 0.008$). No significant difference in the standard deviation of R_{leaf}, LMA, g_{dark} or $[\mathrm{Mg}]_{leaf}$ was detected between specialist and generalist species.

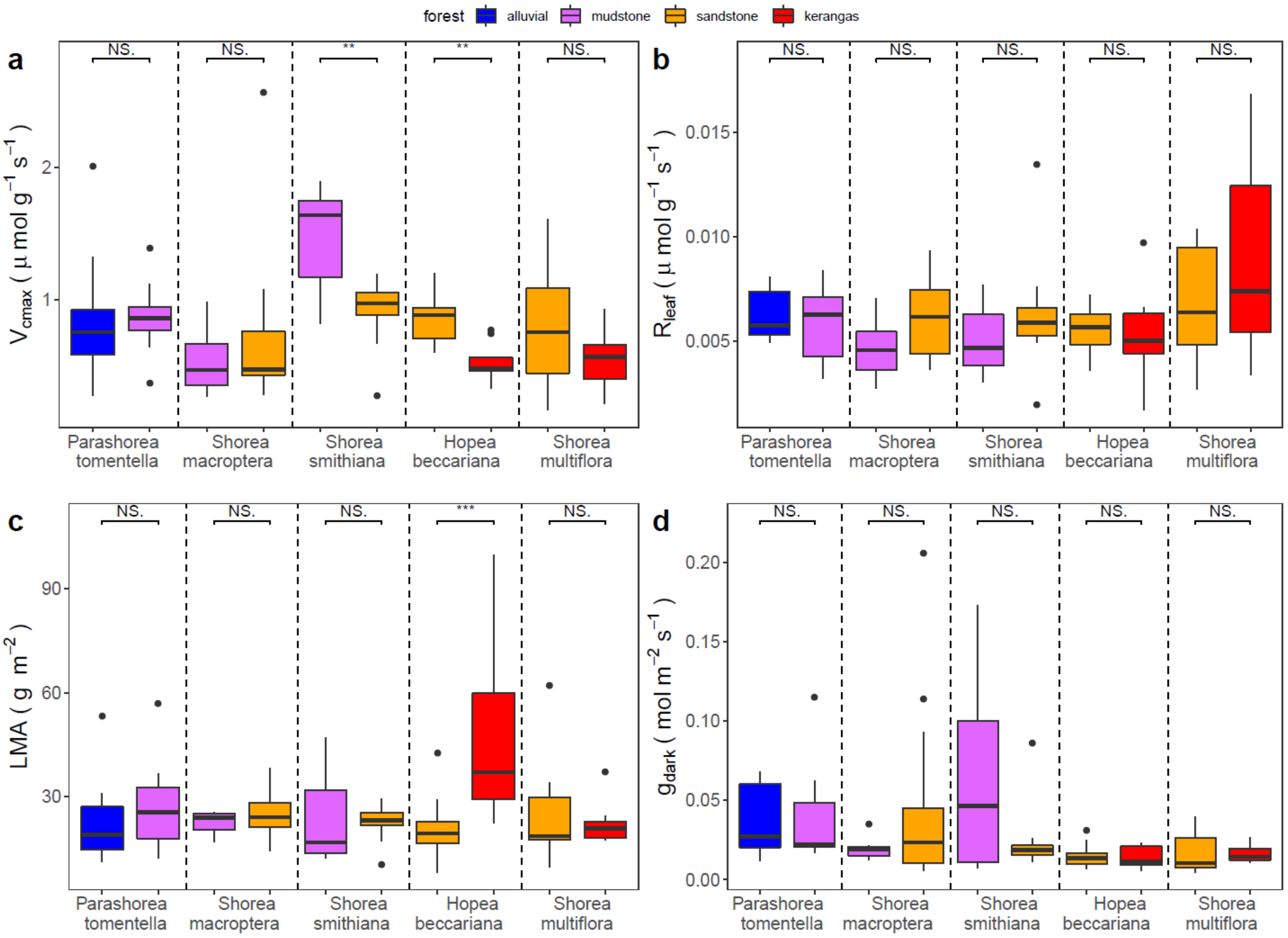

Figure 3.5: Boxplots showing intraspecific differences in V_{cmax} (a), R_{leaf} (b), leaf mass per area (LMA; c) and minimum stomatal conductance (g_{dark}; d) between forests (alluvial – blue, mudstone – purple, sandstone – orange, kerangas – red) for five generalist species. Species were classified according to stem density across the forests (see methods for details). Pairwise comparisons between forests were made for each species using Wilcoxon signed rank tests. Asterisks represent significance levels: NS – $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. 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 1.5*interquartile range.

3.5 Discussion

Our study demonstrates that soil properties are important controls on dipterocarp leaf physiology in Bornean lowland forests. Photosynthetic capacity (V_{cmax}) and leaf dark respiration (R_{leaf}) of dipterocarp trees scale with nutrient availability, although the identity of the nutrient(s) constraining metabolism differed among forest types (Figure

3.2). This constraint on metabolism appears to restrict vertical changes in leaf physiology in response to light gradients, with remarkably little variation in V_{cmax} associated with tree height across all forest types studied (Figure 3.3). The low explanatory power of height on leaf traits (Figure 3.4), surprisingly, suggests limited size-related plasticity and limited effects of local light environments on leaf physiological traits in both specialist and generalist Bornean dipterocarp trees ranging from 5 to 160 cm diameter. Furthermore, generalist species also had limited leaf trait plasticity between forest types (Figure 3.5), although greater variance in leaf nutrient concentrations may support more variable V_{cmax} in generalist species compared to specialists.

3.5.1 Variations in leaf physiology across the edaphic gradient

Most leaf traits, including leaf nutrient concentrations, V_{cmax}, LMA and g_{dark} varied with soil fertility as predicted by the leaf economic spectrum (Wright *et al.*, 2004). Leaves in more fertile forests (alluvial and mudstone) had more acquisitive traits (higher V_{cmax}, higher g_{dark} and lower LMA) than those in low fertility forests (sandstone and kerangas; Figure 3.1). Our findings show that canopy dipterocarp trees follow similar soil-related variation in leaf traits to saplings and other tree families in Bornean forests (Baltzer *et al.*, 2005; Russo *et al.*, 2010; Katabuchi *et al.*, 2012; Dent & Burslem, 2016; Weemstra *et al.*, 2020) and that interspecific variation in traits was significant.

In contrast, R_{leaf} 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_{leaf} in all forests except the alluvial forest, where R_{leaf} was related more closely to $[N]_{leaf}$. This contrasts patterns observed in other regions of the tropics, where leaf nutrient concentrations scale with variation in R_{leaf} across forests because of the respiratory costs typically associated with increases in photosynthetic capacity (Atkin *et al.*, 2015; Rowland *et al.*, 2017). Greater R_{leaf} in the nutrient-poor sandstone and kerangas forests may suggest other factors are driving variation in R_{leaf} in Bornean lowland forests. As R_{leaf} 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_{leaf} in the sandstone and kerangas forests, independent of maximum photosynthetic capacity. The gradient in water availability across the four forest types (SI Figure 3.10) may also explain variation in g_{dark}, as drier conditions select for water conservation and lower leaf conductance (Russo *et al.*, 2010; Schuster *et al.*, 2016; Duursma *et al.*, 2019; Machado *et al.*, 2021). 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.

3.5.2 Nutrient limitation of photosynthetic capacity varies with edaphic conditions

Highly contrasting relationships between leaf nutrient concentrations and maximum photosynthetic capacity were found across our study gradient (Figure 3.2). We observed strong relationships of V_{cmax} with $[N]_{\mathrm{leaf}}$ and $[P]_{\mathrm{leaf}}$ in the nutrient rich alluvial and mudstone forests, whereas V_{cmax} in the nutrient poor kerangas forest was related with cation availability, particularly $[Ca]_{\mathrm{leaf}}$ and $[Mg]_{\mathrm{leaf}}$ (Figure 3.2). 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 3.2). Our results support the notion that V_{cmax} scales more closely with $[N]_{\mathrm{leaf}}$ when $[P]_{\mathrm{leaf}}$ is high (Walker *et al.*, 2014). However, we show that cation availability can also be an important control on V_{cmax}. This supports the emerging perspective from studies across the tropics that multiple nutrients may limit productivity (Sayer & Banin, 2016; Wright, 2019). 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).

3.5.3 Limited vertical leaf trait variation and acclimation to light availability in Bornean forests

In contrast to strong relationships between leaf function and nutrient availability, we did not find as strong relationships between leaf function and tree height, which is the more typical pattern for tropical forest trees (Meir *et al.*, 2002; Domingues *et al.*, 2007; Cavaleri *et al.*, 2010). This may suggest limited acclimation to light in Bornean forests (Table 3.3, Figure 3.3). Some traits including R_{leaf}, LMA and leaf nutrient concentrations did show significant increases with tree height (Table 3.3), suggesting these traits respond to light availability (Poorter *et al.*, 2009; Atkin *et al.*, 2015) or are constrained by height-related increases in hydraulic resistance and gravity (Koch *et al.*, 2004). However, these few cases tended to be caused by a subset of studied species (SI Figure 3.7). Nevertheless, the effect size and variance explained by tree height in our statistical models was low compared to the amount of variance explained by forest type and species (Table 3.3; Figure 3.4), suggesting niches may be more strongly partitioned according to edaphic gradients than light environments. We found no significant forest type-height interaction for any trait except $[N]_{\text{leaf}}$, $[P]_{\text{leaf}}$ and $[K]_{\text{leaf}}$, suggesting that species found within forests with taller canopies and steeper gradients in light availability do not have greater vertical gradients in leaf traits. This provides additional support for the absence of strong environmental niche partitioning with respect to the vertical light gradient for dipterocarps. The absence of a significant change in mass-based V_{cmax} with tree height aligns with the strong theoretical and evidence basis for this trend from Amazonian forests, where area-based increases in V_{cmax} are explained by changes in LMA with height (SI Figure 3.5; Chazdon & Pearcy, 1991; Meir *et al.*, 2002; Domingues *et al.*, 2007; Cavaleri *et al.*, 2010; Lloyd *et al.*, 2010). Even within species, we see very limited adjustment of leaf physiology with tree height (SI Figure 3.7), suggesting the large intraspecific variation we observe may be driven by local edaphic and topographic conditions rather than light availability (SI Figure 3.6). Alternatively, greater canopy height and smaller tree crowns of Asian forests combined with large variations in topography, as observed in Sepilok, may increase horizontal light penetration to the sub-canopy (Loubota Panzou *et al.*, 2020). This horizontal light flux could actually dampen the gradient in vertical light availability. However, logistical challenges associated with accurately measuring and quantifying light availability in tropical forest canopies meant direct measures of light gradients were not possible in this study.

3.5.4 Leaf physiology is conserved within generalist species

Some dipterocarp species within the Sepilok reserve are able to persist across more than one forest type (Baltzer *et al.*, 2005; Margrove *et al.*, 2015; Dent & Burslem, 2016). Yet, we found that most leaf traits (V_{cmax}, R_{leaf}, LMA, g_{dark}) were highly conserved even within these generalist species that crossed from slightly richer to slightly poorer environments. Generalist species predominantly did not shift their mean leaf-level physiology in response to different forest environments, except *Hopea beccariana* (V_{cmax} and LMA) and *Shorea smithiana* (LMA only; Figure 3.5), suggesting either a low degree of trait plasticity within the Dipterocarpaceae family or that adjustment of these traits is not needed for species to persist across forest types. It should be noted that no dipterocarp species is abundant across the full environmental gradient in Sepilok and that even these generalist species are specialised to a narrow range of environmental conditions. Our results indicate it is the high turnover of species between forest environments (Nilus, 2004) that drives between-forest differences in trait values rather than physiological adjustment in co-occurring generalist species. Rather than possessing greater trait plasticity, generalist species may cross forest type boundaries by establishing in small pockets of equivalent soils in different forests. For example, alluvial-mudstone generalist species avoid inundation in the alluvial forest by persisting in marginally elevated microsites (Born *et al.*, 2014; Born *et al.*, 2015). We show that generalists have greater variance in leaf nutrient concentrations ($[N]_{\text{leaf}}$, $[P]_{\text{leaf}}$, $[Ca]_{\text{leaf}}$) and V_{cmax} than specialist species, indicating greater variation of microhabitats inhabited. However, the focus on leaf physiology alone in our study prevents us from testing whether generalist species possess plasticity in other key traits, such as longer leaf lifespans, reduced growth rates, and differences in wood and hydraulic traits (Dent & Burslem, 2009; Russo & Kitajima, 2016; Zhang *et al.*, 2020) or are associated with different communities of mycorrhizal partners (Peay *et al.*, 2015; Liu *et al.*, 2018), which might allow them to tolerate and compete in a wider range of environmental conditions. Alternatively, adult traits may be relatively unimportant if establishment preferences are determined at the seedling stage (Grubb, 1977), or source-sink dynamics facilitate persistence of individuals in non-preferred habitats.

The high niche specificity of dipterocarps to edaphic conditions could potentially leave some species vulnerable to global environmental changes that alter edaphic conditions, such as logging, land use and climate changes (Qie *et al.*, 2017; Rowland *et al.*, 2018a; Swinfield *et al.*, 2020). The highly specific niche requirements may make restoration of lowland mixed dipterocarp forests challenging because the heterogeneity in edaphic conditions needs to be accounted for to achieve effective restoration (Kettle, 2009). Ultimately, any strategy for conservation of dipterocarp species must include maintenance of intact soil environments and areas of undisturbed primary forest.

3.6 Conclusions

Overall, we show that dipterocarp species investigated here found in Bornean lowland forests appear to have limited environmentally-driven plasticity in leaf physiology, suggesting they have highly specialised environmental niches, especially with respect to nutrient availability (Katabuchi *et al.*, 2012). 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. We found that leaf traits in dipterocarps changed across edaphic gradients, with photosynthetic capacity and respiratory rates constrained by leaf nutrient concentrations rather than variation in light regimes determined by canopy height. Our findings highlight the mechanisms for environmental niche partitioning according to nutrient availability in dipterocarp species. Our results also have important implications for the modelling of carbon fluxes in tropical forests as we show different nutrients can constrain photosynthesis and respiration between forest types, including cations, contrasting long-held theories of nitrogen and phosphorus limitation in tropical forests (Vitousek, 1984; Vitousek & Farrington, 1997). We find 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.

Chapter 4: Selective logging increases belowground allocation and dominance of tropical forest seedling communities

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4.1 Abstract

Selective logging is a common form of disturbance to tropical forests, changing micro-environmental conditions and potentially the plant community composition of lowland tropical forests. Recruitment of seedlings is important for the recovery of logged forests, but we lack an understanding of how logging effects seedling physiology, mortality and selection processes, which limits efforts to enhance the resilience and restoration of logged forests. We studied 14 traits of 399 woody plant seedlings from 15 species growing in forests 27 to 39 years after selective logging (n = 204) and compared them to traits of seedlings in neighbouring unlogged primary forests (n = 195) in Sabah, Malaysian Borneo. We also censused seedlings from 183 1 m^2 plots for ~1.5 years (4 censuses) immediately following a mast fruiting event to estimate species annual mortality rates. Seedlings in logged forests had greater community-weighted means (CWM) of belowground biomass allocation and leaf thickness, but lower CWM leaf area per unit shoot area than those in old-growth forest. Specialists of old-growth forest also increased belowground biomass allocation but had reduced foliar nutrient concentrations, higher leaf mass per area and lower specific maximum root length when they recruited in logged forest. Mortality rates did not differ significantly between logged and unlogged forests when compared across all individuals, but they were higher in logged forests for the seven old-growth specialists. Higher foliar nitrogen concentrations reduced mortality in logged forests. Species found in logged forests had a wider range of trait values, but local 1 m^2 functional diversity was reduced because of greater spatial heterogeneity in the dominance of pioneer species. At the community scale, seedlings allocate relatively more biomass to roots and less to leaves in logged forest, which suggests that below-ground resources may be more limiting than light in this environment. Active intervention may be required for old-growth specialists to recruit and for functional diversity and long-term resilience to future environmental change to be maintained in selectively logged tropical forests.

4.2 Introduction

The extent of human-modified forests now exceeds that of intact primary forests across most of the tropics (Laurance *et al.*, 2014). Logging represents a major driver of forest degradation with >20% of tropical forests logged within five years of the turn of the 21st century (Asner *et al.*, 2009). The majority (95%) of tropical timber extraction occurs via selective logging (from herein logging), whereby only the largest and most valuable trees are extracted and a forested landscape of non-target trees is left unharvested (Asner *et al.*, 2009; Edwards *et al.*, 2014). Depending on timber extraction volumes, logged forests can retain much of their functional similarity for animals and can provide valuable habitat and migration corridors for many, although not all, animal species (Meijaard *et al.*, 2005; Wells *et al.*, 2007; Edwards *et al.*, 2011; Putz *et al.*, 2012; Wearn *et al.*, 2017). The effect of logging on plant communities, however, is more varied. Logged forests have been shown to possess similar species diversity of trees >10 cm diameter at breast height (DBH) (Verburg & van Eijk-Bos, 2003; Hector *et al.*, 2011; de Avila *et al.*, 2015; Osazuwa-Peters *et al.*, 2015; Both *et al.*, 2019; Yguel *et al.*, 2019; Hayward *et al.*, 2021), but significantly less diverse sapling communities when compared to nearby unlogged forests (Okuda *et al.*, 2003; Hayward *et al.*, 2021). Both tree and sapling communities of logged forests, however, experience shifts in species and functional composition (Baraloto *et al.*, 2012; Carreño-Rocabado *et al.*, 2012; Osazuwa-Peters *et al.*, 2015; Both *et al.*, 2019; Yguel *et al.*, 2019; Hu *et al.*, 2020), but the effects of logging on seedling communities remains largely unknown. An increased understanding of seedling function and mortality is crucial for predicting long-term shifts in taxonomic and functional composition of logged forests and to improve management for their recovery (Chazdon, 2003; Bagchi *et al.*, 2011).

On the island of Borneo, logging is actively being undertaken in 42% of its forests (Gaveau *et al.*, 2014). The abundance of valuable timber species and rapid post-colonial economic development has resulted in greater timber exports from Borneo than from Africa and Amazônia combined (Brookfield & Byron, 1990; Curran *et al.*, 2004). Timber of species from the Dipterocarpaceae family is especially valuable, with 97% of large canopy dipterocarps harvested during logging events in Indonesian Borneo (Curran *et al.*, 1999; Curran & Webb, 2000). Dipterocarps represent the dominant family of Bornean lowland forests, comprising >20 % of trees and >40 % of forest basal area (Lee *et al.*, 2002; Slik *et al.*, 2003), whilst also contributing to notably high aboveground carbon stocks, wood production rates and great canopy heights (Banin *et al.*, 2012; Banin *et al.*, 2014; Shenkin *et al.*, 2019). Bornean forests rely predominantly on mast flowering and fruiting events for recruitment, with many species reproducing simultaneously at 2-6 year intervals (Sakai, 2002). The loss of large reproductively mature trees as a consequence of logging has reduced the frequency and intensity of these mast events (Curran *et al.*, 1999). The recruitment of dipterocarp and other large tree species during these increasingly rare mast events is therefore of critical importance for the recovery of forest structure, aboveground carbon storage and economically valuable timber.

Logging practices typically remove the largest trees from a forest (Slik *et al.*, 2013), reducing total forest basal area (Riutta *et al.*, 2018) and changing vertical forest structure (Cazzolla Gatti *et al.*, 2014; Milodowski *et al.*, 2021). The removal of canopy trees increases canopy openness of forests and understory light availability, with foliar density, as measured by plant area index, >50 % lower in heavily logged forests (Milodowski *et al.*, 2021). Given that most seedlings in intact tropical forests rely on diffuse light and sunflecks for much of their photosynthesis (Chazdon & Pearcy, 1991), logging causes a large increase in direct light availability for seedlings. Following disturbance events, such as logging, light demanding species frequently emerge and outcompete shade tolerant species (Slik *et al.*, 2002). Logging has been shown to shift community weighted mean traits of established trees to be more acquisitive (Baraloto *et al.*, 2012; Carreño-Rocabado *et al.*, 2012; Both *et al.*, 2019). Given this, we might expect a similar shift in seedling traits to occur in response to increased light availability following logging. Seedlings of pioneer species (sensu Swaine & Whitmore, 1988) typically have a greater capacity to acclimate photosynthesis under higher light environments than seedlings of non-pioneer species that are vulnerable to photoinhibition (Riddoch *et al.*, 1991; Strauss-Debenedetti & Bazzaz, 1991; Lovelock *et al.*, 1994; Zipperlen & Press, 1996; Silvestrini *et al.*, 2007). Whilst seedlings of some non-pioneer species might be able to respond to increases in light availability, responses are likely to be dependent on water and nutrient availability (Bungard *et al.*, 2000; Brenes-Arguedas *et al.*, 2011; Kupers *et al.*, 2019).

Along with light, changes to the canopy structure following logging also changes several other abiotic environmental conditions. Logging reduces the microclimatic buffering provided by the subcanopy, with hotter and drier conditions increasing understory vapour pressure deficits (Hardwick *et al.*, 2015; Blonder *et al.*, 2018; Jucker *et al.*, 2018b; De Frenne *et al.*, 2021). Timber is frequently extracted from tropical forests using heavy machinery that also causes increased soil erosion (Baharuddin *et al.*, 1995; Sidle *et al.*, 2004), soil compaction (Ziegler *et al.*, 2006) and surface run-off (Baharuddin *et al.*, 1995). These changes to physical soil properties may reduce the availability of water and nutrients to seedlings. Logging can cause additional nutrient losses alongside soil erosion via leaching, gaseous emissions and direct removal of nutrients in timber and leaf litter from the largest trees' crowns (Quinton *et al.*, 2010; Cleveland *et al.*, 2011). Changes to soil conditions following logging can also drive changes to the fungal communities of tropical forests (McGuire *et al.*, 2015; Chen *et al.*, 2019), affecting access to nutrients via reduced litter decomposition and reduced mycorrhizal associations (McGuire *et al.*, 2015; Both *et al.*, 2017). Greater abiotic stress, including reduced nutrient availability and higher vapour pressure deficits, is expected to promote a shift towards more conservative traits that promote resource retention over acquisition. Community weighted mean values of specific leaf area and foliar P concentrations were lower in canopy trees in logged than nearby unlogged Bornean forests, which indicates a shifter towards a more conservative strategy in response to nutrient limitation (Swinfield *et al.*, 2020). Seedlings are likely to experience contrasting selective pressures in logged forests from increased light availability and greater abiotic stress, but it remains unknown whether and how seedlings respond to these selective pressures.

It is well-established that plants display a fast-slow continuum of life history and functional trait strategies (Wright *et al.*, 2004; Reich & Cornelissen, 2014; Salguero-Gomez *et al.*, 2016). Seedlings of most old-growth tropical forest species typically have high shade tolerance and low mortality rates, whilst pioneer species tend to be more shade intolerant and have faster growth rates and more acquisitive traits in open, disturbed sites (Swaine & Whitmore, 1988). Given a shift towards more open canopies and greater light availability in logged forests, it might be expected that seedling communities would shift towards expressing more acquisitive aboveground strategies, with traits such as lower leaf mass per area (LMA) and larger leaf area (Poorter & Bongers, 2006; Boonman *et al.*, 2020; Umaña *et al.*, 2021a). However, it remains unknown whether the release from light limitation offsets the costs of increased abiotic stress caused by logging that could promote more conservative traits, such as higher LMA and lower leaf area : shoot area to conserve water (Mencuccini *et al.*, 2019). Meanwhile lower soil water and nutrient availability in logged forests are likely to select for specific root trait strategies (Boonman *et al.*, 2020). Shifts in biomass allocation towards greater belowground investment may be necessary to uptake enough water and nutrients in order to capitalise on the increased light availability in logged forests

(Larson & Funk, 2016; Umaña *et al.*, 2020a). Greater root length to shoot length ratios (RS) and root mass fractions (RMF) are common in drier environments as a strategy to access deeper water (Markesteijn & Poorter, 2009; Larson & Funk, 2016; Boonman *et al.*, 2020), whilst higher RMF and tougher leaves are strategies to overcome nutrient limitation in seedlings (Andersen *et al.*, 2014). Revealing how traits at both the community and species levels differ between logged and primary forests and how they affect mortality rates can give important insights into how logging changes selection pressures.

Old-growth forests of Borneo are typically dominated by dipterocarp species that tend to be highly specialised, confined to a narrow set of environmental conditions and have low trait plasticity (Nilus, 2004; Bartholomew et al. in review, Bittencourt et al. in review). Novel environmental filters introduced by logging, such as increased drought sensitivity, may therefore prevent the seedlings of many old-growth species, such as dipterocarps, from recruiting (Qie *et al.*, 2019). However, it remains unknown whether species that dominant old-growth forests can adjust their traits and avoid mortality in logged forests. High mortality of these species in logged forests could reduce taxonomic and functional diversity and redundancy, with negative impacts on ecosystem processes and resilience to environmental change (Tilman, 1997; Schmitt *et al.*, 2020). Whilst logging has been found to change community weighted mean traits, it did not change functional diversity in established tree communities (Both *et al.*, 2019). However, the recruitment of some trees in these communities is likely to have preceded any logging activities, preventing us from predicting the long-term impacts of logging on forest dynamics and the necessary intervention needed for successful restoration of old-growth forests. Revealing the extent of plasticity and survival rates of seedlings from old-growth species, as well as changes to functional diversity and redundancy, will be critical for predicting the ability of forests to recover and to identify what intervention is required to accelerate the recovery of logged forests.

In this study, we compare functional traits of 399 seedlings from 15 species following a general masting event in North Borneo between old-growth primary forests and neighbouring forests 27-39 years following selective logging. We measured 14 leaf and root traits, including foliar nutrient concentrations, relative above- versus belowground investment and key traits from the plant economics spectrum (e.g. LMA; Reich & Cornelissen, 2014). More specifically, we answer the following questions:

1) How does selective logging affect seedling community-weighted mean traits?
2) Do old-growth species adjust traits in response to selective logging?
3) How does selective logging affect seedling mortality and does this vary between species found in both primary and logged forests and those restricted to one forest type?
4) Does logging change how functional traits affect mortality?
5) How does selective logging affect functional diversity and redundancy?

4.3 Methods

4.3.1 Study site

This study was carried out in the unlogged primary forest of Danum Valley Conservation Area (DVCA) and the adjacent selectively logged forest of Ulu Segama Forest Reserve (USFR; 4˚ 58’ N, 117˚ 52’ E). DVCA is located in the upper catchment of the Segama River in Sabah, Malaysia and is comprised of 438 km^2 of lowland dipterocarp forest and lower montane rainforest (Marsh *et al.*, 1997; Reynolds *et al.*, 2011). More details of the DVCA forest can be found in Newbery *et al.* (1997) and Walsh and Newbery (1999). The reserve borders a 10,000 km^2 logging concession that has been selectively logged (Reynolds *et al.*, 2011). Mean annual rainfall at this site is 2305 mm and the mean daily temperature is 25.8 ˚C (Fick & Hijmans, 2017).

The region of USFR adjacent to DVCA that was sampled for this study was logged between 1981 and 1993 (Foody & Cutler, 2003). This region was divided into annual logging coupes of approximately 27 km^2 with all commercially valuable trees of >60 cm diameter at breast height harvested (Foody & Cutler, 2003). Logging intensity was typically high (mean 118 m^3 ha^{-1} from 1970 to 1990) but it varied between and within coupes (Foody & Cutler, 2003). Trees were extracted by tractor on moderate terrain and by high-lead on steep slopes (Pinard *et al.*, 2000). In 1993, an additional trial of Reduced Impact Logging (RIL) was established, whereby climbers were cut prior to felling, trees were directionally felled, and harvest and skid-trails were planned to minimise damage to non-target vegetation (Pinard & Putz, 1996; Pinard *et al.*, 2000). Silvicultural intervention was undertaken in a subset of coupes to actively restore the forest as part of the Innoprise-FACE Foundation Rainforest Rehabilitation Project

(INFAPRO; Face the Future, 2011). For all other coupes the forest was left to recover naturally (Face the Future, 2011). More details about the active restoration can be found in Face the Future (2011) and Hayward *et al.* (2021).

4.3.2 Seedling inventory and mortality rates

Seedling plots of size 1 m^2 were established within both the primary forest of DVCA and the logged forest of USFR in September to October 2019 following a mast fruiting event. In the unlogged primary forest, 87 seedling plots were established within the ForestGEO Danum Valley 50 ha forest dynamics plot (Anderson-Teixeira *et al.*, 2015; Davies *et al.*, 2021). Meanwhile, 96 seedling plots were established in the logged forest (52 actively restored; 44 naturally regenerating) within the Indicators of Forest Sustainability (INDFORSUS) project research plots (Foody & Cutler, 2003; Philipson *et al.*, 2020). Seedlings were censused four times between September 2019 and March 2021: (1) September-October 2019, (2) November-December 2019, (3) January-May 2020 and (4) February-March 2021. Each seedling was identified to species level in the field and verified by taxonomic experts at the Forest Research Centre, Sepilok herbarium. Species-level mortality rates were calculated for each seedling plot following Sheil *et al.* (1995):

$$m = 1 - (N_1/N_0)^{1/t} \quad (1)$$

m = mortality per year; N_1 *= population at end census;* N_0 *= population at start census; t = years between censuses.*

The populations at the first and last census was used, except when all seedlings were found dead in the last census. For these cases, the time interval was calculated up until the first census when no seedlings remained alive. For instances when the population increased following the first census because of late germination, the start census was set to that with the greatest population. Mortality rates were calculated for the 15 species that were sampled for traits (see below) with initial abundance ranging from 1 to 95 individuals (mean = 12.5 individuals).

4.3.3 Trait sampling

We measured traits of 399 seedlings from 15 species in January-February 2020 across the primary (n = 195 seedlings) and logged (n = 204 seedlings) forests (SI Table 4.1). The precise age of seedlings was unknown, but most seedlings germinated approximately six months prior to sampling shortly after the mast fruiting event.

Seedlings were sampled from 75 1m^2 seedling plots (46 primary; 26 logged). Of the 26 plots in logged forests, 19 plots are found within actively restored forests and seven in forests with no active intervention. It was not possible to sample seedlings from many of the logged forest plots because of high mortality in the six months between the masting event and our sampling campaign, or because of difficult access to the plots. Species selection followed a mixed approach to ensure that species representing >80 % of seedlings on the plots were sampled and to allow intraspecific comparisons between forest types to be made. Seven species (*Agelaea* sp., *Dryobalanops lanceolata*, *Koompassia excelsa*, *Parashorea malaanonan*, *Shorea johorensis*, *Shorea leprosula* and *Shorea parvifolia*) were found in >1 seedling plot and sampled in both primary and logged forest, except for *D. lanceolata* that was only sampled in logged forest because seedlings could not be located in the primary forest. These seven species are herein referred to as common species. Three additional species were sampled only from primary forest (*Parashorea tomentella*, *Shorea seminis* and *Spatholobus* sp.) and five additional species only from logged forest (*Buchanania sessifolia*, *D. lanceolata*, *Intsia bijuga*, *Pterospermum javanicum*, *Shorea fallax* and *Shorea macrophylla*). Most of the studied species, including the nine dipterocarp species, grow to canopy or emergent trees except for *B. sessifolia* that grows up to 20 m and *Agelaea* sp. and *Spatholobus* sp. that are lianas. For each species at each plot, three seedlings were collected just outside of the permanent seedling plot. We avoided collecting inside the plots to allow continued monitoring of population dynamics. In order to get sufficient material for foliar nutrient analyses, an additional ten seedlings were collected and combined with the three seedlings used for trait measurements prior to analysis. Where seedlings were unavailable in the immediate vicinity because of high mortality, additional samples were taken c. 20-40 m from the seedling plot to allow for replication and improved estimates of the species' mean trait value.

We measured 14 traits on each seedling: leaf mass fraction (LMF), root mass fraction (RMF), leaf mass per area (LMA), leaf thickness, leaf force to punch (LFP), leaf area to shoot area ratio (LA:SA), root length to shoot length ratio (RS), specific maximum root length (SMRL), leaf calcium (Ca_{leaf}), magnesium (Mg_{leaf}), nitrogen (N_{leaf}), phosphorus (P_{leaf}), and potassium (K_{leaf}) concentrations per unit mass and leaf nitrogen to phosphorus ratio (N:P). Seedlings were collected in the morning before being transferred to the Danum Valley Field Centre for trait measurements. Seedlings were cut in the field immediately after harvest at the base of the stem to separate above- and belowground organs before being sealed in moist ziplock bags to minimise water loss during transfer. For each seedling, the length of the longest root and shoot length were measured using a ruler and shoot diameter was measured just below the first branch using precision callipers. Shoot diameter was converted into shoot cross-sectional area based on the assumption that all shoots were circular. To calculate leaf area, all leaves were scanned using a flatbed scanner (CanoScan LiDE 120, Canon Inc., Tokyo, Japan) and analysed using ImageJ software in the R package LeafArea (Katabuchi, 2015). Leaf thickness was measured on three leaves, where available, using precision callipers avoiding any major veins and a mean was calculated. LFP was measured at three points on the leaf using a Chantillon DFXII Digital Force Gauge with a 1 mm^2 flat head rod (AMETEK Sensors, New York, USA) and the mean was calculated. Leaves, shoots and roots were air-dried before being transferred to the Forest Research Centre, Sepilok, where they were dried to constant weight in an oven at 50 ˚C before being weighed. LMF and RMF were calculated by dividing dry leaf and dry root mass by total dry mass, respectively. LMA was calculated by dividing dry leaf mass by leaf area. LA:SA was calculated by dividing leaf area by the cross-sectional area of the shoot, RS by dividing root length by shoot length and SMRL by dividing maximum root length by dry root mass.

The leaves of the sampled seedlings were combined with the additional sample material from the same plot before being analysed for foliar nutrient concentrations at the Forest Research Centre, Sepilok. Leaves were ground using a SM2000 Heavy-duty Cutting Mill (Retsch, Haan, Germany) to pass through a 100-mesh (212 μm) sieve. The leaf samples were digested using a hydrogen peroxide-sulfuric acid digestion (Allen, 1989). N_{leaf} and P_{leaf} were measured colorimetrically using an Astoria-Pacific Flow Analyzer (Astoria-Pacific, OR, USA). Ca_{leaf}, K_{leaf} and Mg_{leaf} were measured spectrometrically using a SpectroArcos FHX22 (Spectro Analytical Instruments, Kleve, Germany). A subsample of the leaves was dried at 105 ˚C to constant weight to calculate the percentage moisture content and to correct laboratory analyses to an oven dry basis. N:P was calculated by dividing N_{leaf} by P_{leaf}.

4.3.4 Data analysis

To test for differences in community-level traits between primary and logged forests, we calculated and compared community weighted mean (CWM) trait values. CWMs are calculated by weighting species mean trait values in each forest type by the abundance of that species in each plot (Pla *et al.*, 2012). For species where traits were not measured, the mean value for all species in that forest type was used. To compare differences in CWM traits, we used Mann-Whitney tests using the *wilcox.test* function in the R *stats* package (R Core Team, 2020). We used principal component analysis (PCA) to examine axes of variation in foliar nutrient and non-nutrient CWM traits between primary and logged forests using the R package *FactoMineR* (Lê *et al.*, 2008; Husson *et al.*, 2011), with traits centred and scaled to their unit variance. We separated these traits to understand how differences in structural traits affects access to nutrients. Differences between the mean PCA trait axes for primary and logged forests were tested by comparing 95% confidence intervals of the mean CWM using the R package *factoextra* (Kassambara & Mundt, 2017).

To test for intraspecific adjustment of traits between primary and logged forests, we fitted linear mixed effects models using the R package *lme4* (Bates *et al.*, 2014). Each trait was modelled with forest type (primary versus logged) as a fixed effect and seedling plot nested in species as a random intercept effect to account for our sampling design. For foliar nutrients, species was included as the random intercept. We compared models with and without the forest fixed effect using log-likelihood tests and the Akaike Information Criterion (AIC; Sakamoto, 1994). We additionally tested for taxonomic differences in the size and direction of trait adjustments to logging by comparing the full model with random species intercept and/or a random slope effect to a generalised least squares model following Zuur *et al.* (2009). Low sampling effort for some species meant testing for a species random slope effect was not possible for some traits. In order to understand how each species adjusts their traits, we additionally compared traits between primary and logged forests using Mann-Whitney tests, analysing each species separately, whilst accepting the limitations of the sample size and statistical power.

We calculated the mean seedling mortality rate for each species in both primary and logged forests and compared differences in species-level mean mortality rates between forest types using a Mann Witney test. In order to understand whether differences in mortality rates observed at the community level were driven by differences in species composition or by differential mortality of species that are found in both forest types, we repeated the test for the seven species found in both forests. We used general linear models with a binomial error structure to understand which traits predicted mortality rates in each forest, using species-level trait means and mortality rates at each sampled plot. We did not include data for samples collected >5 m from the plot. All 14 traits and their interaction with forest type were included in the full model. The best model was selected by backwards stepwise selection according to AIC scores using the *stepAIC* function in the R package *MASS* (Venables & Ripley, 2002).

We calculated species evenness, functional diversity and functional redundancy for each seedling plot using the R package *SYNCSA* (Debastiani & Pillar, 2012). Gini-Simpson's Index was used as a measure of species evenness (Simpson, 1949). Rao's quadratic entropy (Rao's Q) was used as a measure of functional diversity and is calculated by an Euclidean dissimilarity matrix of functional traits (Rao, 1982). Functional Redundancy is calculated as the difference between Simpson's index and Rao's Q (Bello *et al.*, 2007; Pillar *et al.*, 2013). Differences between primary and logged forests were compared using Mann Whitney tests for each diversity index. We additionally investigated the trait space occupied by the community in primary and logged forests using a principal component analysis of species mean trait values, following the same procedure outlined for CWMs. All data analysis was undertaken in R statistical software v. 3.6.3 (R Core Team, 2020).

4.4 Results

4.4.1 Community weighted mean traits

We found significant shifts in the community weighted mean (CWM) for five of 14 measured seedling traits between primary and logged forests (Table 4.1). RMF ($p = 0.009$) and RS ($p = 0.033$) were higher in logged forests, whilst LMF ($p < 0.001$), leaf thickness ($p = 0.040$) and LA:SA ($p = 0.002$) were lower in logged forests compared to primary forests. CWMs of foliar nutrient concentrations, LMA, LFP and SMRL did not differ significantly between primary and logged forests.

Table 4.1: Mean ± standard error for seedling CWM trait values in primary (n = 49) and logged (n = 26) forests. P values are derived from Mann Whitney tests comparing the mean CWM between the two forest types with significant differences at $p < 0.05$ in bold.

Trait	Acronym	Units	Primary	Logged	P
Leaf Mass Fraction	**LMF**	**g g^{-1}**	**0.451 ± 0.003**	**0.415 ± 0.008**	**<0.001**
Leaf Mass per Area	LMA	g m^{-2}	34.6 ± 0.5	34.3 ± 1.0	0.450
Leaf Thickness		mm	**0.075 ± 0.002**	**0.065 ± 0.003**	**0.040**
Leaf force to punch	LFP	N	1.39 ± 0.03	1.38 ± 0.04	0.7739
Leaf area: Shoot area	**LA:SA**	**cm^{2} mm^{-2}**	**6.88 ± 0.64**	**4.48 ± 0.59**	**0.002**
Root Mass Fraction	**RMF**	**g g^{-1}**	**0.155 ± 0.002**	**0.175 ± 0.007**	**0.009**
Root Length: Shoot Length	**RS**	**mm mm^{-1}**	**0.389 ± 0.01**	**0.441 ± 0.02**	**0.033**
Specific Maximum Root Length	SMRL	mm g^{-1}	142.6 ± 5.1	162.0 ± 14.9	0.949
Leaf N	N_{leaf}	mg g^{-1}	21.8 ± 0.6	22.8 ± 0.8	0.097
Leaf P	P_{leaf}	mg g^{-1}	1.65 ± 0.03	2.14 ± 0.19	0.054
Leaf Ca	Ca_{leaf}	mg g^{-1}	5.23 ± 0.14	5.65 ± 0.43	0.819
Leaf K	K_{leaf}	mg g^{-1}	11.8 ± 0.3	13.1 ± 0.6	0.610
Leaf Mg	Mg_{leaf}	mg g^{-1}	2.91 ± 0.1	3.19 ± 0.3	0.652
Leaf N:P	N:P	g g^{-1}	13.3 ± 0.3	12.6 ± 0.8	0.382

The first axes of a principal component analysis (PCA) of CWM traits explained 63.4% of the variance in the data (Fig. 4.1a; SI Table 4.2a). The first PCA dimension was explained by covariance in resource acquisition traits – LA:SA (24.0%), SMRL (23.8%), leaf thickness (21.8%) and LMA (14.6%), whilst the second PCA dimension was explained by root investment – RMF (41.0%) and RS (39.4%). We found a significant shift in the overall trait strategy between primary and logged forests, with no overlap of the 95% confidence interval of the mean CWM on dimensions one and two of our trait PCA (Fig 4.1a; SI Table 4.2a). Seedling communities in logged forests

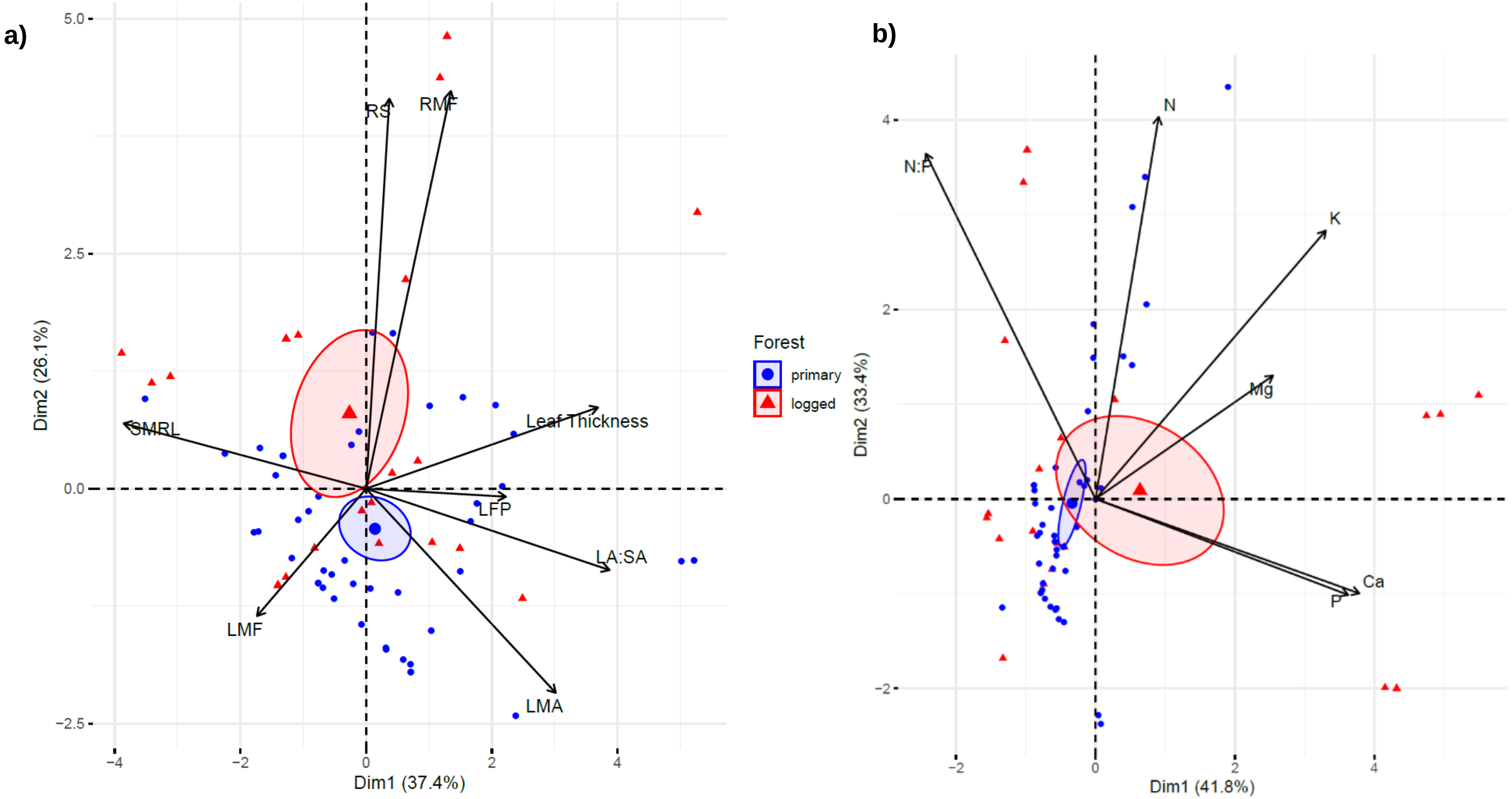

Figure 4.1: Principal component analysis for community-weighted mean (CWM) trait values for (a) non-nutrient traits and (b) foliar nutrient concentrations. For weighting of each variable on each dimension, see SI Table 4.2. Ellipses represent the 95% confidence interval for the mean CWM for primary (blue circles) and logged (red triangles) forests. Points represent the CWM for each seedling plot, with the larger point representing the mean.

had more acquisitive traits (i.e. lower LMA, thinner leaves, higher SMRL; Dimension 1) and greater investment in roots over leaves (Dimension 2) than seedling communities in primary forests. There was no shift in CWM when visualising foliar nutrient concentrations with a PCA that differentiated between primary and logged forests (Fig. 4.1b; SI Table 4.2b). No significant differences in CWMs trait values were found when comparing between actively restored and naturally regenerating logged forests (SI Figs 4.1-4.2).

4.4.2 Intraspecific adjustment of traits

We tested for intraspecific adjustment of traits for the six species that were sampled in both primary and logged forests using mixed effect models. We found significant shifts in nine of 14 traits between forest types (Table 4.2; SI Figs 4.3-4.4). Seedlings in logged forests had 1.47 g m^{-2} higher LMA ($p = 0.012$) and 26.6 mm g^{-1} lower SMRL ($p = 0.013$) compared to those in primary forests. Seedlings also increased investment in roots over leaves by increasing RMF by 0.024 ($p = 0.016$) and by reducing LMF by 0.038 ($p < 0.001$) in logged forests compared to primary forests. Foliar nutrient concentrations were significantly lower in logged forests for all nutrients except Mg_{leaf}, although significant decreases in Mg_{leaf} were observed for *P. malaanonan* and *S. parvifolia*, and increases in Mg_{leaf} in *K. excelsa* and *S. leprosula* in logged forests compared to primary forests (Table 4.2). N:P was 0.624 higher ($p = 0.013$) in logged forests than primary forests. For traits where a species random slope effect model could be fitted, we found a significant random species slope effect in our models for all traits where a significant difference between logged and unlogged forests was found, and hence found intraspecific adjustment of traits to vary between species (Table 4.2). A significant reduction in foliar nutrient concentrations in logged forests was detected in all six species except *S. johorensis*, but not all nutrients were reduced in each species (Table 4.2). *S. johorensis* and *S. leprosula* did not differ significantly in any non-nutrient traits between forests. A significant increase in RMF was detected for *Agelaea* sp., *K. excelsa* and *P. malaanonan*, a significant reduction in LMF in *P. malaanonan* and *S. parvifolia* and a significant increase in LMA in *S. parvifolia* in logged forests. Whilst we detected few significant differences in traits between forests at the individual species-level, low sample sizes per species ($n = 3$ to 30) gave limited power to detect trait differences. We also detected significant differences ($p < 0.05$) in mean trait values between actively restored and naturally regenerating forests for the two species sampled across both restoration treatments. *Agalaea* sp. had higher LMA and leaf N:P, and lower LMF, LFP, N_{leaf}, K_{leaf} and P_{leaf} in actively restored forests, whilst *S. leprosula* had higher leaf N:P and lower RS, RMF, Ca_{leaf}, Mg_{leaf} and P_{leaf} in actively restored forests (SI Figs 4.5-4.6).

4.4.3 Seedling mortality rates

We compared seedling mortality rates between primary and logged forests for all species sampled for functional traits. The mean of species' mean annual mortality rates were not significantly different when comparing all species (primary: 0.686 ± 0.07, logged: 0.752 ± 0.06, p = 0.417), but were significantly higher in logged forest when only comparing the seven species that were common in both forest types (primary: 0.591 ± 0.06, logged: 0.785 ± 0.07, p = 0.038; Fig. 4.2; SI Table 4.3). *Agelaea* sp. had the lowest mean annual mortality rate of all species in both forest types but was still higher in logged (0.443) than primary (0.261) forest. The two species from the Fabaceae family (*I. bijuga* and *K. excelsa*) both had complete mortality in the logged forest, whilst all species from the Dipterocarpaceae family had higher mean annual mortality rates in logged forests (all >0.7) than in primary forests (SI Table 4.3). We found seedlings with higher concentrations of N_{leaf} had lower mortality rates in logged forests ($R^2 = 0.356$, p = 0.032), but found no significant relationships between mortality and any traits in primary forests (Fig. 4.3; SI Table 4.4).

Table 2: Summary of results comparing mean trait values between primary and logged forests for the six species that were sampled in both forest types. Traits were modelled using linear mixed models with forest as a fixed effect and seedling plot nested in species as a random intercept effect, except for foliar nutrients where only a species-level random intercept was used. Mean and standard error (SE) values are presented for the primary forest and the difference (Δ) for logged forests where inclusion of forest type significantly increased the model fit according to log-likelihood tests. The difference in AIC scores (ΔAIC) and p-values between models are presented. Models with a species random intercept and/or slope effect were additionally used to test for a taxonomic effect. The difference in mean trait value in logged compared to primary forest is presented for each species, with asterisks representing the significance level from Mann Whitney tests (*: p < 0.05, **: p < 0.01, ***: p < 0.001). Species mean trait values are presented in SI Table 4.6. Significant effects are presented in bold. Dashes for the species random slope are presented when sampling effort was insufficient for the model to be fitted.

Trait	**Units**	**Primary Forest**		**Δ Logged Forest**				**Species Random Intercept (p)**	**Species Random Slope (p)**	**Intraspecific differences in mean trait value**					
		Mean	**SE**	**Mean**	**SE**	**ΔAIC**	**P**			**AGELAEA**	**KOOMEX**	**PAR2MA**	**SHORJO**	**SHORL1**	**SHORP1**
LMF	$g\ g^{-1}$	0.442	0.02	**-0.038**	**0.01**	-9.83	**<0.001**	**<0.001**	**0.035**	-0.042	-0.038	**-0.092*****	0.007	-0.009	**-0.043****
LMA	$g\ m^{-2}$	31.975	2.74	**1.473**	**0.57**	-4.37	**0.012**	**<0.001**	-	-1.100	1.902	1.083	1.153	0.233	**3.137****
Leaf thickness	mm	0.074	0.01			-0.57	0.109	**<0.001**	0.997	-0.010	0.020	-0.010	-0.010	-0.010	0.000
LFP	N	1.337	0.11			1.48	0.471	**<0.001**	-	0.152	0.127	0.200	-0.200	0.100	-0.100
LA:SA	$cm^{2}\ mm^{-2}$	5.988	1.54			1.37	0.427	**<0.001**	-	-0.719	0.440	-2.140	0.373	0.432	-0.365
RMF	$g\ g^{-1}$	0.165	0.01	**0.024**	**0.01**	-3.76	**0.016**	**<0.001**	**0.003**	**0.062***	**0.112***	**0.050***	0.016	-0.007	0.022
RS	$mm\ mm^{-1}$	0.430	0.05			1.59	0.521	**<0.001**	0.873	0.063	0.088	0.017	0.038	-0.024	-0.006
SMRL	$mm\ g^{-1}$	152.41	17.71	**-26.64**	**10.48**	-4.20	**0.013**	**<0.001**	-	-25.61	-65.77	-17.91	-16.38	-3.85	-28.38
N_{leaf}	$mg\ g^{-1}$	25.335	2.98	**-1.518**	**0.29**	-24.95	**<0.001**	**<0.001**	**<0.001**	**-4.383****	**-4.977****	-1.449	-0.828	-0.046	**-1.417*****
P_{leaf}	$mg\ g^{-1}$	1.723	0.09	**-0.147**	**0.03**	-21.52	**<0.001**	**<0.001**	**<0.001**	**-0.649****	**-0.449****	-0.072	0.003	0.042	**-0.113*****
Ca_{leaf}	$mg\ g^{-1}$	5.394	0.52	**-0.672**	**0.16**	-14.76	**<0.001**	**<0.001**	-	-1.001	**-0.982***	**-1.158****	-0.297	**-1.219****	**-0.849****
K_{leaf}	$mg\ g^{-1}$	13.335	1.45	**-0.684**	**0.20**	-9.74	**0.001**	**<0.001**	**0.001**	**-3.135****	-0.689	-0.523	0.002	-0.003	**-0.556***
Mg_{leaf}	$mg\ g^{-1}$	2.967	0.36			0.70	0.254	**<0.001**	**<0.001**	-0.436	**0.714***	**-0.409*****	0.066	**0.192***	**-0.243***
N:P	$g\ g^{-1}$	14.841	1.64	**0.624**	**0.25**	-4.11	**0.013**	**<0.001**	**<0.001**	**3.922***	**3.386****	0.085	-0.349	-0.599	0.308

LMF - Leaf Mass Fraction; LMA - Leaf Mass per Area; LFP - Leaf Force to Punch; LA:SA - Leaf Area: Shoot Area; RMF - Root Mass Fraction; RS - Root Length: Shoot Length; SRL - Specific Root Length

AGELAEA – *Agalaea sp.*; KOOMEX – *Koompassia excelsa*; PAR2MA – *Parashorea malaanonan*; SHORJO – *Shorea johorensis*; SHORL1 – *Shorea leprosula*; SHORP1 – *Shorea parvifolia*.

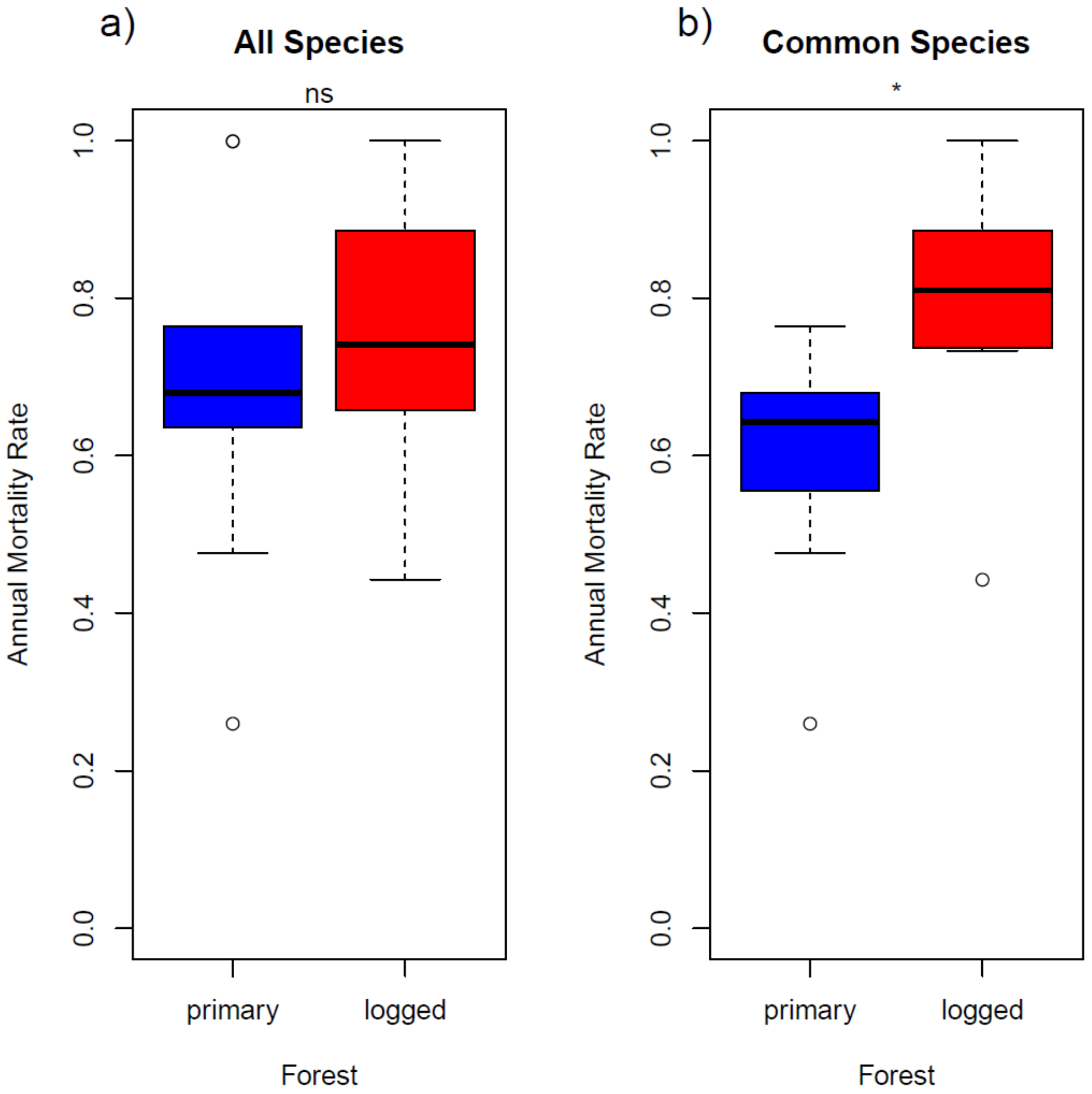

Figure 4.2: Mean annual mortality rate of post-mast seedlings over 1.5 years in primary (blue) and logged (red) forests for all species (a) and the seven species found in both forests (b). Asterisks represent significant differences between forests from Mann Whitney tests (ns: $p \geq 0.05$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$).

4.4.4 Trait space, functional diversity and redundancy

We visualised the trait space occupied by species in primary and logged forest using a principal components analysis of species trait means (Fig. 4.4). The first three dimensions of this PCA captured 66.9% of the variance in traits (SI Table 4.5). The first dimension was explained by several resource acquisition traits and foliar nutrients (LMA, SMRL, LA:SA, leaf thickness, Mg_{leaf}, Ca_{leaf} and K_{leaf}). The second dimension was explained by investment in leaf biomass (LMF) and strength (LFP), as well as

N_{leaf}, P_{leaf} and K_{leaf}, whilst the third dimension was explained by investment in roots (RMF and RS) and leaf N:P (SI Table 4.5). The seedling community of logged forest occupied greater trait space on all of the first three dimensions than seedling communities of primary forest. Species found exclusively in logged forests were located at the edge of the community trait space, including *S. macrophylla* with high LMA and low foliar nutrient concentrations (dimension 1), *I. bijuga* with high foliar nutrients and low root investment (dimension 2 and 3), and *B. sessilifolia* and *P. javanicum* with low root investment (dimension 3).

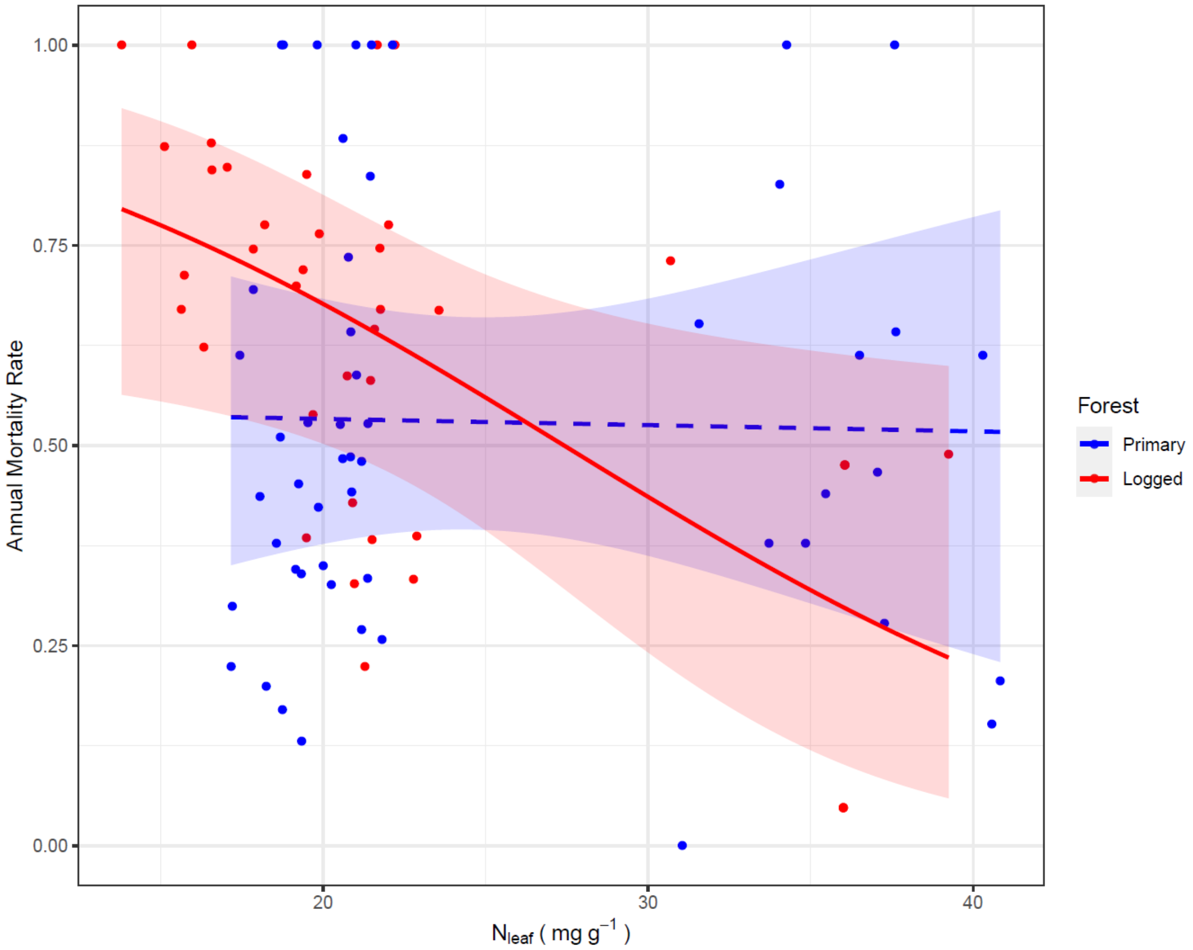

Figure 4.3: Foliar nitrogen concentrations (N_{leaf}) were the best predictor of seedling annual mortality rates over the first 1.5 years in logged forests (R^2 = 0.356). A significant negative relationship ($p = 0.032$) between mortality and N_{leaf} was found in logged forests (solid line) but not in primary forests (dashed line) from a general linear model fit with a binomial error structure. Shading around the lines represents the 95% confidence interval for the relationship. For model co-efficients, see SI Table 4.4.

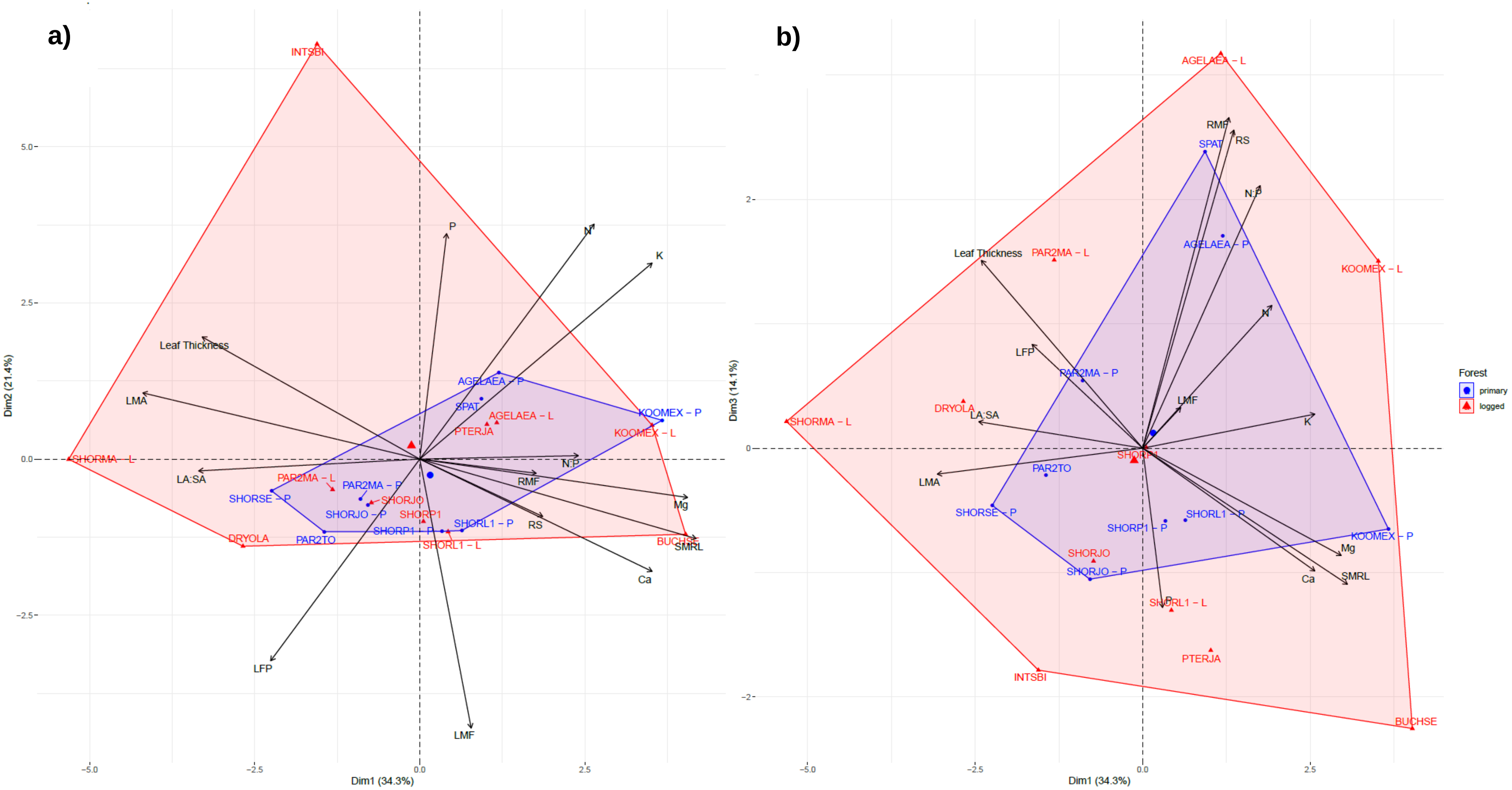

Figure 4.4: Principal component analysis of species mean trait values in primary (blue dots) and logged (red triangles) forests for dimensions 1 and 2 (a), and dimensions 1 and 3 (b). Species are indicated using their species code with a suffix of P or L to indicate primary and logged forests, respectively, for species sampled in both – see SI Table 4.1 for details. The mean for all species is indicated by a larger point. Trait space is indicated by the minimum convex polygon for each forest type. For variable contributions to each dimension, see SI Table 4.5.

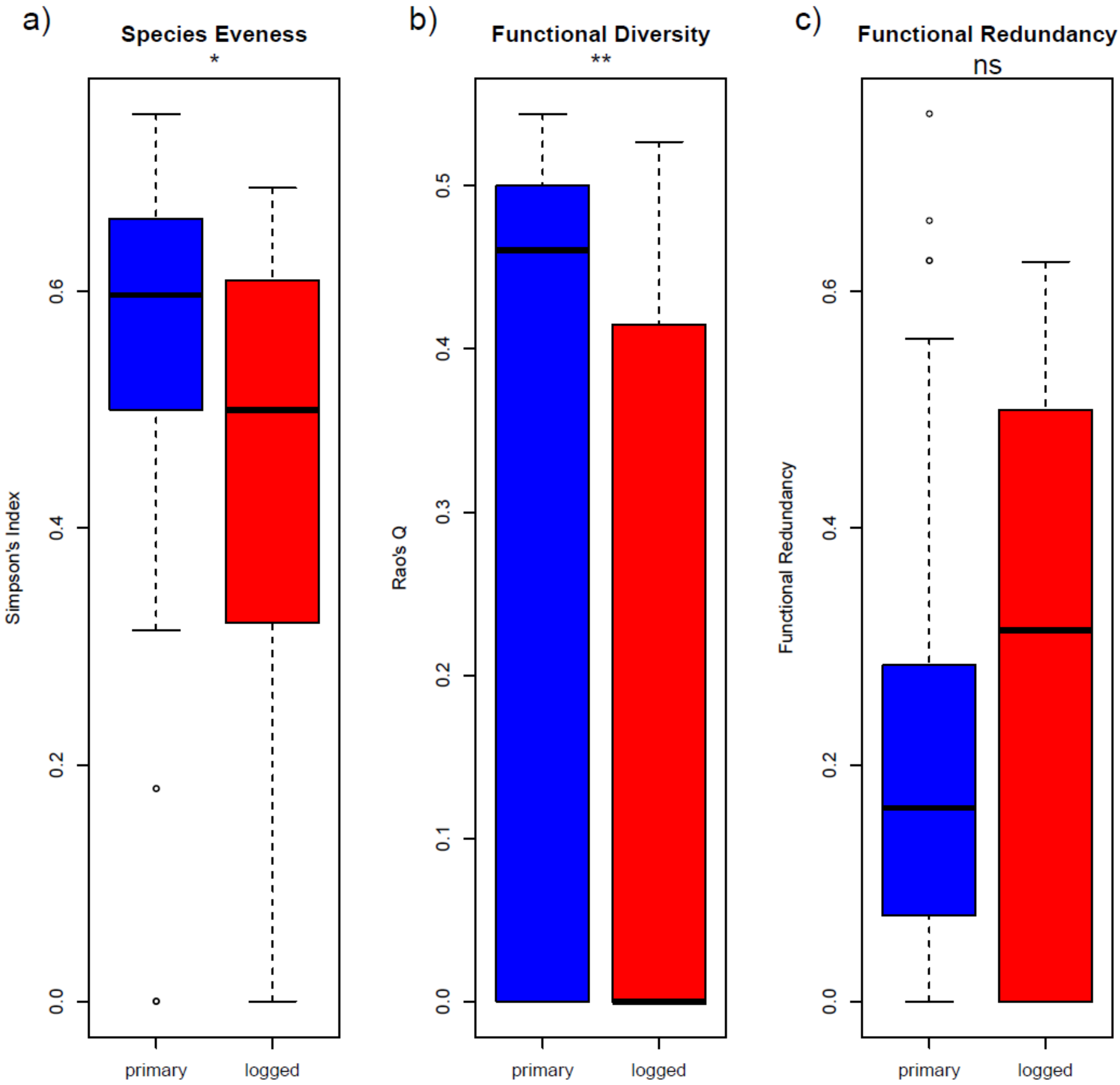

Figure 4.5: Species evenness (a), functional diversity (b) and functional redundancy (c) of primary (blue) and logged (red) seedling communities. Asterisks represent significant differences between the two forests from Mann-Whitney tests (ns: $p \geq 0.05$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$).

We tested whether the greater trait space occupied by logged forests resulted in greater functional diversity at the 1 m^2 plot scale. Despite greater trait space occupied by species in logged forest, mean functional diversity of 1 m^2 seedling plots, quantified by Rao's Q, was significantly lower in logged forests than primary forests (primary: 0.325 ± 0.03, logged: 0.173 ± 0.04, $p = 0.005$, Fig. 4.5b). This shows more similar functional traits are found among seedlings in logged forests than primary forests. Species evenness was also significantly lower in logged forests (primary: 0.541 ± 0.03, logged: 0.465 ± 0.04, $p = 0.024$, Fig. 4.5a). However, seedling communities in logged forests did not have lower functional redundancy than seedling communities in primary forests, highlighting differences in functional diversity are explained by differences in species evenness (primary: 0.216 ± 0.03, logged: 0.292 ± 0.04, p = 0.224, Fig. 4.5c).

4.5 Discussion

Our results reveal changes to seedling traits and functional diversity 27 to 39 years following selective logging in a North Bornean forest. Seedlings found in logged forests invest more resources in roots (higher RMF and lower LMF) than those of unlogged primary forest, at both the community level and for individuals compared within species (Fig. 4.1, Tables 4.1-4.2). Community weighted means (CWM) of some traits associated with the fast-slow plant economics spectrum, such as SMRL and LMA, did not shift significantly between logged and primary forests, with no differences in mean foliar nutrient concentrations or annual mortality rates observed (Fig. 4.2; Table 4.1). No significant differences in CWM traits were also found between actively restored and naturally regenerating logged forests (SI Figs 4.1-4.2). However, seedlings common to both forests did experience higher post-masting mortality rates over the first 1.5 years and lower foliar nutrient concentrations in logged forests, including in actively restored forests (Fig. 4.2 & SI Fig. 4.6, Table 4.2). A concurrent shift towards more conservative traits was also observed in common species, indicating an inability to overcome the changes in microclimatic conditions and resource availability caused by logging. Differences in seedling mortality rates within logged forests declined with increasing foliar nitrogen concentrations, but variation in short-term seedling mortality in primary forests could not be explained (Fig. 4.3). Species in logged forests occupied a larger overall trait space because of the additional presence of earlier successional species (Fig. 4.4). However, lower species evenness and functional diversity in logged forests at the local 1m^2 scale (Fig. 4.5) reveal that seedling communities in logged forest become locally dominated by a few species.

4.5.1 Logging promotes belowground biomass investment

Seedling communities of logged forests express divergent traits to those of unlogged primary forests, with a shift towards greater biomass investment in roots over leaves at both the community and intraspecific level (Fig. 4.1 & SI Fig. 4.1, Tables 4.1-4.2). Greater investment in belowground biomass in seedlings is indicative of reduced light limitation and increased water and nutrient limitation (Wurzburger & Wright, 2015; Kramer-Walter & Laughlin, 2017; Waring & Powers, 2017; Boonman *et al.*, 2020;

Umaña *et al.*, 2020a; Umaña *et al.*, 2021b). Logging of the largest trees in tropical forests can reduce foliar density by >50%, greatly increasing understory light availability (Pfeifer *et al.*, 2016; Milodowski *et al.*, 2021). Light acts as an important control on seedling mortality rates, with the survival of both shade tolerant and intolerant species increasing with increasing light availability (Philipson *et al.*, 2014). We did not detect a significant difference in whole-community seedling mortality rates between primary and logged forests, but greater light availability may allow seedlings to divert investment towards belowground organs in order to overcome shortage of below-ground resources in logged forests.

Changes to soil environments caused by logging can reduce nutrient availability (Baharuddin *et al.*, 1995; Swinfield *et al.*, 2020) and is likely to have occurred at our study site as indicated by lower leaf nutrient concentrations in logged forests in the common species (Table 4.2). These changes to the abiotic environment result from both the direct removal of trees from a forest (Quinton *et al.*, 2010; Swinfield *et al.*, 2020) and the indirect impacts of heavy-machinery, skid-trails and log falls on the environment (Baharuddin *et al.*, 1995; Sidle *et al.*, 2004; Ziegler *et al.*, 2006). We found that seedling communities displayed a greater biomass allocation in roots but did not shift root morphology (SMRL), indicating greater nutrient limitation in logged forests of Danum Valley (Kramer-Walter & Laughlin, 2017). Studies of canopy trees in Bornean forests detected shifts in foliar nutrient concentrations and greater phosphorus limitation following logging (Both *et al.*, 2019; Swinfield *et al.*, 2020), but we could not detect these shifts in seedling CWM traits. Instead, reductions in foliar nutrients could only be found in species common to both forests. This might indicate that seedlings of dominant species in logged forests are adapted to maintain nutrient uptake despite reductions in nutrient availability.

Greater water limitation for seedlings in logged forests could also be driving the significant increase in belowground investment and the reduction in community-level LA:SA (Mencuccini *et al.*, 2019). Logging can increase water stress via changes to both the microclimate and soil physical properties (Baharuddin *et al.*, 1995; Ziegler *et al.*, 2006; Hardwick *et al.*, 2015; De Frenne *et al.*, 2021) and can increase drought sensitivity of seedlings (Qie *et al.*, 2019). The loss of canopy trees following logging will increase understory radiation, temperature and vapour pressure deficit, elevating evaporative stress (Blonder *et al.*, 2018; De Frenne *et al.*, 2021). Meanwhile, soil compaction and greater surface run-off in logged forests may further exacerbate reduced soil water availability (Baharuddin *et al.*, 1995; Ziegler *et al.*, 2006). Combined, these changes may reduce water availability and increase demand for seedlings that triggers adjustments to LA:SA to reduce the surface area for evaporative loss and to increase specific rates of water supply (Mencuccini *et al.*, 2019). These shifts in overall trait strategy however did not have direct effects on overall mortality rates.

4.5.2 Intraspecific responses to logging

Given the response of CWM traits of seedlings to logging, we evaluated whether these changes were driven by the observed alterations to species composition (Fig 4.5a) or by intraspecific adjustment of traits. We found that seedlings of species that could persist in both primary and logged forests did shift biomass allocation towards roots, but 10 of the other 12 traits measured did not follow the same pattern as CWMs. These results suggest that changes in species composition rather than intraspecific responses drive the shifts in CWMs (Table 4.1-4.2). Common species did not modify RS or LA:SA, but instead displayed a greater LMA and reduced SMRL in logged forests. High LMA and low SMRL are resource conservative traits and may be indicators of stress in these species (Poorter *et al.*, 2009; Reich & Cornelissen, 2014). We found common species are stressed by logging with significantly higher annual mortality rates compared with primary forests (Fig. 4.2), but this could not directly be explained by trait variation. Many species that dominate old-growth forests, such as dipterocarps, are highly specialised and restricted to narrow environmental conditions (Bartholomew et al. in review; Bittencourt et al. in review). Changes to the abiotic environment driven by logging may push these specialised species towards the edge of their abiotic niche and reduce their capacity to survive. We find that common species do not adjust their traits to mirror the CWM, suggesting they respond to different selection pressures compared to species that dominate logged forests.

Higher seedling mortality of common species may be driven by a reduced ability to uptake nutrients from the environment. Our data shows common species experience nutrient limitation in logged environments with reductions in foliar nutrient concentrations that were not detected in CWMs (Table 4.2). Many of the dominant species in old-growth Bornean forests are dipterocarps that require associations with ectomycorrhizal fungi to access nutrients (Brearley, 2012), and are particularly dependent on them at the seedling stage (Smits, 1994). As logging can reduce mycorrhizal diversity and abundance (McGuire *et al.*, 2015), these specialised dipterocarp species may not have access to an appropriate community of soil and root-associated microbial symbionts to access sufficient nutrients for survival. Alternatively, these common species may have higher growth rates in logged forests that could dilute foliar nutrient concentrations and explain the patterns we observe.

We found foliar nitrogen concentrations (N_{leaf}) were the best predictor of seedling mortality in logged forests (Fig. 4.3), indicating access to nitrogen acts as a key environmental filter in logged forests. Seedlings with higher N_{leaf} may be able to capitalise on the greater light availability by increasing photosynthetic capacity in logged forests (Poorter & Bongers, 2006). Higher nitrogen availability has previously been found to increase the capacity of dipterocarp seedlings to respond to elevated irradiance with photodamage occurring when nitrogen availability is low (Bungard *et al.*, 2000). Maintaining nitrogen supply may therefore be needed to survive in the higher light environment of logged forests. Alternatively, lower nitrogen availability may increase phosphorus limitation by reducing phosphatase production (Olander & Vitousek, 2000; Treseder & Vitousek, 2001) or may reduce assimilation of non-structural carbohydrates that help alleviate any drought stress enhanced by logging (O'Brien *et al.*, 2014; Qie *et al.*, 2019).

High mortality rates of common species in logged forests have important implications for their long-term recovery. If species dominant in old-growth forests fail to recruit in logged environments, we may observe halted succession and a permanent shift towards earlier successional communities in logged tropical forests (Qie *et al.*, 2019). As selective logging practices do not remove the entire tree community, there may be a long lag period before any shifts in community composition are detected at later ontogenetic stages (Hayward *et al.*, 2021). This might explain why shifts towards lower specific leaf area (the inverse of LMA) and lower foliar nutrients were detected at the community level for saplings and canopy trees (Both *et al.*, 2019; Swinfield *et al.*, 2020) but not seedling communities (this study), with many old-growth specialist species still dominating the pattern of canopy but not seedling CWMs.

4.5.3 Impacts of logging on functional and taxonomic diversity

Our data reveal that a larger trait space is occupied by seedlings in logged forests at the landscape scale than in old-growth primary forests (Fig. 4.3). Logging practices can increase environmental heterogeneity of forests through spatially variable impacts on canopy cover, microclimate and soil structure (Blonder *et al.*, 2018). Differences in logging intensity that frequently occur at landscape scales will further enhance environmental heterogeneity with more than seven-fold variation in logging intensity occurring across our study site (Foody & Cutler, 2003; Hayward *et al.*, 2021). This wider environmental space may therefore support a greater range of functional traits at the landscape scale as more environmental niches are available to be filled (Fig. 4.3).

However, we found that logging reduced local (1 m^2) scale functional diversity of seedling communities (Fig. 4.5b), which was driven by an increase in species dominance (Fig. 4.5a). As logging reduces water and nutrient availability and increases micro-environmental extremity (Blonder *et al.*, 2018; Swinfield *et al.*, 2020), novel environmental filters could be acting to reduce both functional and taxonomic diversity (Craven *et al.*, 2018). Functional redundancy was low in both primary and logged forests (Fig. 4.5c), meaning any shifts in species composition could alter the long-term function of these forests. Reduced evenness of seedling communities in logged forests may also have occurred because of a reduction in the number of reproductively mature trees. As many species in tropical forests, especially canopy and emergent trees, only begin to reproduce at large diameters, we may expect that few trees contribute to each seedling community in logged forests, whilst seedling communities in primary forests will have come from multiple parent trees. As functional diversity is important for maintaining ecosystem processes and resilience to disturbance (Tilman, 1997; Schmitt *et al.*, 2020), logged forests may be more vulnerable to future environmental changes, such as climate change, especially when functional redundancy is low.

4.5.4 Restoration of logged forests

The restoration of logged forests typically concentrates on altering the vegetation structure by planting trees, cutting lianas or thinning of sapling communities (Cerullo *et al.*, 2018). Whilst active restoration can accelerate the recovery of aboveground biomass of logged forests (Philipson *et al.*, 2020), we found no evidence to suggest that active restoration enhances natural regeneration of old-growth forests. CWMs of all traits did not differ between actively restored and naturally regenerating forests (SI Figs 4.1-4.2) and both common species (*Agelaea* sp. and *Shorea leprosula*) showed more conservative traits in actively restored forests (SI Figs 4.5-4.6). Tree planting and liana cutting therefore appear to have little impact on seedling dynamics in logged forests 20 years later.

Overall, natural regeneration was altered by logging in Bornean forests, irrespective of current restoration techniques. Species dominant in old-growth forests, including economically important timber species, are particularly vulnerable to logging and experience higher mortality rates in logged forests. Greater investment in roots and the importance of foliar nitrogen concentrations in determining mortality in logged forests indicates belowground stress from reduced nutrient and water availability acts as a key environmental filter in logged environments. More acquisitive trait strategies of earlier successional species appear less vulnerable to logging, with resultant shifts towards earlier successional communities likely to occur under current management strategies. Increased localised dominance patterns may also be expected even if overall diversity does not change at the landscape scale. Our findings indicate that amelioration of belowground conditions or modifications to current vegetation management strategies may therefore be necessary for natural seedling recruitment in logged forests to resemble that of old-growth forests (Chazdon, 2003; Philipson *et al.*, 2020).

Chapter 5: Small tropical forest trees have a greater capacity to adjust carbon metabolism to long-term drought than large canopy trees

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Author Contributions: DB, LR, MM, RO and PM designed the data collection, ACLD and PM designed the drought experiment, DB, LR, ACLD, PRLB, IC, PBC, TFD, RCM, LVF, and OAAR all contributed to data collection and all authors contributed to editing the manuscript.

5.1 Abstract

The response of small understory trees to long-term drought is vital in determining the future composition, carbon stocks and dynamics of tropical forests. Long-term drought is, however, also likely to expose understory trees to increased light availability driven by drought-induced mortality. Relatively little is known about the potential for understory trees to adjust their physiology to both decreasing water and increasing light availability. We analysed data on maximum photosynthetic capacity (J_{max}, V_{cmax}), leaf respiration (R_{leaf}), leaf mass per area (LMA), leaf thickness and leaf nitrogen and phosphorus concentrations from 66 small trees across 12 common genera at the world's longest running tropical rainfall exclusion experiment and compared responses to those from 61 surviving canopy trees. Small trees increased J_{max}, V_{cmax}, R_{leaf} and LMA (71%, 29%, 32%, 15% respectively) in response to the drought treatment, but leaf thickness and leaf nutrient concentrations did not change. Small trees were significantly more responsive than large canopy trees to the drought treatment, suggesting greater phenotypic plasticity and resilience to prolonged drought, although differences among taxa were observed. Our results highlight that small tropical trees have greater capacity to respond to ecosystem level changes and have the potential to regenerate resilient forests following future droughts.

5.2 Introduction

Climate change can simultaneously affect multiple environmental variables across ecosystems globally (IPCC, 2019). However, little is known about how trees respond to multiple environmental shifts, especially in tropical forests (Niinemets, 2010; Bonal *et al.*, 2016). Both episodic and sustained droughts have been shown to cause mortality of large canopy trees in Amazonia (Nepstad *et al.*, 2007; Phillips *et al.*, 2010; Bennett *et al.*, 2015; Meir *et al.*, 2015; Rowland *et al.*, 2015a), resulting in canopy openings and changes in the understory environment (Chazdon & Fetcher, 1984; Brown, 2009; Pfeifer *et al.*, 2016). Small understory trees must therefore respond to concurrent reductions in soil moisture availability and increased light availability to survive, compete and grow under drought conditions. The ability of these small trees to adjust their physiology in response to multiple environmental shifts could be critical for predicting the future of tropical forests.

If canopy trees are susceptible to mortality during drought under future climates, it becomes important to understand the response of understory trees to drought conditions within higher light environments, and concomitant changes in air temperature and VPD. However, most of our current knowledge of tropical tree drought responses is focused on either large canopy trees or seedlings (e.g. Poorter & Hayashida-Oliver, 2000; Nepstad *et al.*, 2007; Schuldt *et al.*, 2011; O'Brien *et al.*, 2014; Rowland *et al.*, 2015b; Feldpausch *et al.*, 2016; O'Brien *et al.*, 2017). Some studies have investigated the impacts of short-term drought events on tropical understory trees (e.g. Phillips *et al.*, 2010; Newbery *et al.*, 2011), but, to our knowledge, no studies to date have investigated the effects of prolonged drought in tropical forests on understorey trees also exposed to elevated light conditions. This represents a gap in our knowledge as understory trees tend to have very different resource requirements to adult trees and seedlings (Sterck *et al.*, 2014). If we are to fully predict the fate of tropical forests and improve climate predictions from the latest generation of demography-based vegetation models, it is critical to understand the physiological responses of understory trees in drought-affected forests (Moorcroft *et al.*, 2001; Smith *et al.*, 2008; Fisher *et al.*, 2018; Moore *et al.*, 2018).

Differences in physiology, microenvironments and resource requirements will likely lead to different drought responses in small understory trees compared with large canopy trees (Kitajima & Poorter, 2008). Small trees tend to be particularly sensitive to reductions in soil moisture availability (Ruger *et al.*, 2012; Kitajima *et al.*, 2013; Quevedo-Rojas *et al.*, 2018), because of smaller total carbon reserves (Hartmann *et al.*, 2018) and shallower rooting depths (Stahl *et al.*, 2013; Brum *et al.*, 2018). However, vulnerability to drought may actually be lower in small trees, as carbon reserves per unit biomass may be greater (Hartmann *et al.*, 2018). An ability to maintain a positive balance between carbon assimilation and use will ultimately be critical for these small trees to survive and avoid carbon starvation under drought conditions (O'Brien *et al.*, 2014; McDowell *et al.*, 2018). The adjustment of functional traits related to carbon metabolism, including maximum photosynthetic capacity (J_{max} and V_{cmax}) and leaf respiration (R_{leaf}), is important for buffering long-term reductions in soil moisture availability. Under drought stress, some trees have been shown to reduce photosynthetic capacity because of drought-induced impairment or for nutrient re-allocation for stress repair (Damour *et al.*, 2008; Damour *et al.*, 2009), whilst others have been shown to maintain photosynthetic capacity to optimise carbon assimilation during wetter periods (Rowland *et al.*, 2015b). In response to this, R_{leaf} can increase under drought conditions to support stress-related repair or support osmoregulation (Rowland *et al.*, 2015b), however perhaps more typically R_{leaf} has been found to decrease during drought stress in response to reduced photosynthesis (Atkin & Macherel, 2009; Ayub *et al.*, 2011). The extent of plasticity in these carbon metabolic traits could determine the likelihood of small trees surviving long periods of reduced soil moisture availability. However, these traits are not simply controlled by drought stress, but are also highly sensitive to light availability (Poorter *et al.*, 2009; Atkin *et al.*, 2015; Hasper *et al.*, 2017). Consequently, the light environment of a tree should also be considered when understanding responses to drought.

Tropical forests display strong vertical gradients in light availability with small understory trees generally adapted to shade conditions relying on diffuse light and unpredictable, fleeting sunflecks for the majority of their carbon assimilation (Chazdon & Pearcy, 1991; Leakey *et al.*, 2003). Under normal conditions, tropical trees are able to acclimate their leaf physiology to the steep gradient in irradiance experienced through the vertical profile of the canopy, with photosynthetic capacity and LMA increasing with light availability (Meir *et al.*, 2002; Poorter *et al.*, 2009; Cavaleri *et al.*, 2010; Domingues *et al.*, 2010). Trees modify their leaf physiology to optimise the balance between carbon gain and carbon and water loss, in order to maximise growth, reproduction and competitiveness. Both large and small understory trees in tropical forests have been shown to be highly responsive and plastic to changes in their light environment (Kitajima *et al.*, 2013; Quevedo-Rojas *et al.*, 2018), suggesting light is likely to be the most limiting factor for photosynthesis in intact tropical forests. However, if another factor, such as water availability, also becomes limiting, these trees may no longer be able to acclimate to high light levels, potentially leading to negative impacts of increasing light on growth and survival. Increases in light availability under drought conditions may result in excessive photon flux density, elevated leaf temperatures and elevated VPD, inducing photoinhibition (Kamaluddin & Grace, 1992; Mulkey & Pearcy, 1992; Krause *et al.*, 1995), prolonged stomatal closure (Reynolds-Henne *et al.*, 2010) and xylem embolism. To avoid these negative consequences of concurrent high light and drought stress, small understory trees may need to modify their physiology in different ways compared to canopy trees.

Insights from the same eastern Amazon throughfall exclusion experiment used in this study showed the responses of large trees to drought were indeed influenced by the light environment (Rowland *et al.*, 2020). Large trees that had also experienced increased canopy exposure following mortality events, experienced reductions in photosynthetic capacity under drought conditions, whilst those that did not maintained photosynthetic capacity (Rowland *et al.*, 2020). However, large trees will have experienced relatively minor shifts in their light environment when compared to small understory trees. These larger trees may also be more exposed to hydraulic stress from the drought, which may limit their ability to respond positively to elevated light (Bittencourt *et al.*, 2020), although they may already be acclimated to higher VPD conditions at the top of the canopy so may not experience hydraulic stress from sudden shifts in VPD that will occur in the understory. Studying how small understory trees adjust their leaf physiology to concurrent shifts in water and light availability and how these responses differ from large canopy trees may also give new insights into the potential for forest regeneration following drought events.

Here, we use data from a 15-year tropical forest drought experiment located in eastern Amazonia, to test how long-term drought affects carbon metabolism and leaf morphology in small understory trees. By comparing data on maximum photosynthetic capacity (J_{max} and V_{cmax}), leaf dark respiration (R_{leaf}), leaf mass per area and leaf thickness from 66 small understory trees (1-10 cm DBH) against those from 61 surviving canopy trees across 12 genera between a throughfall exclusion (TFE) experiment and neighbouring control plot, we test the following hypotheses:

1) Small understory trees respond to canopy openings following long-term drought stress by increasing photosynthetic capacity (J_{max} and V_{cmax}) in response to elevated light availability.
2) Small understory trees increase leaf dark respiration and LMA in response to long-term drought stress.
3) Leaf physiological traits (J_{max}, V_{cmax}, R_{leaf} and LMA) are more responsive to reduced soil moisture availability and canopy openings following prolonged soil moisture deficit in small understory trees than large trees.

5.3 Methods

5.3.1 Study site

This study was carried out at the world’s longest running TFE experiment in Caxiuanã National Forest Reserve, Para, Brazil (1°43′S, 51°27’W). The experiment is located in seasonally dry *terra firme* forest with an annual precipitation of 2000-2500 mm. Here, a pronounced dry season occurs between June and November, where average precipitation drops to <100 mm per month. The experiment consists of two plots: the TFE plot (1 ha) where 50% of incoming canopy throughfall has been excluded using clear plastic panels at 1-2 m height since 2002, and a neighbouring control plot (1 ha) located <50 m from the TFE. The two plots were both trenched around the perimeter to a depth of 1-2 m to minimise horizontal throughflow. Both plots have been continuously maintained and monitored since 2001. For experimental details, see (Fisher *et al.*, 2007; da Costa *et al.*, 2010; Rowland *et al.*, 2015b; Meir *et al.*, 2018). Reduced soil moisture availability on the TFE plot compared with the control plot has been shown previously with lower mean pre-dawn leaf water potentials on the TFE plot (SI Fig. 5.1) (Bittencourt *et al.*, 2020).

5.3.2 Sampling

From August to September 2017, we sampled 66 small trees (1-10 cm diameter at breast height; 1.3 m DBH; 2.7-23.0 m height) across the two plots: 30 from the TFE and 36 from the control. We selected individuals from 12 of the most common genera within the two plots (*Duguetia, Eschweilera, Inga, Iryanthera, Licania, Manilkara, Minquartia, Ocotea, Protium, Tetragastris, Swartzia, Vouacapoa*) in accordance with a corresponding study on large tree carbon metabolism and storage (SI Table 5.1a; Rowland *et al.*, 2020). All species represent canopy or emergent trees when mature. In order to minimise edge effects within the plots, we sampled trees located within one quarter of each 1 ha plot (i.e. 0.25 ha), with all trees located at least 20 m from the plot perimeter. For each genus, individual tree selection was designed to cover a range of sizes from 1 to 10 cm DBH. Two people independently assessed the relative canopy position of each tree and assigned it as either shaded or in a canopy gap according to whether the leaves experienced vertical shading or not. All canopy position assessments were recorded at approximately the same time each day, and the presence of leaves directly above the target tree were used to minimise bias from different sun positions at the time of measurement.

We selected an additional 61 large trees (>20 cm DBH: range 20.2-67.9 cm) from a parallel study across eight corresponding genera (*Eschweilera, Inga, Licania, Manilkara, Minquartia, Protium, Swartzia, Tetragastris*) to compare responses of large trees against a subset of 48 small trees for the same eight genera (SI Table 5.1b). For more details about large tree sampling, see Rowland *et al.* (2020).

5.3.3 Gas exchange measurements

During the peak dry season (August-September 2017), we collected a branch of approximately 1 m length from the top of the crown of each tree, using pole pruners. For the majority of the trees (> 95%), the branches were cut between 09:00 and 10:00 hrs, but on some occasions, branches were cut between 10:00 and 13:00. Once harvested, branches were immediately placed in water and were cut twice underwater to restore water supply to the leaves (Domingues *et al.*, 2010). The branches were subsequently left to stabilise in full sunlight for a minimum of 30 minutes. Following stabilisation, we selected non-senescing, fully formed leaves to be measured using two cross-calibrated portable photosynthesis systems (LI-6400XT and LI-6800, LI-COR, Nebraska, USA). For each tree, we measured one leaf for estimates of photosynthetic capacity and one neighbouring leaf for dark-adapted leaf respiration (R_{leaf}).

We performed photosynthetic CO_2 response curves (A-C_i) to estimate maximum photosynthetic capacity. We placed a leaf within the leaf chamber of a portable photosynthesis system and measured net photosynthetic assimilation (A) and leaf internal carbon dioxide (CO_2) concentration (C_i). We generated A-C_i curves by manipulating CO_2 concentrations within the leaf chamber (400, 200, 75, 400, 800, 1200, 2000 ppm), whilst providing a photosynthetic active radiation (*PAR*) of 1500 μmol m^{-2} s^{-1}, a temperature of 28 ˚C and a relative humidity of 60-70%. Light response curves carried out on a subset of the samples (n = 8) ensured 1500 μmol m^{-2} s^{-1} *PAR* represented saturating light conditions for the leaves (data not shown). In order to maintain data quality, A-C_i curves were aborted if stomatal conductance (g_s) dropped below 0.03 mol m^{-2} s^{-1} (following Rowland *et al.*, 2015b). No difference between measurements of photosynthetic capacity or R_{leaf} on cut versus uncut branches have been found in previous studies at this site (Rowland *et al.*, 2015b), suggesting our measurements reflect true values of *in situ* leaves and differences between the two plot treatments. We waited for steady-state conditions within the leaf chamber to be reached before any gas exchange measurements were recorded. Using these data, we estimated the maximum rate of electron transport (J_{max}) and the maximum rate of carboxylation (V_{cmax}) standardised to 25 ˚C following the equations from the C_3 photosynthesis model of Farquhar *et al.* (1980) as in Sharkey *et al.* (2007) using the *optim* function from the *stats* package in R statistical software (R Core Team, 2020). Ten trees were removed from our sample where A-C_i curves could not be fitted.

Dark-adapted leaf respiration (R_{leaf}) was measured on a leaf adjacent to that used to measure maximum photosynthetic capacity. Leaves were wrapped in aluminium foil for a minimum of 30 minutes before the portable photosynthesis system was used to measure R_{leaf}. We maintained stable leaf chamber conditions of 400 ppm CO_2 concentration, 0 μmol m^{-2} s^{-1} *PAR* and 28 ˚C for all respiration measurements. Following stabilisation within the leaf chamber, three measurements of respiration were recorded at five second intervals, then standardised to 25 ˚C using a Q10 value of 2.2 following Rowland *et al.* (2015b) and a mean value was calculated.

5.3.4 Leaf morphological traits

After completing leaf gas exchange measurements, we removed each of the leaves used to measure A-C_i curves and R_{leaf} from the branch and placed them in a sealed airtight plastic zip-lock bag. Moist cotton wool was placed in the bag to maintain high levels of humidity and prevent any water loss from the leaf. We scanned leaves using a flatbed scanner (CanoScan LiDE 120, Canon Inc., Tokyo, Japan) and calculated the area of each leaf using ImageJ software (Schneider *et al.*, 2012). Leaves were then placed in an oven to dry for 24 hours at 70 ˚C, to constant mass. We measured dry leaf mass using a precision balance and calculated leaf mass per area (LMA, g m^{-2}) by dividing dry leaf mass by leaf area. We used LMA from the leaves used to measure A-C_i curves and R_{leaf} to estimate maximum photosynthetic capacity and R_{leaf}, respectively, on a mass basis. We measured leaf thickness at three different points on fully hydrated leaves using digital callipers avoiding any major veins and calculated the mean. We averaged the LMA and thickness for the A-C_i and R_{leaf} leaves to generate an estimate for the overall branch.

5.3.5 Leaf nutrient analyses

We collected an additional sample, depending on leaf size, of 3-20 leaves adjacent to the leaves used for the gas exchange measurements to quantify leaf nitrogen and phosphorus concentrations ($[N]_{leaf}$, $[P]_{leaf}$). Following collection, leaves were dried in an oven for 24 hours at 70 ˚C to constant mass before being combined with the leaves used for gas exchange measurements. Major veins were then removed, and the remaining foliar matter was ground to a fine powder using a ball mill. Nitrogen concentrations were measured using the semi-micro Kjeldahl method (Malavolta, 1997), whilst phosphorus concentrations were measured using a Femto 600+ Spectrophotometer using the ammonium metavandate method (Malavolta, 1997). All analyses were tested against laboratory standards. We divided the gas exchange parameters on a mass basis by leaf nutrient concentrations to estimate leaf photosynthetic and respiratory nutrient use efficiency.

5.3.6 Data analysis

5.3.6.1 Small tree physiological responses

We used linear mixed effects models, using the package *lme4* (Bates *et al.*, 2014), to test for treatment (TFE vs control) and taxonomic effects on leaf gas exchange, morphological, nutrient content and nutrient-use efficiency traits in small trees (n = 66). Taxonomy was included as a random intercept effect in our models, whilst the TFE treatment was incorporated as a fixed effect. We tested for a genus and a species nested within genus taxonomic effect by comparing the full linear mixed effects model to a generalised least squares model, following Zuur *et al.* (2009) using the *nlme* package (Pinheiro *et al.*, 2012). When genus was not significant, linear models were used to test the significance of the fixed effects. For each trait response variable, the treatment effect was tested by comparing the Akaike Information Criterion corrected for sample size (AICc) between models using restricted maximum likelihood in the package *MuMIn* (Bartón, 2018).

Since traits may be coordinated, we additionally used standardised major axis regression (SMA) to test the effect of the TFE trait trade-offs. We tested for differences in the slopes and intercepts of the bivariate trait-trait relationships between small trees on the different treatments using a Wald test in the package *smatr* (Warton *et al.*, 2012). We investigated relationships between the gas exchange measurements and leaf morphological variables and the relationship between J_{max} and V_{cmax}.

5.3.6.2 Small and large tree comparisons

We tested for differences in individual tree-level responses to the TFE treatment for large canopy (n = 61) and small understory trees (n = 48), for the same set of species and genera in which data were available (SI Table 5.1b). We used linear mixed effect models to test the effect of the TFE treatment, tree size (large vs small), canopy shading (canopy gap vs fully shaded) and the interactions between treatment and tree size, and between treatment and canopy shading on leaf gas exchange and morphological traits. We also tested for taxonomic effects by including genus and species nested within genus as random effect variables and comparing to a generalised least squares model, following the same protocol used for small tree analyses (Bartón, 2018). Within this paper, all data represent the mean and associated errors denote standard errors of the mean. All data analyses were undertaken on individual tree-level data in R (R 3.5.1, R Core Team 2020).

5.4 Results

5.4.1 Physiological responses to long-term drought in small understory trees

We found a significant positive effect of the TFE, relative to the control plot, on both mean J_{max} (71.1%; Δ14.18 ± 2.65 μ mol m^{-2} s^{-1}, $P < 0.001$; Fig. 5.1a) and V_{cmax} (29.2%; Δ3.99 ± 1.40 μ mol m^{-2} s^{-1}, $P < 0.01$; Fig. 5.1b) standardised to 25˚C. J_{max} ranged from 7.11 to 41.00 μ mol m^{-2} s^{-1} in the control trees compared with 15.94 to 68.93 μ mol m^{-2} s^{-1} in the TFE trees, whilst V_{cmax} ranged from 7.84 to 26.12 μ mol m^{-2} s^{-1} in the control and 11.52 to 39.19 μ mol m^{-2} s^{-1} in the TFE. We found a 32.2% increase in 25 ˚C standardised leaf dark respiration (R_{leaf}) on the TFE plot compared to the control plot (Δ0.12 ± 0.06 μ mol m^{-2} s^{-1}, $P = 0.045$; Fig. 5.1c), with values ranging from 0.11-0.95 μ mol m^{-2} s^{-1} on the control and 0.06-1.49 μ mol m^{-2} s^{-1} on the TFE. Leaf mass per area (LMA) was 10.68 ± 4.04 g m^{-2} (15.1%) higher for small trees found on the TFE plot ($P < 0.01$; Fig. 5.1d), but mean leaf thickness did not significantly differ between the two treatments (Table 5.1). We found no significant differences in mean leaf nitrogen and phosphorus concentrations ($[N]_{leaf}$ and $[P]_{leaf}$) on a mass-basis between the control and TFE treatments (Fig. 5.1 e-f, Table 5.1). We found a significant effect of genus on the intercept for all of the traits except J_{max} and R_{leaf}, but no significant species-nested-within-genus effect for any traits (SI Table 5.2).

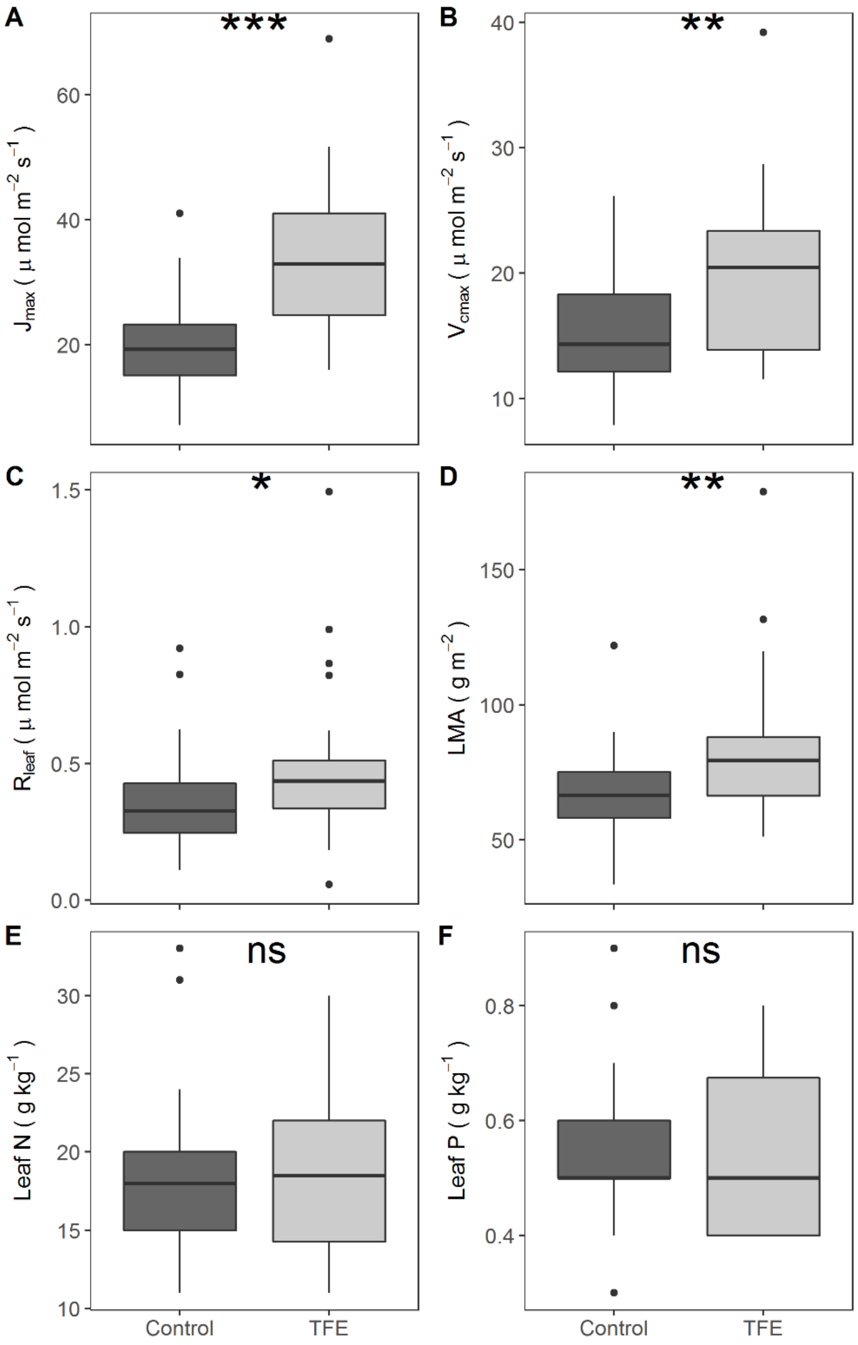


Figure 5.1: Boxplots showing how maximum photosynthetic capacity (J_{max}: a; V_{cmax}: b), leaf dark respiration (R_{leaf}: c), leaf mass per area (LMA: d), leaf nitrogen ($[N]_{leaf}$; e) and leaf phosphorus ($[P]_{leaf}$; f) differed between the control and TFE plot for small understory trees (1-10 cm DBH). Asterisks represent significant differences from linear mixed effect model tests at different p-values (ns: non-significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). See SI Table 5.2 for full model details. 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 whiskers.

Table 5.1: Parameter estimates for the minimal adequate models explaining J_{max}, V_{cmax}, R_{leaf}, leaf mass per area (LMA) and leaf thickness for large (>20 cm DBH; n = 61) and small (1-10 cm DBH; n = 48) trees. The intercept represents the trait value when the fixed effects are zero: large control trees that are not shaded. Canopy position represents the difference when a tree is shaded, plot represents the difference between the TFE treatment compared to the control and tree size represents the difference for small trees compared to large trees. Coefficient estimates ± the standard error are presented for each fixed effect and refer to the differences between the factor levels indicated in brackets for each column and the overall intercept. The genus intercept is given whenever the genus included as a random intercept effect improved the model fit. Species nested within genus was not significant for any traits, so is not included here. Random effect variance for genus ± standard deviation is presented. Total (conditional) R^2 represents the total variation explained by the model and is partitioned into the variation explained by the fixed effects (marginal R^2) and fixed plus random-effects (conditional R^2). Asterisks represent the significance level of each variable: ns $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Dashes represent variables that were not retained in the minimal adequate model but were tested in the initial fully saturated model. See Methods and SI Table 5.3 for more details about model selection.

Trait	**Intercept**	**Canopy Position**	**Plot**	**Tree Size**	**Size : Canopy interaction**	**Size : Plot interaction**	**Genus intercept**	**Fixed Effect (marginal) R^2**	**Total (conditional) R^2**
		(shaded)	(TFE)	(small)	(TFE : shaded)	(TFE : small)			
J_{max}		***	*	***	-	***	*		
	55.68 ± 2.93	-14.90 ± 3.29	-7.52 ± 3.01	-18.82 ± 3.84		18.88 ± 4.56	20.28 ± 4.50	0.526	0.596
V_{cmax}		**	ns	***	-	**	**		
	29.96 ± 1.83	-5.82 ± 1.89	-3.27 ± 1.72	-7.59 ± 2.18		6.69 ± 2.58	10.70 ± 3.27	0.336	0.482
R_{leaf}		-	ns	***	-	-	-		
	0.63 ± 0.04		0.09 ± 0.05	-0.23 ± 0.05				0.188	0.188

LMA	103.91 ± 6.81	-	* 8.19 ± 4.10	*** -30.66 ± 4.60	-	-	*** 266.90 ± 16.34	0.267	0.527
Leaf thickness	0.18 ± 0.01	-	-	-	-	-	** 0.0005 ± 0.022	0	0.232

Using standardised major axis (SMA) regression to compare differences in the relationships between J_{max}, V_{cmax}, R_{leaf}, and LMA across the two experimental plots, we found no significant trait-trait relationships, except for J_{max}-V_{cmax} (SI Table 5.3). An increase in the log_{10}-transformed electron transport rates relative to carboxylation on the TFE treatment compared with the control was observed (TFE = 1.72 ± 0.07 , Control = 1.36 ± 0.08, Wald = 8.503, df = 1, $P = 0.004$; Fig. 5.2), but no difference in the slope of the relationship ($P = 0.757$).

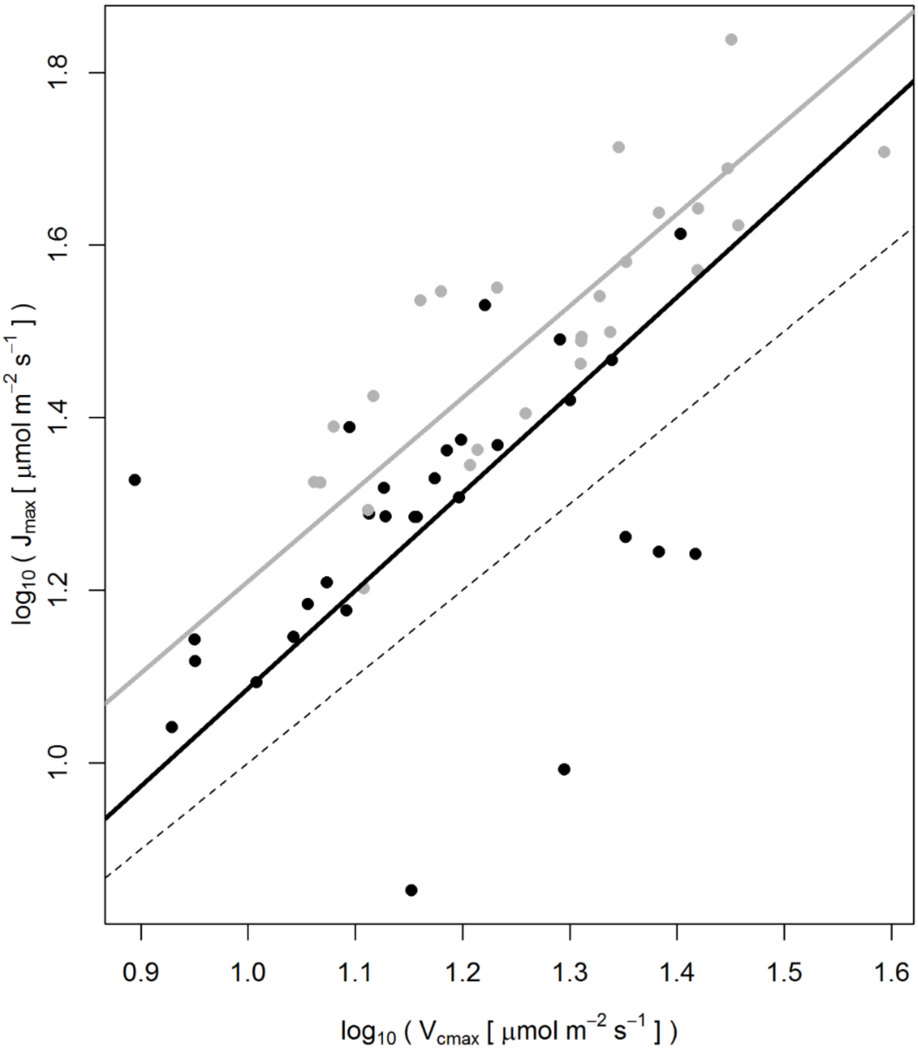


Figure 5.2: Standardised Major Axis (SMA) regression between J_{max} and V_{cmax} on a log_{10} scale for small understory trees (1-10 cm DBH) on the control plot (black) and the TFE plot (grey). The dashed line represents a 1:1 ratio. A significant difference in the elevation ($p < 0.01$) and a shift in the data ($p < 0.001$) between the treatments were found, but no significant difference between the slopes was found ($p = 0.757$).

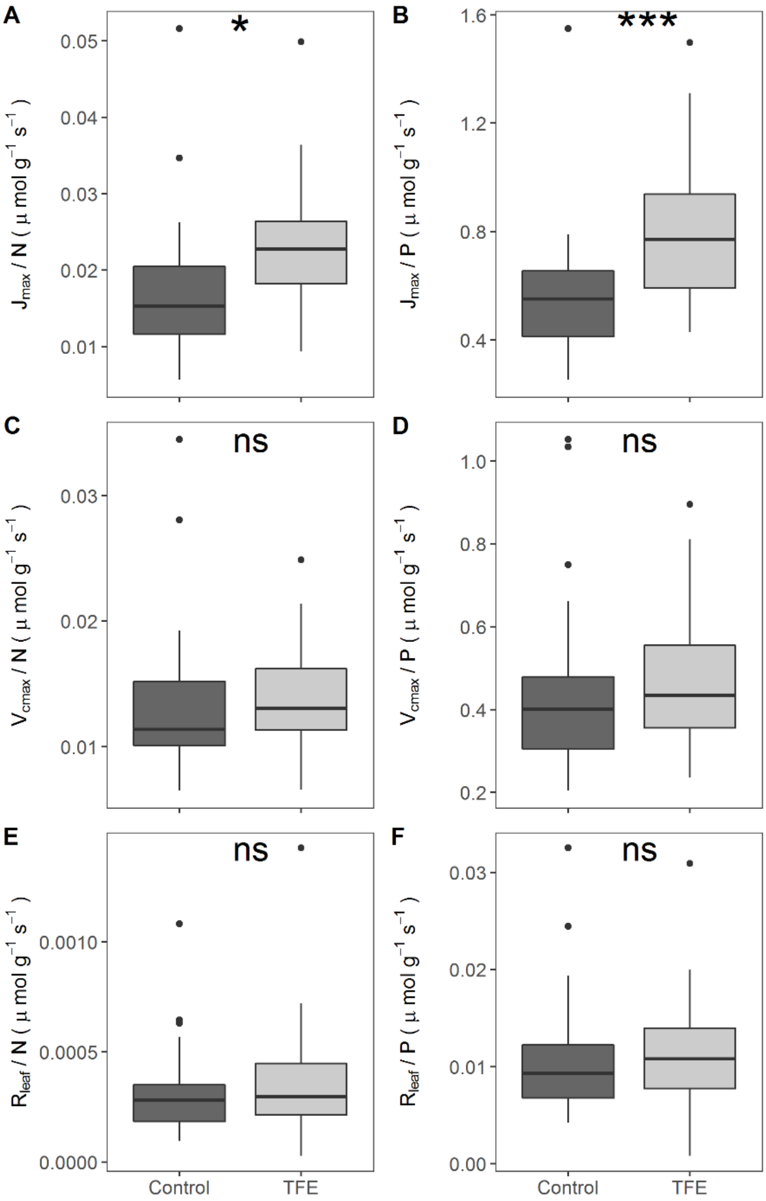


Figure 5.3: Boxplots showing how J_{max} (a, b), V_{cmax} (c, d) and R_{leaf} (e, f) nutrient use efficiency (NUE) changed between the control and TFE treatment for nitrogen (a, c, e) and phosphorus (b, d, f). NUE was calculated by dividing gas exchange parameters on a mass basis by leaf nutrient concentrations. Asterisks represent significant differences from linear mixed effects models between the two treatments (ns: non-significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). 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 1.5*interquartile range.

We found no relationship between J_{max}, V_{cmax} or R_{leaf} with $[N]_{leaf}$ or $[P]_{leaf}$ on either plot (SI Table 5.3). However, the TFE trees significantly increased J_{max} on a mass basis per unit N_{leaf} and unit P_{leaf} relative to the control (Fig. 5.3). J_{max} increased per unit nitrogen and unit phosphorus in the TFE trees by 0.006 ± 0.002 μmol g^{-1} s^{-1} and 0.227 ± 0.068 μmol g^{-1} s^{-1}, respectively (J_{max}/N_{leaf}: $P = 0.018$; J_{max}/P_{leaf}: $P < 0.01$; Fig. 5.3). Overall, neither V_{cmax} nor R_{leaf} increased per unit N_{leaf} or P_{leaf} in the TFE trees relative to the control (Fig. 5.3).

5.4.2 Comparison of responses to long-term drought between large canopy and small understory trees

We compared the responses of leaf traits in large (>20 cm DBH) and small (1-10 cm DBH) trees to the TFE treatment and to canopy shading using linear mixed models. We found a significant effect of tree size and the TFE treatment on J_{max}, V_{cmax}, R_{leaf}, and LMA, except for a non-significant effect of the TFE treatment on V_{cmax} and R_{leaf} (Fig. 5.4; Table 5.1). J_{max}, V_{cmax}, and R_{leaf} were, respectively, 33.8% (Δ18.82 ± 3.01 μmol m^{-2} s^{-1}), 25.3% (Δ7.59 ± 2.18 μmol m^{-2} s^{-1}) and 36.5% (Δ0.23 ± 0.05 μmol m^{-2} s^{-1}) lower in small trees after accounting for canopy shading in the models. Canopy shading had a significantly negative effect on J_{max} and V_{cmax}, but not R_{leaf} or LMA, with maximum photosynthetic capacity higher for trees positioned in the canopy or a canopy gap compared to trees shaded by the canopy (Table 5.1). In addition, a significant interaction between the TFE treatment and tree size for J_{max} and V_{cmax} was found, showing the response of maximum photosynthetic capacity to the TFE treatment to be dependent on tree size after accounting for canopy shading. The TFE effect on small tree J_{max} and V_{cmax} was reduced compared to large trees by 100.3% (Δ18.88 ± 4.56 μmol m^{-2} s^{-1}) and 88.1% (Δ6.69 ± 2.58 μmol m^{-2} s^{-1}), respectively. We found no significant effect of canopy shading, TFE treatment or tree size on leaf thickness. A significant genus effect was present for all leaf traits except R_{leaf}, showing these leaf traits are not solely determined by the environment, but also vary with taxonomy. For example, *Inga* and *Swartzia* had the highest J_{max} and V_{cmax}, respectively, whilst *Protium* had the lowest J_{max} and V_{cmax} of the genera studied, according to the intercepts in our mixed effect models. See Table 5.1 and SI Table 5.4 for effect sizes, standard errors, significance and R^2 values.

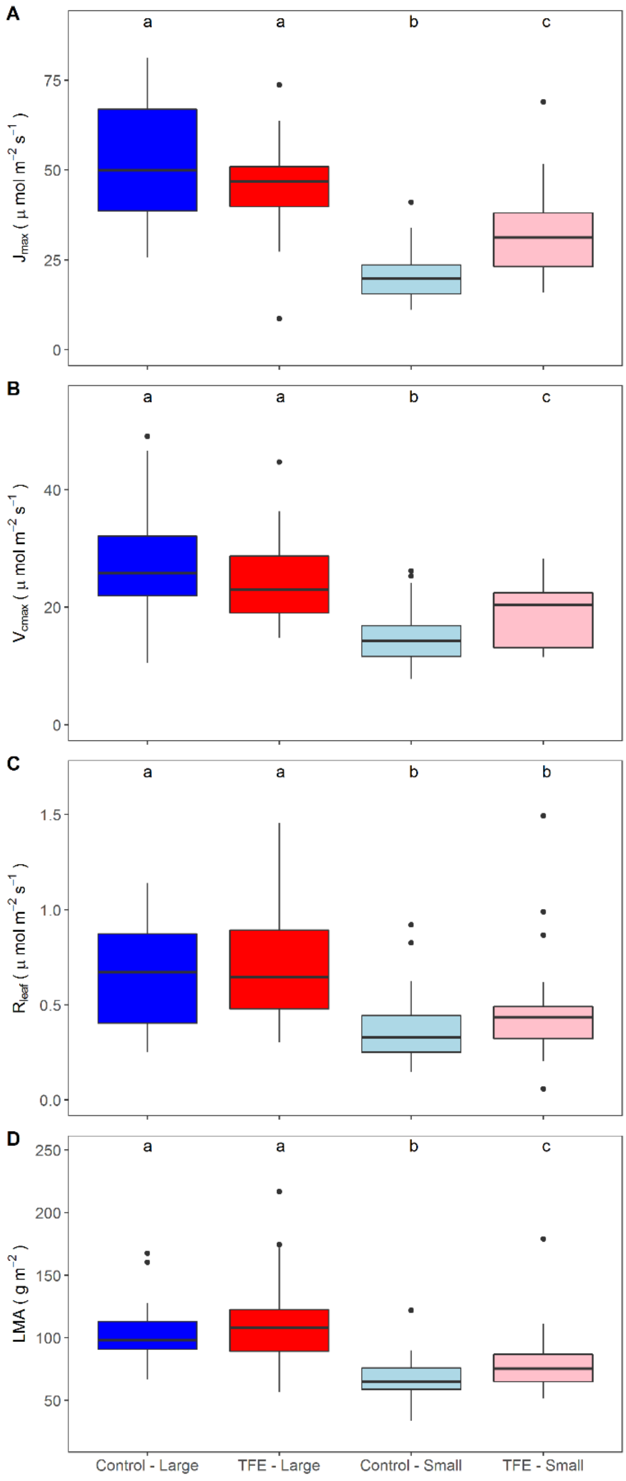


Figure 5.4: Boxplots showing how J_{max} (a), V_{cmax} (b), R_{leaf} (c) and leaf mass per area (LMA; d) change between the control (blue) and TFE (red) treatments for large (>20 cm DBH; red and dark blue) and small (1-10 cm DBH; pink and light blue) trees. Identical letters represent categories where there is no significant difference ($p > 0.05$) from pairwise Wilcoxon rank-sum tests. 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 1.5*interquartile range.

When the above results were repeated separately for the five most common genera in our dataset, we discovered the effect of tree size and the TFE treatment varied for different genera (Fig. 5.5). We show *Eschweilera* and *Swartzia* to have a positive response to the TFE treatment in small trees for J_{max}, with *Swartzia* having the largest (positive) response for V_{cmax} (Fig. 5.5). In contrast our data show *Inga* and *Protium* to exhibit little response to the TFE treatment in small trees for all traits. Different genera also exhibit different degrees of variation in their leaf morphology, showing that the responses to the TFE treatment vary by taxa (Fig. 5.5). Despite relatively small sample sizes, our data indicate similar or greater intraspecific than interspecific variation in leaf traits of small trees, especially photosynthetic capacity on the TFE, with the standard deviation in trait values within species exceeding the standard deviation in species-level means on the TFE in 8/9, 6/9, 4/10, and 2/10 species for J_{max}, V_{cmax}, R_{leaf} and LMA respectively (SI Table 5.5).

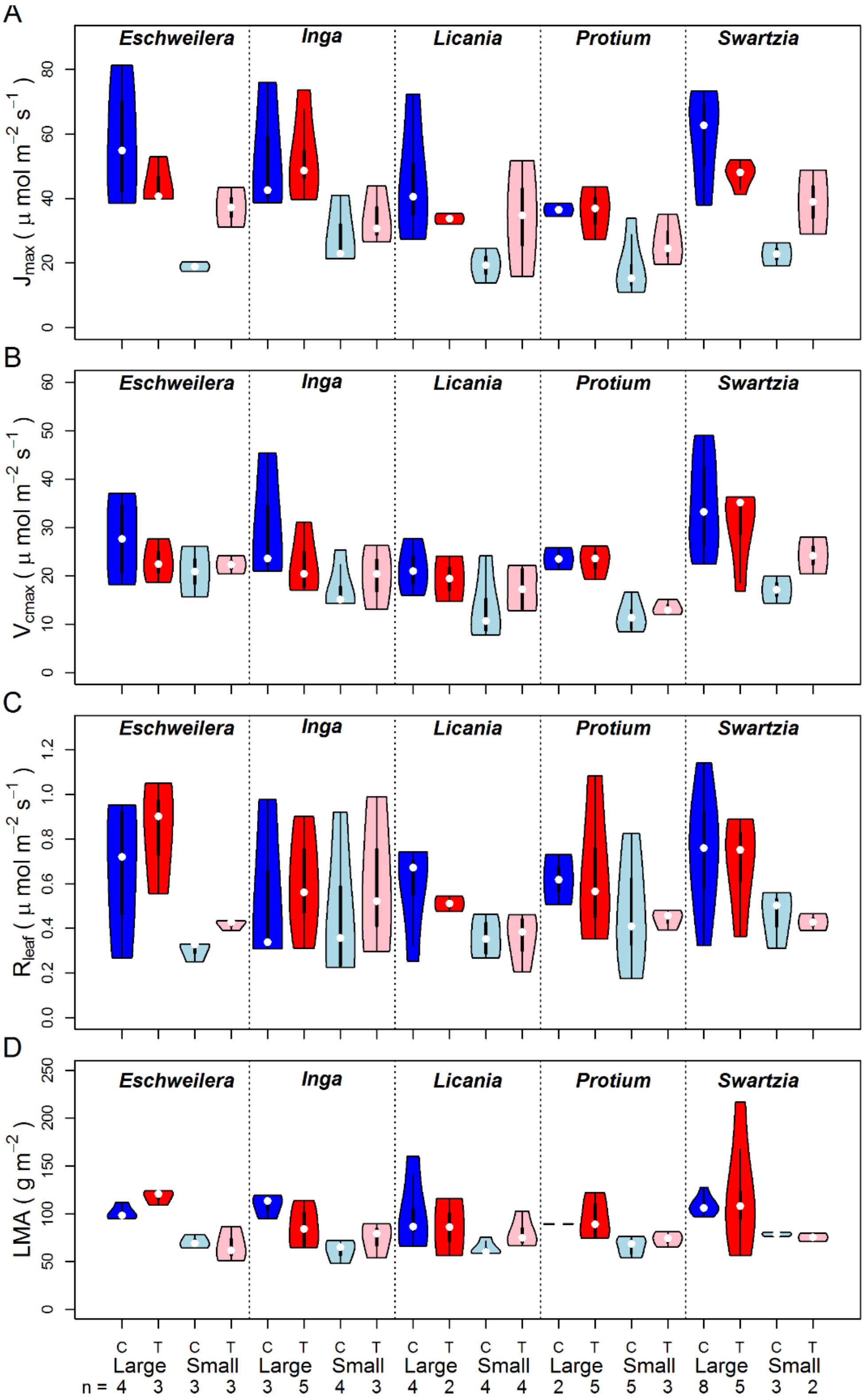


Figure 5.5: Violin plots comparing J_{max} (a), V_{cmax} (b), R_{leaf} (c) and leaf mass per area (LMA; d) between the Control (C) and TFE (T) treatment for large (>20 cm DBH) and small (1-10 cm DBH) trees across the five most common genera: *Eschweilera, Inga, Licania, Protium, Swartzia*. All genera with n ≥ 2 for each of the four categories are presented. White dots represent the median, thick grey lines represent the interquartile range and thin grey lines represent the mean ± 1.5 standard errors.

5.5 Discussion

We demonstrate that small understory trees (1-10 cm DBH) are more responsive than large canopy trees (>20cm DBH) to prolonged drought conditions. Canopy openings driven by drought-induced mortality of large trees (Rowland *et al.*, 2015a) have allowed small understory trees to increase photosynthetic capacity (J_{max} & V_{cmax}), leaf respiration (R_{leaf}) and leaf mass per area (LMA) in spite of reduced soil moisture availability and no changes in leaf nutrient concentrations (Fig. 5.1 & SI Fig. 5.1 & 5.2). These small understory trees show greater capacity to adjust their leaf physiology than large canopy trees following 15 years of through-fall exclusion (TFE; Fig. 5.4), suggesting responses to drought are dependent on tree size. Measured values of J_{max}, V_{cmax}, R_{leaf} and LMA in this study remained lower in small trees compared to large trees for both treatments, but values for small understory trees under the TFE treatment approach those of large trees for J_{max} and V_{cmax} after accounting for canopy position (canopy gap vs shaded understory) in our statistical models (Table 5.1). This indicates small trees are sufficiently plastic to increase photosynthetic capacity with higher light availability, even under drought conditions.

Maximum photosynthetic capacity was highly responsive to the TFE treatment in small understory trees with a 71% increase in the maximum rate of electron transfer (J_{max}) and a 29% increase in the maximum rate of carboxylation (V_{cmax}; Fig. 5.1). The increase in light availability in the droughted forest and the release from extreme light limitation is likely to be driving these physiological adjustments as light represents an important control on both traits (Hasper *et al.*, 2017). Typically, very little light penetrates the canopy to the understory in tropical forests because of the high leaf area index characteristic of tropical rainforests (Asner *et al.*, 2003). With the opening of the canopy, increased light availability may mean understory trees are no longer dependent on sunflecks for the majority of their photosynthesis (Chazdon & Pearcy, 1991; Leakey *et al.*, 2003). As a consequence, the magnitude of the change in the light environment may be sufficiently great that light acts as a strong selection pressure on photosynthetic capacity in these small trees, even when exposed to long-term drought conditions.

The greater plasticity of J_{max} compared to V_{cmax} and resultant increase in the J_{max} / V_{cmax} ratio on the TFE plot (Fig. 5.2) is highly indicative of a response to light, as the electron transfer reactions are directly involved in capturing light energy (Farquhar *et* *al.*, 1980; Sharkey *et al.*, 2007). A similar shift in the ratio in tropical montane cloud forests compared to lowland tropical forests has been attributed to lower total daily light availability caused by cloud cover, but with periods of intermittent intense light (van de Weg *et al.*, 2012). Following the mortality of canopy trees, the understory may experience similar sporadic periods of intense light, as a consequence of increased sunfleck occurrence and duration. A larger upregulation of J_{max} compared to V_{cmax} may allow these trees to maximise light capture during these prolonged sunflecks, with carboxylation reactions occurring subsequently (Pearcy, 1990). The division of the light dependent and light independent reactions may allow small understory trees to increase overall carbon assimilation whilst avoiding the additional maintenance costs of elevated V_{cmax}.

We show small trees can increase J_{max}, but not V_{cmax}, without additional leaf nitrogen or phosphorus (Fig. 5.1), most likely by increasing nutrient use efficiency (Fig. 5.3). This may occur via a potential re-allocation of nitrogen and phosphorus to optimise photosynthetic capacity (Hasper *et al.*, 2017; Mo *et al.*, 2019). The carboxylation reactions have greater nutrient demand for enzymes, such as RuBisCO, compared to those in the electron transport chain (Evans, 1989; Xu *et al.*, 2012; Raven, 2013). This may allow J_{max} to be more plastic and responsive to changes in light availability than V_{cmax}, without increasing leaf nutrient concentrations. Overall, the reduction in light limitation of photosynthesis in understory trees we observe here could facilitate increased wet-season growth rates as observed previously at this experiment in larger understory trees (Metcalfe *et al.*, 2010; Rowland *et al.*, 2015a). Consequently, the ability of small understory trees to respond to light whilst under soil moisture deficit may allow them to regenerate and recover biomass faster than currently predicted by dynamic vegetation models (Fisher *et al.*, 2007).

The ability of small understory trees to respond to increased light availability in the face of drought, increased leaf temperatures and elevated VPD may have various explanations. Firstly, it is possible that despite the reduced soil moisture concentrations (SI Fig. 5.1), our small trees are less stressed than the adult trees by the drought treatment. This could be a consequence of reduced competition for water following the mortality of large trees (Rowland *et al.*, 2015a), or a result of physiological adjustments to their hydraulic architecture or stomatal conductance. Small trees may be able to avoid drought stress by having stronger stomatal regulation or greater resistance to xylem embolism (Anderegg *et al.*, 2018; Bittencourt *et al.*, 2020). Reduced physiological and architectural constraints also allow small trees to explore more trait combinations than canopy trees that may allow them to be more effective at resisting drought (Reed *et al.*, 2011; Damián *et al.*, 2017). Alternatively, small trees may be able to avoid drought stress by reducing non-maintenance related metabolic activity, such as growth, in the dry season when drought conditions are most pronounced, and maximising growth during the wet season when the soil moisture deficit is reduced. This hypothesis is consistent with previous observations of high wet season and lower dry season diameter growth rates in the trees of smaller size classes on the TFE relative to the control (Metcalfe *et al.*, 2010; Rowland *et al.*, 2015a). Whichever mechanism small trees use, our results suggest that these trees are likely to be able to minimise the impact of the drought, relative to larger trees, in order to facilitate the upregulation of photosynthetic capacity and a release from extreme light limitation.

In addition to upregulation of maximum photosynthetic capacity, we found R_{leaf} to increase in small trees following long-term drought by 32% (Fig. 5.1). These elevated respiratory rates likely reflect the additional maintenance costs of higher photosynthetic capacity under elevated light conditions (Atkin *et al.*, 2015). However, we do not find a direct relationship between R_{leaf} and V_{cmax} or J_{max} in these trees (SI Table 5.3), suggesting elevated R_{leaf} is not simply a consequence of increased photosynthetic capacity. Instead, elevated R_{leaf} may reflect a response to increased stress under reduced water availability, potentially representing a means of drought resistance through increasing carbon metabolism for maintenance respiration (Rowland *et al.*, 2018b). Under water limitation, particularly when combined with increased irradiance, leaves can accumulate harmful reactive oxygen species (ROS) that cause cell damage (Wang & Vanlerberghe, 2013). An upregulation of respiration can provide a mechanism for leaves to purge these harmful ROS and avoid damage to the photosynthetic metabolic machinery (Atkin & Macherel, 2009). These negative effects of ROS are likely to be strongest during the dry season when water availability is particularly low. Here, small understory trees may have increased their R_{leaf} in the dry season to avoid drought stress and facilitate responses to increased light availability. It must also be acknowledged that our results may be influenced by changes in canopy temperature profiles between the plots, with a smaller expected vertical gradient in temperature in the more open canopy of the TFE plot, but measuring this was beyond the scope of this study. We do find large intra-generic variations in R_{leaf} and low explanatory power of the TFE treatment in our statistical models (SI Table 5.2), suggesting this trait is not simply influenced by long-term drought, but also by a range of other unaccounted for factors that are likely species-specific.

An increase in light availability in the understory of the droughted forest is also likely to be the main explanation for the 15% increase in LMA in small trees on the TFE we observe here. LMA is most strongly controlled by light (Poorter *et al.*, 2009), as leaves invest more in proteins that catalyse photosynthesis and produce more carbohydrates under elevated light conditions (Niinemets *et al.*, 1998; Poorter *et al.*, 2009). Higher concentrations of these high molecular weight metabolites will increase the density of cells and hence LMA. However, it should be noted that elevated LMA may also occur in response to reduced water availability, as a water conservation strategy (Wright *et al.*, 2004; Poorter *et al.*, 2009). Unlike photosynthetic capacity and R_{leaf}, LMA has been shown to increase in large trees at the same experiment via increased investment in spongy mesophyll for water storage (Rowland *et al.*, 2015b; Binks *et al.*, 2016), indicating increased LMA in small trees may also be directly associated to lower water availability in the TFE.

We show small trees were more responsive to prolonged drought conditions than large canopy trees, suggesting small trees experience different selection pressures or possess a greater ability to respond to ecosystem level changes in the physical environment. Maximum photosynthetic capacity of small trees increased in response to the TFE treatment – the exact opposite to the response of large trees to the TFE once differences in canopy position have been accounted for in our models (Table 5.1). In fact, only canopy shading prevents small trees from matching the capacity of large trees. Under prolonged drought, small trees experience changes to both their light and water availability, whereas larger canopy trees will predominantly only experience substantial shifts in water availability. The different responses to prolonged drought suggest small trees are responding most strongly to changes in their light environment, whilst large trees are responding to reductions in soil moisture availability. These shifts may reflect changes in the most limiting resource from the understory to the top canopy, with understory trees strongly light limited and canopy trees strongly water or nutrient limited (Chazdon & Fetcher, 1984; Sterck & Schieving, 2011).

Despite a general trend of physiological adjustments to prolonged drought conditions in small understory trees, our results clearly demonstrate that different genera have different abilities to respond to changes in their physical environment. Small *Eschweilera* and *Swartzia* trees displayed the greatest directional change in their traits in response to the TFE, as represented by the increase in carbon metabolism trait values (J_{max} & V_{cmax}; Fig. 5.5). In contrast small *Inga* and *Protium* trees showed very low directional trait variability in response to the TFE. The capacity of a tree to change its traits and potentially acclimate to new environmental conditions is likely to provide a competitive advantage under unstable environmental conditions (Pattison *et al.*, 1998; Lusk *et al.*, 2003), allowing some species to outcompete others. The large positive responses of small *Eschweilera* trees to drought observed here may allow it to maintain its hyperdominance in the Amazon (ter Steege et al. 2013), whilst species that show limited responses, e.g. *Protium*, may become less dominant in future communities. However, it should be noted that we show large intrageneric variation in the responses of trees of all sizes (Fig. 5.5), suggesting taxonomy may not be the only critical factor determining responses to drought-induced changes to the physical environment. Moreover, we focus here on leaf-level physiology and do not measure architectural (e.g. rooting depth) or stomatal responses that may facilitate adaptive responses in genera with low leaf-level plasticity. Further studies investigating recruitment following long-term drought are required to fully understand how taxonomic dominance may change in the future.

5.6 Conclusion

In this study, we highlight the important role of forest structural changes and light in determining physiological responses to long-term drought. Small trees (<10 cm DBH) relative to large trees (>20 cm DBH) display sufficient phenotypic plasticity in leaf morphology and carbon metabolism traits to allow them to respond to increases in light availability despite long-term drought. The ability of small trees to increase their photosynthetic capacity may facilitate increased growth and consequently partial recovery of forest aboveground biomass following earlier drought-induced mortality of large trees (Rowland *et al.*, 2015a). This capacity of small trees to show positive responses to ecosystem-level changes in water and light availability could ultimately allow a more resilient forest to establish and potentially moderate the negative impacts of climate change on the forest ecosystem.

Chapter 6: Synthesis and Conclusions

6.1 Summary of Key Findings

This thesis investigated how the availability of abiotic resources, including nutrients, light and water, affect the local-scale distribution and physiology of trees in intact tropical forests and the responses of tropical trees to environmental change. The main aims of this thesis were to understand the role of environmental variation in supporting high species richness in tropical forests and how changes to that environment, specifically from selective logging and long-term drought, may affect the functioning and community composition of tropical forests. A large focal point of my research was to understand trait plasticity in tropical forest trees, because understanding plasticity and acclimation are crucial in answering one of my core questions – how will plants respond to environmental change?

The first two empirical chapters of this thesis focus on understanding determinants of tree species' niches in intact tropical forests. These chapters utilise natural variation in abiotic environments within large (50 ha) forest dynamic plots (chapter 2) and across a natural edaphic gradient (chapter 3). Overall, the results presented in these chapters identify the important role of niche partitioning in facilitating species coexistence and that local conditions influence along which environmental gradients niches are partitioned. In the last two empirical chapters of this thesis, I utilise long-term manipulations of the environment to investigate the role of environmental change on tropical forests. The results of these chapters identify the vulnerability to environmental change driven by selective logging of species that dominate old-growth forests (chapter 4), but the resilience of small trees to long-term drought conditions (chapter 5). In these chapters, I identify the key changes to the abiotic environment and trait modifications that determine species' responses to environmental change.

In the following paragraphs, I present a summary of the key findings for each empirical chapter and outline how it contributed to the overall aims of this thesis.

6.1.1 Chapter 2: Partitioning of multiple niches supports high species richness in tropical forests

To understand the role of niche partitioning in supporting the exceptional species richness of tropical forest tree communities, I first investigated the local-scale drivers of the distribution of 444 species in three tropical forest sites. The results show that species have strong associations to many environmental variables, revealing the importance of abiotic environmental heterogeneity in supporting the coexistence of highly diverse tree communities. The results identify that the niche is defined by multiple dimensions in 47-78% of species, depending on the study site. These included dimensions not previously studied in combination, notably fine-scale variation in micro-topography, light and nutrient availability (both macro- and micro-nutrients, including various compounds of nitrogen and phosphorus), soil toxicity and abiotic controls on trophic interactions (e.g. soil sodium concentrations; Kaspari, 2020). My statistical models were able to explain the co-existence of 60-86% of abundant species at the study sites with these species having a unique combination of environmental associations shared by no other species. These findings support the theory that species are able to co-exist and avoid competitive exclusion by becoming specialised to niches defined by multiple dimensions. Strong niche partitioning among species in tropical forests can thus support high species richness in these forests.

6.1.2 Chapter 3: Differential nutrient limitation controls leaf physiology, supporting niche partitioning in tropical dipterocarp forests

In order to understand the mechanisms underlying niche partitioning, my third chapter studied how leaf physiology of 13 dipterocarp species varies across an edaphic gradient in Sepilok, North Borneo. Across this gradient, dipterocarp species show a degree of specialism in their distributions, being restricted to either one or two of four forest types. Soil nutrient availability and canopy structure both co-vary across the gradient, meaning the mechanisms driving species turnover across the gradient remained unknown. This chapter aimed to disentangle the drivers of variation in leaf traits (photosynthetic capacity, respiration and structural traits) across the gradient and thus, the key dimension for niche partitioning between dipterocarp species in these forests. Nutrient availability was found to explain greater variation in leaf traits than tree height, implying nutrients rather than light provide the key axis for niche differentiation between species in these forests. The results also reveal that variation in multiple nutrients is important because the influence of specific nutrients on photosynthetic capacity was not consistent between forest types; photosynthetic capacity was correlated with nitrogen in the nutrient-rich alluvial forest, but correlated with base cations in the most nutrient-poor, kerangas forest.

I also examined how more generalist species (those found in two forest types) adjust their traits between environments. My results reveal that leaf trait plasticity is low in these generalist species as limited trait adjustment was identified between forest types. These results suggest leaf function is fixed within dipterocarp species, even those with a more generalist distribution. The distribution of these generalist species may instead be explained by establishment in equivalent micro-environments across forests or by plasticity of other traits. A lack of leaf trait plasticity may leave these species highly vulnerable to environmental change, with the potential for more plastic species to outcompete them. Given that dipterocarp species are the dominant family (Lee *et al.*, 2002; Slik *et al.*, 2003) and represent the tallest trees of South-East Asian forests (Brearley *et al.*, 2017; Shenkin *et al.*, 2019), environmental change could cause major shifts in species composition and forest function if these species are unable to respond to changes in their environment. Overall, this chapter reveals that a wide range of soil types are needed to maintain high beta diversity in tropical forests because different soil types host unique assemblages. Any alterations to these soils, such as from nutrient deposition, could have impacts on forest function, competitive processes and community composition, although experimental manipulation of soil environments is needed to verify these conclusions.

6.1.3 Chapter 4: Selective logging increases dominance of acquisitive seedling traits in tropical forests

Selective logging represents a major driver of environmental change in tropical forests with more than half of tropical forest areas previously logged (Asner *et al.*, 2009; Laurance *et al.*, 2014). Investigating how selective logging affects the functional traits and mortality of seedlings in these forests is critical if we are to understand the long-term impacts on these forests. My results reveal that mortality rates are not significantly higher in logged forests when considering all 15 studied species, but for common species mortality rates are elevated in logged forests. This reveals that species that dominate old-growth forests are less able to recruit successfully in logged forests and we observe a shift towards a greater dominance of earlier successional species. Investigating differences in community weighted mean trait values between primary and logged forests revealed greater investment in belowground resources and more acquisitive leaf traits in logged forests, indicative of a shift from aboveground light limitation towards belowground resource limitation (water availability and/or nutrient availability). Whilst intraspecific comparisons revealed that common species can plastically adjust relative belowground investment, they have more conservative leaf and root traits, implying they are under greater stress in logged forests. Foliar nutrient concentrations were lower in logged forests in common species, but not at the community level, suggesting it is changes to the soil structure that has reduced the ability of common species to access soil nutrients and water and has potentially driven greater mortality rates. By comparing neighbouring primary and logged forests, I reveal that logging pushes some species to the edge of their niche space and could have long-term impacts on the community structure of tropical forests.

6.1.4 Chapter 5: Small tropical forest trees have a greater capacity to adjust carbon metabolism to long-term drought than large canopy trees

Increasing drought frequency, duration and severity represents another major environmental change in the tropical forest biome (Dai, 2012; Trenberth *et al.*, 2013; Hilker *et al.*, 2014; Chadwick *et al.*, 2015; Gloor *et al.*, 2015). Drought increases mortality rates in large tropical forest trees (Phillips *et al.*, 2010; Rowland *et al.*, 2015a), causing the canopy structure to open and light availability in the understory to increase. In this chapter, I use a long-term drought experiment in East Amazonia to understand how concurrent changes to light and water availability will affect small tropical forest trees. Here, I reveal that small trees are able to respond to increases in light availability by increasing photosynthetic capacity and photosynthetic nutrient use efficiency despite reduced water availability. These responses contrasted those of large trees that did not adjust traits under the drought treatment but recorded elevated mortality (Rowland *et al.*, 2015a). My results reveal that trait plasticity provides an important mechanism for small trees to respond to environmental change. Whilst an overall trend of greater resilience was found, I show that different species have varying capacity to respond, with greater responses in hyper-dominant species. These results suggest that the next generation of tropical forest trees may be resilient to drought, but that differences in drought resilience may cause changes to species composition with enhanced dominance of the most dominant species which ultimately may result in species losses.

6.1.5 Co-author publications

Several co-authored papers have also resulted from my PhD research and have contributed important findings which relate to the aims of this thesis (Appendix 1). I briefly outline their contributions here:

6.1.5.1: Divergence of hydraulic traits among tropical forest trees across horizontal and vertical resource gradients in Borneo (Bittencourt et al. in review)

The results presented in this publication complement the findings of Chapter 3 of this thesis.

Understanding water transport and drought resistance represents a key component of a tropical forest tree's niche. In Bittencourt *et al.* (in review), we reveal how changes in topography and edaphic conditions across the edaphic gradient in Sepilok affect the hydraulic traits and water-use niche of tropical forest trees. We reveal that species found on nutrient poorer and sandier soil have greater drought resistance traits (i.e. embolism resistance), providing an important mechanism to allow species to partition their niche with respect to topographic and edaphic variation. By comparing small and large trees in this study, we also revealed how trees plastically adjust their water transport traits to increase water transport efficiency with tree height. This mechanistic understanding reveals how trees can adjust their physiology in order to overcome the greater gravitational stress in taller trees and meet the greater water demand as photosynthesis increases under higher light availability. Overall, we reveal that the hydraulic niche is an important component of a species' niche and plasticity in hydraulic traits is important for responding to changes in the environment with tree height.

6.1.5.2a: The response of carbon assimilation and storage to long-term drought in tropical trees is dependent on light availability (Rowland et al., 2020)

6.1.5.2b: Amazonia trees have limited capacity to acclimate plant hydraulic properties in response to long-term drought (Bittencourt et al., 2020)

6.10.5.2c: Small understorey trees have greater capacity than canopy trees to adjust hydraulic traits following prolonged drought in a tropical forest (Giles et al. in review)

The results presented in these three publications complement the findings of Chapter 5 of this thesis.

Investigating how interactive changes to a species' niche affect responses to environmental change is critical for understanding how forest function and species composition will change in the future. In these three publications (Bittencourt *et al.*, 2020; Giles et al. in review; Rowland *et al.*, 2020), we use the same long-term drought experiment as in chapter 5 and reveal that changes in light availability and tree size play an important role in determining responses to drought. Rowland *et al.* (2020) reveal that large trees modify carbon assimilation and storage under drought conditions, but only if they are exposed to high light radiation. These shifts are likely driven by greater hydraulic stress in these trees that drives them to downregulate photosynthetic capacity and change non-structural carbohydrate storage strategies. Bittencourt *et al.* (2020) support these findings by showing that plasticity in hydraulic traits decreases with tree size and leaves large trees more vulnerable to embolism formation and ultimately drought-induced mortality. Further evidence of greater plasticity in hydraulic traits of small trees was found by Giles *et al.* (in review) where we discovered greater drought resistance traits in small trees compared with large trees. These studies reveal how variations in trait plasticity can determine responses to environmental change, with large trees more vulnerable to long-term drought than small understory trees in this location. Moreover, all studies revealed taxonomic variation in trait responses, suggesting taxonomic variation in trait plasticity could drive changes in community composition under environmental change.

6.2 Cross-cutting questions

My research cuts across several key themes. In this section, I synthesise the results of this compendium of research to answer important cross-cutting questions.

6.2.1 Does niche partitioning support species coexistence and high species richness in tropical forests?

Tropical forests host some of the most biodiverse ecosystems globally (Terborgh, 1992), but explaining the co-existence of these species has remained a longstanding challenge in ecology. Three main hypotheses have been proposed to explain the exceptional species richness of tropical forests: conspecific negative density dependence (CNDD; Janzen, 1970; Connell *et al.*, 1971), neutral theories (Hubbell, 2001) and niche partitioning theory (Whittaker, 1965; Hutchinson, 1978). CNDD hypothesises that specialised natural enemies, including herbivores and pathogens, act to reduce the population of common species and increase the survival rate of rare species, thereby promoting co-existence of species rich communities (Janzen, 1970; Connell *et al.*, 1971). CNDD has been widely studied in tropical forests and has been found to act as an important control of tree recruitment and species co-existence (Harms *et al.*, 2000; Comita & Hubbell, 2009; Bagchi *et al.*, 2010; Terborgh, 2012;

Bagchi *et al.*, 2014; Hulsmann *et al.*, 2021). Meanwhile, neutral theories hypothesise that species richness can be high in tropical forests because of random drift of species abundances and can occur irrespective of differences in species' niches (Hubbell, 2001). Evidence to support neutral theories as a mechanism for species co-existence, however, remains limited (Clark *et al.*, 2007). Instead, neutral models have been found to perform better at explaining differences in species population and range sizes (Bell, 2001; Volkov *et al.*, 2003). Niche partitioning theory hypothesises that species divide an n-dimensional niche space based off access to resources, allowing species to co-exist by avoiding competitive exclusion (Whittaker, 1965; Hutchinson, 1978). Niche partitioning of several key resources has been found previously in tropical forests (e.g. Denslow, 1980; Harms *et al.*, 2001; Paoli *et al.*, 2006; John *et al.*, 2007), but a supposedly small number of niche dimensions in autotrophic species has represented a major barrier to support this theory. I find strong evidence to suggest niche partitioning provides an important mechanism to facilitate high species richness and identify many dimensions of niche space that are partitioned between tropical forest tree species. Both niche partitioning and CNDD are thus likely to work in combination to maintain the high species richness of tropical forest tree communities.

In Chapters 2 and 3, soil nutrient availability was identified as a key axis for species to differentiate their niches and to facilitate species co-existence. Both the distribution (chapter 2) and physiology (chapter 3) of many species could be explained by soil nutrient availability. Tropical forests are traditionally considered to be phosphorus-limited because of their presence on old-weathered soils (Vitousek, 1984; Vitousek & Farrington, 1997). Phosphorus has previously been found to be an important control on species distributions and productivity in tropical forests (Condit *et al.*, 2013; Turner *et al.*, 2018). I found further support that phosphorus acts as a key control on species distributions (chapter 2), photosynthetic capacity and respiration (chapter 3). Phosphorus was found to be an important driver of the distribution of >30% of species in Barro Colorado Island (BCI) with these species showing positive or negative associations to total soil phosphorus concentrations (chapter 2). Meanwhile, relationships between leaf phosphorus concentrations and photosynthetic capacity (mudstone and sandstone) and respiration (mudstone, sandstone and kerangas) were found across the edaphic gradient in Sepilok, showing leaf metabolism to be correlated with availability of phosphorus in these forests (chapter 3). Variation in phosphorus availability can thus provide a key axis for niche partitioning between species with different phosphorus affiliations.

Phosphorus was not the only determinant of species distributions and physiology identified, though. In addition to phosphorus, nitrogen and cations (calcium, magnesium and potassium) are important macro-nutrients needed for key metabolic processes, such as photosynthesis and respiration (Hawkesford *et al.*, 2012). Availability of these macro-nutrients might therefore determine rates of metabolism and species-level performance. In chapter 3, I found the element correlated with photosynthesis and respiration changed across the gradient in nutrient availability in Sepilok, with leaf metabolism in the most nutrient-rich forests (alluvial forests) correlated with nitrogen instead of phosphorus. Photosynthetic capacity was correlated with calcium and magnesium in kerangas forests and correlated with nitrogen, phosphorus, calcium and potassium in sandstone forests. These variations in nutrient limitation provide the opportunity for species to differentiate their niche based off access and use of these resources. Soil cation availability was found to be a key determinant of species distributions in Danum Valley, suggesting cations play an important role in niche partitioning in Bornean forests (chapter 2). Both nitrogen and phosphorus can be found in multiple forms in soil, e.g. nitrogen can exist as nitrates or ammonium. We found these different chemical forms of nitrogen and phosphorus could both be partitioned between species in some forests, although affiliation to specific chemical forms was not found to be universal across species or sites (chapter 2).

This thesis also identified several other key micro-nutrients that can provide axes for niche partitioning between species. In chapter 2, iron was found to be an important driver of local-scale species distributions in both Pasoh (24% of species) and BCI (28% of species). Other elements, such as aluminium, boron, chromium, manganese, nickel and sodium, were also found to determine local scale distributions of more species that null expectations. This highlights the important role of micro-nutrition, soil toxicity and nutrient controls on herbivore abundance in determining tropical tree species' niches (John *et al.*, 2007; Kaspari, 2020; Manara *et al.*, 2020).

Topography was also identified as a key axis of differentiation between species in tropical forests. The number of species significantly associated with topography was found to increase with topographic variation, with up to 40% of species showing an elevational preference at Danum Valley (chapter 2). In Sepilok, micro-topographic variation has created two distinct forest types in close proximity with different floristic compositions found in neighbouring alluvial and mudstone forests (Born *et al.*, 2014). In chapter 3, I found differences in physiological traits (e.g. leaf respiration and leaf mass per area) and leaf nutrient concentrations between these forests despite no differences in soil nutrient availability, highlighting how topography can modify physiology. Alluvial forests are found on flat floodplains, whilst mudstone forests are found on small hills that do not sporadically flood. These differences in flooding patterns likely provide a key dimension for niche partitioning between species of these two forests. Edaphic conditions, such as soil texture and water holding capacity also frequently vary with micro-topography and can affect water and nutrient availability. In Bittencourt et al. (in review), we found hydraulic traits, such as embolism resistance, varied across the Sepilok edaphic gradient, suggesting hydraulic niche segregation occurs in these forests and is an important mechanism that drives species turnover across edaphic gradients.

Whilst topography and soil nutrient availability were found to provide important dimensions for niche partitioning, the effect of canopy structure and light availability on niche partitioning was more variable. Canopy structure metrics explained the distribution of more species in Danum Valley than BCI or Pasoh. However, almost all significant associations in Danum Valley were negative associations to canopy gaps, suggesting species do not partition high and low light environments evenly (chapter 2). Vertical partitioning of light environments also appears to be low in Bornean forests. Tree height was found to have low explanatory power of most traits in Bornean forests, with soil nutrient availability explaining considerably more variation in leaf traits (chapter 3). In contrast, partitioning of light environments in Neotropical forests may be higher. Both positive and negative associations to canopy gaps were found at BCI, suggesting some species prefer higher light conditions (chapter 2). In the Amazon, species were also found to be highly responsive to light availability, even when under drought conditions. Small trees increased photosynthetic capacity, leaf respiration and hydraulic efficiency in response to a more open canopy, whilst large trees did not show equivalent shifts under drought conditions (chapter 5; Giles et al. in review). This highlights the presence of vertical niche partitioning between small and large trees in these forests.

Overall, niche partitioning appears to be an important mechanism that acts to support high species richness in tropical forests, with many different abiotic environmental variables partitioned between species. Greater environmental heterogeneity can enhance niche partitioning, with the importance of different variables typically dependent on their variability. Niche partitioning was able to explain the presence of up to 86% of abundant species with these species sharing their combination of species-environment associations with no other species (chapter 2). Niche partitioning is likely to be an important driver of the high specialisation of many tropical tree species and the mechanism driving high beta diversity across environmental gradients in tropical forests (Cao *et al.*, 2021). Whilst niche partitioning may be high between abundant species, we could not differentiate the niche of some species and also did not study rare species in this thesis, meaning other mechanisms such as CNDD likely work in combination with niche partitioning to support highly diverse tropical forest communities.

6.2.2 How do tropical forest trees respond to changes in their environment?

I investigated how tropical forest trees respond to multi-dimensional changes in their environment in both intact and disturbed environments. Across a natural edaphic gradient in Sepilok, I found that generalist species largely did not adjust their leaf physiology between different forest types (chapter 3). Trait plasticity in leaf physiology was unable to explain why some species were able to fill a wider environmental niche in these forests, with greater tolerance of unfavourable conditions or plasticity in other traits, such as root traits, likely facilitating survival across a wider range of environments. Alternatively, these generalist species might be able to pick out small pockets of equivalent environments in both forest types. For example, the two mudstone-sandstone generalist species (*Shorea macroptera* and *S. smithiana*) were only observed in the valleys of sandstone forests, where higher nutrient and water availability is likely to be found close to small streams. Further research would be needed to confirm these fine-scale habitat preferences of generalist species in the Sepilok forest.

Trait plasticity with respect to tree height was also low in dipterocarp forests, with limited adjustment of leaf traits with tree height (chapter 3). I found height-related variation in most leaf traits to be small, except for leaf mass per area (LMA) and area-based photosynthetic capacity and respiration. This confirms that plasticity in LMA is a key adaptation to allow trees to respond to changes in their environment with height (Cavaleri *et al.*, 2010) and to increase metabolic rates per unit area. I also found no significant interaction effect between tree height and forest type on leaf traits, except leaf nitrogen, phosphorus and potassium concentrations, implying that differences in canopy structure and soil nutrient availability do not alter how traits change with tree height.

Whilst light availability naturally changes through the ontogenetic development of a tree, changes in light availability can occur because of disturbances. Long-term drought conditions are known to kill the largest trees in a forest (Phillips *et al.*, 2010; Rowland *et al.*, 2015a), creating a more open canopy with greater understory light availability. In chapter 5, I found that light was an important control on leaf physiology in Amazon trees under drought conditions and that small trees (1-10 cm DBH) can respond to increasing light availability despite reduced water availability. Small trees increased area-based photosynthetic capacity, leaf dark respiration and LMA in order to increase productivity under high light conditions. Increasing nutrient use efficiency, modifying the relative investment into the light dependent versus carboxylation reactions (chapter 5) and increasing hydraulic efficiency (Giles *et al.* in review) were important mechanisms that allowed these small trees to take advantage of the additional light available. These positive responses to increased light availability however were restricted to small trees, with large trees either not shifting their traits or downregulating metabolism in response to drought under high light (Bittencourt *et al.*, 2020; Rowland *et al.*, 2020). The ability of small trees to respond to respond to long-term drought conditions may enhance the resilience of these forests to shifting climatic conditions.

Selective logging represents another disturbance that changes canopy structure and increases understory light availability in tropical forests (Milodowski *et al.*, 2021). In chapter 4, I found varying responses in leaf traits to logging with intraspecific shifts towards higher LMA in old-growth species, but shifts towards lower LMA in community weighted means. In seedlings, it appears that increased light availability may enhance stress on shade-tolerant species and shift community composition towards species that have a preference for higher light environments. Overall, it appears that the ability to respond to changes in light availability vary with ontogenetic development, peaking in trees of intermediate size (1-10 cm DBH).

Selective logging also changes the soil environment, reducing nutrient and water availability (Swinfield *et al.*, 2020). Seedling communities were found to shift investment towards belowground resources and to increase specific maximum root length (chapter 4). These adaptations were likely important in maintaining leaf nutrient concentrations and water uptake and to avoid elevated mortality rates, as common species that had lower specific root length had lower leaf nutrient concentrations and higher mortality rates. Overall, variation in several traits are likely to be important for trees to be able to respond to natural and human-induced changes in their environment.

6.2.3 How will environmental change affect species composition of tropical forests?

Not all species are predicted to have the capacity to respond to environmental change. Many tree species in tropical forests are highly specialised and sensitive to changes in their abiotic environment. In Pasoh, Danum Valley and BCI, a high proportion of species (47-78%) were found to be associated to multiple environmental variables (chapter 2). As environmental change can affect multiple different abiotic conditions, these specialist species will be more likely to be pushed to the edge of their niche and unable to survive.

In South-East Asian forests, dipterocarps are the dominant family and have highly specialised distributions. Some species are more generalist in their distribution and can survive across a slightly wider range of environmental conditions. However, at Sepilok I found that trait plasticity is low even in these more generalist species, suggesting dipterocarps may be highly vulnerable to environmental change and habitat loss if forest cover loss is concentrated on certain soil types (chapter 3). In Borneo, selective logging is widespread and is a major driver of environmental change (Gaveau *et al.*, 2014). In logged forests, dipterocarp and other dominant species of old-growth forests were found to have higher seedling mortality rates than earlier successional species (chapter 4). As a result, logging and other environmental changes are likely to cause a shift in tree communities with earlier successional species increasing their dominance. Logging also reduced local scale functional diversity, resulting in shifts towards more homogenous communities.

In Amazonian forests, species also showed varying capacity to respond to long-term drought conditions (chapter 5). We found significant taxonomic effects when studying changes in carbon metabolism and hydraulic traits of both large and small trees (chapter 5; Bittencourt *et al.* (2020); Rowland *et al.* (2020); Giles *et al.* (in review)). However, in contrast to Bornean forests, the hyper-dominant species showed the greatest capacity to respond to changes in their environment. These findings support previous studies from Amazonia and Africa that found drought increases the dominance of dry-affiliated species (Fauset *et al.*, 2012; Esquivel-Muelbert *et al.*, 2019; Aguirre-Gutierrez *et al.*, 2020). My findings indicate there is likely to be an increase in the dominance of the species that are pre-adapted to the novel conditions created by environmental change across tropical forests.

6.3 Perspectives and Challenges

The findings of this thesis present important developments towards our understanding of tropical forest ecology and unlock new areas for future research. Meanwhile, several research challenges were identified that constrain the conclusions that can be drawn. I outline some of the main challenges and areas for future research here.

6.3.1 Disentangling niche dimensions

The niche of tropical forest trees is complex and multi-dimensional, with variation in environments interacting in intricate ways to determine tree physiology and function. Many different environmental variables co-vary within tropical forests across environmental gradients, making it difficult to disentangle their effects on species distributions and physiology. In chapter 2, several soil nutrient, topographic and canopy structure variables were correlated and had to be condensed into principal components for statistical models to be fit. This made it challenging to understand the exact drivers of species distributions. In Sepilok, soil nutrient availability, soil texture, water availability, topography and canopy structure all vary across the edaphic gradient. This posed a challenge when trying to explain the drivers of trait variation, with leaf nutrient concentrations and tree height providing the best available proxies for nutrient and light availability. Meanwhile, selective logging and drought both cause considerable changes to many environmental variables, making it difficult to isolate individual mechanistic drivers of observed responses. The effects of environmental variation on species distribution and physiology are also likely to occur in interactive and non-linear ways. Whilst the interactive effects of environmental variation were studied in some chapters, it was not possible to include interactions in my species distribution models (chapter 2) because complex model structures already existed. This limits our ability to fully understand the niche of tropical forest trees.

In order to disentangle the different dimensions of species niches, both natural environmental gradients and experimental manipulations will be important. In some tropical forests, orthogonal gradients in environmental resources exist. For example, across the Isthmus of Panama, natural gradients in phosphorus and precipitation exist, allowing for these effects on species distributions and physiology to be disentangled whilst also allowing interactive effects to be studied. Distinct associations to both precipitation and phosphorus availability have been found across these gradients (Condit *et al.*, 2013), as well as variation in structural leaf and wood traits (Umaña *et al.*, 2020b). Future research should focus on identifying equivalent orthogonal gradients in other regions to see if these patterns hold elsewhere and orthogonal gradients in other resources to disentangle their effects. Meanwhile, additional research that focuses on more mechanistic metabolic and hydraulic traits across these gradients can improve our understanding of the mechanisms underlying niche differentiation across environmental gradients.

Whilst natural gradients are important, long-term experimental manipulations are needed to provide a full mechanistic understanding of how species differentiate their niche. Large-scale experiments are rare in tropical forests and have focused on a small sub-set of environmental variables. For example, nutrient manipulation experiments have predominantly focused on soil nitrogen, phosphorus and potassium (Newbery *et al.*, 1999; Sayer *et al.*, 2012; Wright *et al.*, 2018; Wright, 2019), with other cation additions only being implemented at few sites, e.g. the Amazon Fertilisation Experiment (Lugli *et al.*, 2021). Whilst these elements are important drivers of forest productivity, other elements are increasingly being recognised as important drivers of species distributions (e.g. John *et al.*, 2007). Experiments that manipulate other micro-nutrients will be important for understanding what role these elements play in determining species niches and their role on tree physiology. Experiments that interactively change the environment, e.g. drought plus fertilisation, will also help to identify how environments interact to affect species function and improve predictions of responses to environmental change.

6.3.2 Taxonomic coverage

Tropical forests are the most biodiverse forests globally (Terborgh, 1992). Whilst this diversity stimulates interesting questions, it also poses a major challenge when trying to understand the ecology of these forests. In chapter 2, I modelled the distribution of all species with an abundance of >6 individuals ha^{-1} at three forest sites, identifying the local-scale drivers of the distribution of 444 species. Whilst this level of taxonomic coverage is high compared to most studies, it still represents less than one quarter of all species found at the studied sites. The extreme rarity of most species posed a major challenge as modelling data with an over-abundance of zeros is difficult. Consequently, it was beyond the scope of this thesis to understand the niche of most species. Limits to sampling effort meant taxonomic coverage across all other chapters was also incomplete (13-15 species) – although higher than much previous research, it is not sufficient to allow extrapolation across the whole community. Large intraspecific variation further compounded the problem, limiting our ability to comprehensively predict variation in traits and responses to environmental change. Low taxonomic coverage can create biases in results (e.g. Rowland *et al.*, 2015b; Rowland *et al.*, 2020), meaning future research should try to expand on the taxonomic coverage whenever possible. Novel technologies and low-cost sensors can increase sampling efforts and should be implemented in future research (e.g. Pereira *et al.*, 2020). Meanwhile, novel methods and statistics should be developed to improve our understanding of the ecology of rare species.

6.3.3 Spatial coverage

Limits to the spatial coverage of this research represented another challenge when trying to extrapolate findings across all tropical forests. Each chapter of this thesis utilised data from permanent forest dynamics plots. Whilst these represent an important method for understanding long-term dynamics of forests, their small spatial extent (max. 50 ha) means findings from these plots may not be representative of tropical forests more widely. For example, most of our understanding of the impacts of long-term drought on tropical forests comes from the experimental plot in Caxiuanã studied in chapter 5. This experiment is located on *terra firme* forest in East Amazonia, a region with high seasonality in precipitation and more dry-affiliated and drought tolerant species (Esquivel-Muelbert *et al.*, 2017a; Esquivel-Muelbert *et al.*, 2017b). Consequently, the responses we observe in chapter 5 may not be replicated elsewhere and should therefore be interpreted with caution when trying to understand drought impacts more broadly within Amazonia and pan-tropically. Equivalent caution should also be taken when interpreting the findings of the other chapters presented in this thesis as they also represent highly localised research. Integration between remote sensing and field based measurements is becoming increasingly important for increasing spatial coverage (Jucker *et al.*, 2018b; Philipson *et al.*, 2020; Swinfield *et al.*, 2020) and should continue to be used to upscale our understanding of tropical forest ecology.

6.3.4 Long-term dynamics

One of the major challenges in tropical forest research is understanding long-term dynamics. Whilst this thesis uses two long-term manipulations of the environment (chapter 4: 27-39 years post-logging; chapter 5: 15 years of experimental drought), these remain short-term when considered with respect to the average 200-400 year life span of tropical forest trees (Martínez-Ramos & Alvarez-Buylla, 1998). Long-term experiments, such as those used in this thesis remain rare. For example, most drought experiments in tropical forests have been short-lived, with only Caxiuanã providing insights beyond 6 years (Meir *et al.*, 2015). In order to understand long-term dynamics and responses to environmental change, continued monitoring of long-term studies should endure. For example, continued monitoring of populations at both studies presented in chapters 4 and 5 will provide insights into long-term changes in recruitment and species composition. Whilst funding challenges may prevent some experiments from continuing long-term, efforts to continue monitoring beyond the lifespan of the experiment can also provide insights into how species recover from environmental change. This will identify whether disturbances push ecosystems beyond critical thresholds or return to equilibrium following environmental changes.

6.4 Implications and Conclusions

Tropical forests are of global importance because of their contribution to the global carbon cycle, their exceptional biodiversity and the global and local ecosystem services they deliver. These forests, however, are increasingly threatened by global environmental change. This thesis helps contribute to our understanding of tropical forests and how they are likely to respond to environmental change with implications for conservation and ecosystem restoration. By increasing our understanding of the niche of tropical forest tree species, it is possible to improve restoration efforts so that the appropriate species are matched to the environment of restoration sites. The high specialisation and multiple dimensions of species-environment associations means careful matching of the species to the environment is likely to be important for the success of restoration projects.

The high specialisation of tropical forest species is also likely to leave many species vulnerable to environmental change. Both selective logging and long-term drought conditions could change the species composition of tropical forests without intervention. Old-growth specialist species are likely to have low rates of natural regeneration in logged forests because of high seedling mortality. Meanwhile, whilst hyper-dominant species show positive responses to long-term drought, the ability of rarer species to respond remains uncertain. Efforts that ensure these old-growth specialist and rarer species survive are likely to be important to avoid shifts in species composition that cause tropical forests to become dominated by few generalist species. Planting of these species may not be enough though. Instead, conservation and restoration efforts may also need to focus on maintaining and recovering the abiotic environment. Various aspects of the abiotic environment were found to determine the distribution of many species and to support high species richness in tropical forests. Changes to the soil environment caused by selective logging were found to reduce nutrient access of common species with implications on seedling mortality rates. Recovery of intact soil and canopy environments could be critical for the success of restoration in logged forests.

Despite the great challenges that face conservation and restoration practitioners, the findings of this thesis reveal some resilience within tropical forests. In some regions, small trees may have trait plasticity that may allow them to naturally regenerate following the loss of large trees during drought events. Despite reduced recruitment of old-growth specialist species in logged forests, earlier successional species also appear to be able to respond to environmental changes and may be able to make some important contributions to ecosystem services, such as carbon cycling and habitat for wildlife. Overall, this thesis provides evidence to suggest that whilst intervention is likely to be needed to maintain and recover biodiverse communities under environmental change, tropical forests appear to have some innate resilience that provides hope that they will be able to survive environmental change.

Appendix 1: Co-authored publications

Several co-authored papers have been developed during the timeframe of my PhD. The following papers have been published, are in review or are in preparation for submission. The abstracts are presented here alongside the full author list and author contributions.

Amazonia trees have limited capacity to acclimate plant hydraulic properties in response to long-term drought

Bittencourt P.R.L., Oliveira R.S., da Costa A.C.L., Giles A.L., Coughlin I., Costa P.B., Bartholomew D.C., Ferreira L.V., Vasconcelos S.S., Barros F.V., Junior J.A.S., Oliveira A.A.R., Mencuccini M., Meir P. & Rowland L. (2020) Amazonia trees have limited capacity to acclimate plant hydraulic properties in response to long-term drought. *Global Change Biology*, **26**, 3569-3584.

Abstract

The fate of tropical forests under future climate change is dependent on the capacity of their trees to adjust to drier conditions. The capacity of trees to withstand drought is likely to be determined by traits associated with their hydraulic systems. However, data on whether tropical trees can adjust hydraulic traits when experiencing drought remain rare. We measured plant hydraulic traits (e.g. hydraulic conductivity and embolism resistance) and plant hydraulic system status (e.g. leaf water potential, native embolism and safety margin) on >150 trees from 12 genera (36 species) and spanning a stem size range from 14 to 68 cm diameter at breast height at the world's only long running tropical forest drought experiment. Hydraulic traits showed no adjustment following 15 years of experimentally imposed moisture deficit. This failure to adjust resulted in these drought-stressed trees experiencing significantly lower leaf water potentials, and higher, but variable, levels of native embolism in the branches. This result suggests that hydraulic damage caused by elevated levels of embolism is likely to be one of the key drivers of drought-induced mortality following long-term soil moisture deficit. We demonstrate that some hydraulic traits changed with tree size, however, the direction and magnitude of the change was controlled by taxonomic identity. Our results suggest that Amazonian trees, both small and large, have limited capacity to acclimate their hydraulic systems to future droughts, potentially making them more at risk of drought-induced mortality.

Author contributions

P.R.L.B., R.S.O., M.M., P.M. and L.R. conceived the research ideas, developed the project and wrote the manuscript. P.M. and A.C.L.D. conceived and performed experiment. L.A.G., I.C., B.P.C., D.C.B., S.S.V., L.V.F., A.R., A.A.R., J.A.S.J., L.R. and P.R.L.B. contributed to data collection and all authors contributed to manuscript preparation.

The response of carbon assimilation and storage to long-term drought in tropical trees is dependent on light availability

Rowland L., Costa A.C.L., Oliveira R.S., Bittencourt P.R.L., Giles A.L., Coughlin I., Britto Costa P., Bartholomew D., Domingues T.F., Miatto R.C., Ferreira L.V., Vasconcelos S.S., Junior J.A.S., Oliveira A.A.R., Mencuccini M. & Meir P. (2020) The response of carbon assimilation and storage to long-term drought in tropical trees is dependent on light availability. *Functional Ecology*, **35**, 43-53.

Abstract

1. Whether tropical trees acclimate to long-term drought stress remains unclear. This uncertainty is amplified if drought stress is accompanied by changes in other drivers such as the increases in canopy light exposure that might be induced by tree mortality or other disturbances.

2. Photosynthetic capacity, leaf respiration, non-structural carbohydrate (NSC) storage and stomatal conductance were measured on 162 trees at the world's longest running (15 years) tropical forest drought experiment. We test whether surviving trees have altered strategies for carbon storage and carbon use in the drier and elevated light conditions present following drought-related tree mortality.

3. Relative to control trees, the surviving trees experiencing the drought treatment showed functional responses including: (a) moderately reduced photosynthetic capacity; (b) increased total leaf NSC; and (c) a switch from starch to soluble sugars as the main store of branch NSC. This contrasts with earlier findings at this experiment of no change in photosynthetic capacity or NSC storage. The changes detected here only occurred in the subset of drought-stressed trees with canopies exposed to high radiation and were absent in trees with less-exposed canopies and also in the community average. In contrast to previous results acquired through less intensive species sampling from this experiment, we also observe no species-average drought-induced change in leaf respiration.

4. Our results suggest that long-term responses to drought stress are strongly influenced by a tree's full-canopy light environment and therefore that disturbance-induced changes in stand density and dynamics are likely to substantially impact tropical forest responses to climate change. We also demonstrate that, while

challenging, intensive sampling is essential in tropical forests to avoid sampling biases caused by limited taxonomic coverage.

Author contributions

L.R., M.M., R.S.O. and P.M. designed the data collection; A.C.L.d.C. and P.M. designed the drought experiment; L.R., A.C.L.d.C., P.R.L.B., I.C., P.d.B.C., D.B., A.G., T.F.D., R.C.M., L.V.F., S.S.V., J.A.S.J. and A.A.R.O all contributed to data collection and all authors contributed to writing the manuscript.

Small understorey trees have greater capacity than canopy trees to adjust hydraulic traits following prolonged drought in a tropical forest

Giles, A. L., Rowland L., Bittencourt P. R. L. , Bartholomew, D. C., Coughlin I., Costa P. B., Domingues T., Miatto, R.C, Barros, F. V., Ferreira L. V., Groenendijk, P., Oliveira A. A. R., da Costa A. C. L., Meir P., Mencuccini M., Oliveira R. S. (in review) Small understorey trees have greater capacity than canopy trees to adjust hydraulic traits following prolonged drought in a tropical forest. *Tree Physiology.*

Abstract

Future climate change predictions for tropical forests highlight increased frequency and intensity of extreme drought events. However, it remains unclear whether the different niches occupied by large and small trees create distinct strategies that confer differential drought tolerance. The future of tropical forests is ultimately dependent on the capacity of small trees (<10 cm in diameter) to adjust their hydraulic system to tolerate drought. We evaluated multiple hydraulic traits indicative of drought tolerance of small trees across nine common Neotropical genera at the world's longest-running tropical forest throughfall-exclusion experiment and compared their responses with surviving large canopy trees. Small understorey trees in both the Control and the throughfall exclusion treatment (TFE) had significantly lower minimum stomatal conductance and maximum hydraulic leaf-specific conductivity relative to large trees of the same genera, as well as significantly greater branch hydraulic safety margin (HSM), percentage loss of conductivity (PLC) and embolism resistance, demonstrating they occupy a distinct hydraulic niche. Surprisingly, in response to the drought treatment, small trees increased specific hydraulic conductivity by 56.3% and leaf : sapwood area ratio by 45.6%. The greater HSM of small understorey trees relative to large canopy trees likely enabled them to adjust other aspects of their hydraulic systems to increase hydraulic conductivity and take advantage of increases in light availability in the understorey, driven by the drought-induced mortality of canopy trees. Our results demonstrate that differences in hydraulic strategies between small understorey and large canopy trees drive hydraulic niche segregation. Small understorey trees can adjust their hydraulic systems in response to changes in water and light availability indicating natural regeneration of tropical forests following long-term drought may be possible.

Author contributions

ALG collected and compiled the data alongside LR, PRLB, IC, PBC, PG, LVF, DDV, JASJ, DCB and ACLdC. LR designed the study with MM, ACLdC, PM , ALG and RO. ALG, PRLB and LR performed the statistical analysis and ALG, LR and RO wrote the paper, all other authors substantially contributed to revisions.

Divergence of hydraulic traits among tropical forest trees across horizontal and vertical resource gradients in Borneo

Bittencourt, P. R. L., Bartholomew, D. C.**,** Banin, L. F., Bin Suis, M. A. F., Nilus, R., Burslem, D. F. R. P., Rowland, L. (in review) Divergence of hydraulic traits among tropical forest trees across horizontal and vertical resource gradients in Borneo. *New Phytologist.*

Abstract

- Fine-scale topographic-edaphic gradients are common in tropical forests and drive high spatial turnover in species composition and marked changes in forest structure and function. We evaluate how hydraulic traits of dipterocarp species relate to vertical and spatial niche specialization along such a gradient.
- Along a marked topographic-edaphic gradient with uniform climate in Borneo, we measured 6 key hydraulic traits in >150 individuals of differing heights in 13 dipterocarp species. We investigated how hydraulic traits relate to habitat, tree height and their interaction across this gradient
- We found that embolism resistance increases in forests on nutrient poor, sandy soil, but varied with tree height. In contrast, water transport efficiency did not change with habitat, instead showing significant increases with tree height across all trees along the gradient. Habitat and height did not interact for the traits we measured; however habitat type controlled trait-trait coordination.
- Our data reveal that variability in the hydraulic traits of dipterocarp trees is driven by a complex combination of topographic-edaphic conditions, tree height and taxonomic identity. Our work indicates that hydraulic traits play a significant role in shaping the topographic-edaphic and vertical niche specialization of dipterocarp species.

Author contributions

P.R.L.B., D.C.B., L.R., L.F.B and D.F.R.P.B. designed the data collection, P.R.L.B. and D.C.B. contributed to data collection, P.R.L.B. did the statistical analysis and wrote the manuscript and all authors contributed to reviewing the manuscript.

Preventing extinctions of the world's trees – *in situ* and *ex situ* conservation.

Rivers, M.C., Bartholomew, D. C., Beech, E., Barstow, M., Davies, K., Jänicke, S., Smith, P., Oldfield, S. (in review) Preventing extinctions of the world's trees – in situ and ex situ conservation. *Nature Ecology and Evolution.*

This paper is an output from my three-month internship undertaken at Botanic Gardens Conservation International as part of my PhD.

Abstract

Trees are essential to Earth, but increasingly under threat. We present the first global assessment of the conservation status and extent of *in situ* (protected areas) and *ex situ* (botanic gardens and seed banks) conservation for all tree species. Our research shows that 38% of tree species are threatened with extinction. Eighty percent of trees are found in a protected area, including 70% of threatened species. Meanwhile, 30% of trees are found in *ex situ* collections. However, these conservation actions fail to fully complement each other, and 25% of threatened tree species have neither *in situ* nor *ex situ* protection. Tropical species are underrepresented in both types of conservation. We consider the results in relation to global conservation targets. We call for a greater focus on the conservation of threatened tree species with complementarity of *in situ* and *ex situ* conservation, together with policy, education, capacity building and livelihood measures.

Author contributions

M.C.R. and D.C.B. led on analysis, development and manuscript drafting; E.B., M.B., K.D. made substantial contributions to manuscript preparation; S.J. contributed to the analysis and interpretation of data; P.S. and S.O. contributed to the conceptual development of the work and manuscript preparation.

Red List of Bornean Endemic Dipterocarps

David Bartholomew, Megan Barstow, Agusti Randi, Vilma Bodos, Daniele Cicuzza, Pui Kiat Hoo, Suzika Juiling, Eyen Khoo, Yulita Kusumadewi, Ling Chea Yiing, Andi Maryani , Colin Maycock , Reuben Nilus, Joan Pereira, Julia Sang, Iyan Robiansyah, John B Sugau, Sasikumar Tanggaraju and Sandy Tsen (2021) Red List of Bornean Endemic Dipterocarps.

This red list publication is an output from my three-month internship undertaken at Botanic Gardens Conservation International as part of my PhD.

Executive Summary

The Red List of Bornean Endemic Dipterocarps provides and analyses IUCN Red List assessments for all dipterocarp species restricted to the island of Borneo. Trees of the Dipterocarpaceae family dominate the forests of South-East Asia, meaning the conservation of this family is of vital importance for protecting the biodiversity of the region. Borneo represents the centre of dipterocarp diversity with 269 accepted species, including 162 endemics.

Of the 162 species assessed, 134 species (83%) are of conservation concern. This includes 99 species that are threatened with extinction (Vulnerable, Endangered or Critically Endangered). If Data Deficient species are assumed to have equivalent probability of being threatened as all other assessed species, 62.3% of Bornean endemic dipterocarps are assessed as threatened. Eighteen species (11%) are Critically Endangered and require urgent conservation action.

The majority of assessed species are experiencing a population decline caused by a multitude of threats. The high-quality timber and local abundance of dipterocarps across Borneo mean they are widely logged and traded internationally. Unsustainable logging practices have caused rapid population declines of many species. The other primary threats to Bornean endemic dipterocarps are forest conversion for agro-industrial oil palm and wood pulp plantations, roads and increased fire frequency.

Currently, 146 (90%) of Bornean endemic dipterocarp species are protected *in situ*, including 85% of threatened species. Rates of *ex situ* conservation are considerably lower, with only 32 threatened species (32%) found in *ex situ* collections. This falls short of Target 8 of the Global Strategy for Plant Conservation that states that at least

75% of threatened species should be held in *ex situ* collections. Ten species, all of which are threatened, have no formal protection *in situ* or *ex situ*.

This publication identifies Bornean endemic dipterocarps that are most at risk of extinction, including 18 Critically Endangered species that require immediate conservation action. A diverse set of conservation priorities that are needed to protect these species from the array of threats they face are outlined. These assessments should be used to inform policy and conservation actions in the region to protect and prevent the loss of Borneo's unique dipterocarp diversity.

Author contributions

M.B. conceived the idea for the report and organised the red list publications, A.R., V.B., D.C., P.K.H., S.J., E.K., Y.K., L.C.Y., A.M., C.M., R.N., J.P., J.S., I.R., J.B.S., S.Ta. and S.Ts. assessed the species, D.B. led the data analysis, D.B. and M.B. wrote the report, V.B., D.C., Y.K., A.R., I.R. and L.C.Y. contributed case studies and all authors contributed to reviewing the report.

Appendix 2: Supporting Information of Chapter 2

Supplementary Methods

Model equations

Species distributions were modelled by a different equation at each site because of differences in data availability (not all soil co-variates were measured at each site) and differences in co-variate autocorrelation. Principal component analysis was used to condense auto-correlated co-variates at each site, with different co-variates contributing to the main axes at each site (see Table 2.2). The following equations were used to model the distribution of all species at each site:

BCI:

Species Abundance ~ Aspect + Elevation + TPI + TWI + topography PC1 + canopy PC1 + canopy PC2 + NH_4 + NO_3 + PO_4 + B + Cu + Fe + Na + P + soil PC1 + spatially structured random effect + spatially unstructured random effect *(1)*

Danum Valley:

Species Abundance ~ Aspect + Elevation + TPI + TWI + topography PC1 + canopy PC1 + canopy PC2 + NH_4 + NO_3 + PO_4 + B + Cr + Fe + Mn + Na + Ni + P + soil PC1 + soil PC2 + spatially structured random effect + spatially unstructured random effect *(2)*

Pasoh:

Species Abundance ~ Aspect + TPI + TWI + topography PC1 + Gap Fraction at 2m + canopy PC1 + canopy PC2 + NH_4 + NO_3 + PO_4 + Al + Ca + Fe + K + Mg + Mn + Na + P + pH + spatially structured random effect + spatially unstructured random effect *(3)*

In order to make direct comparisons between the three sites, models were re-run for all species using a model with co-variates with data available at all sites and that were not autocorrelated at any site ($r < 0.7$):

Species Abundance ~ Aspect + Elevation + TPI + TWI + Gap Fraction at 2m + Gap Fraction at 10m + maximum canopy height + NH_4 + NO_3 + PO_4 + Ca + Fe + Mn + Na + P + spatially structured random effect + spatially unstructured random effect *(4)*

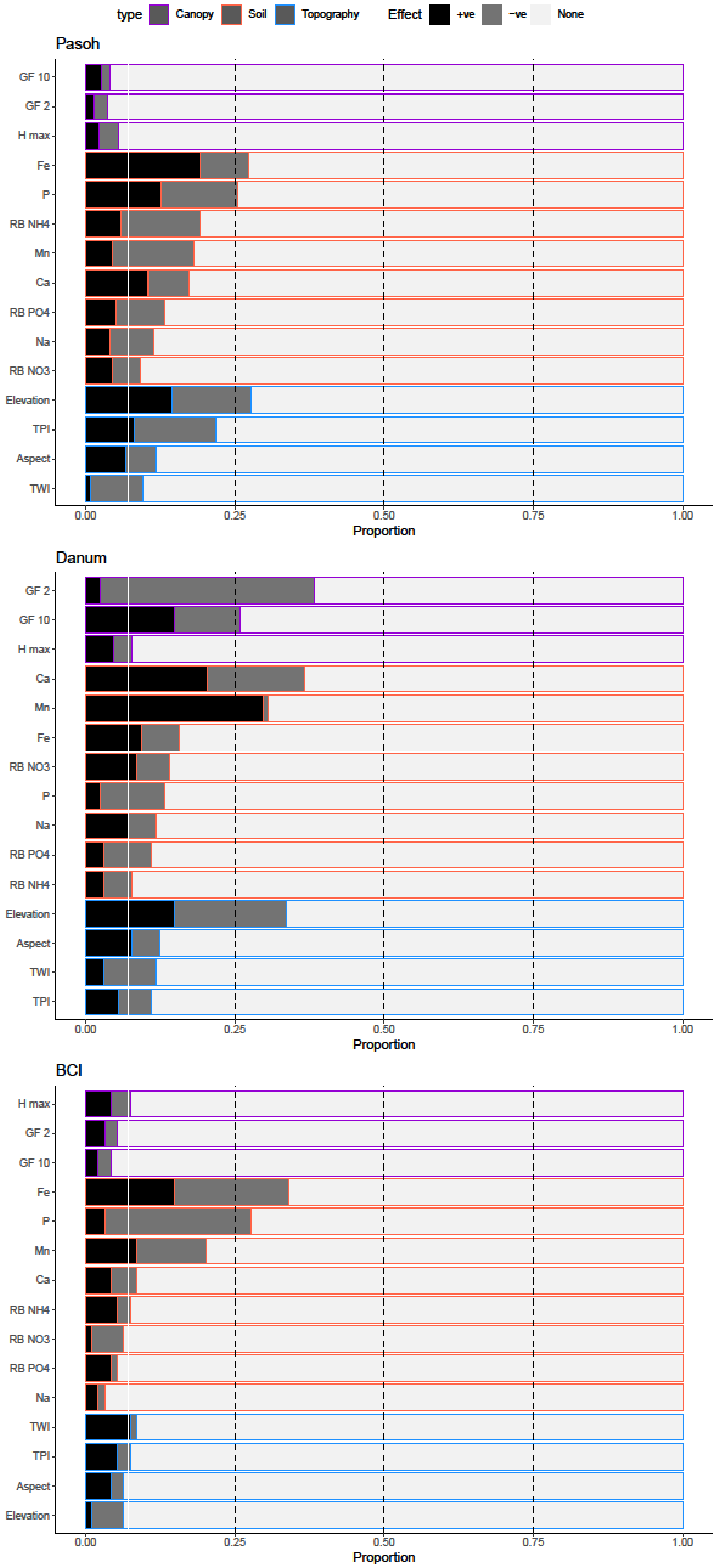
SI Table 2.1: Details of the Airborne LiDAR surveys used to generate digital elevation models and canopy height models used in this study.

Site	**Date of Flight**	**Sensor**	**Flying altitude (m)**	**Reference**
Barro Colorado Island	15 August 2009 to 10 September 2009 (11 overflights)	Optech ALTM 3100 onboard an aeroplane	457	STRI, NSF DEB0939907, J. Dalling, S. Hubbell and S. Dewalt
Danum Valley	November 2016	Leica ALS50-II lidar sensor onboard a Dornier 228-201 aeroplane	1400 - 2400	Jucker *et al.* (2018a)
Pasoh	26 April 2018	RieglLMS-Q680i LiDAR system onboard EC120 Helicopter	600	Omar *et al.* (2020)

SI Table 2.2: Data transformations for environmental co-variates used in the species distribution models at each site. Dashes represent no data transformation, whilst NAs represent cases where the co-variate was not included at that site.

Environmental co-variate	Barro Colorado Island	Danum Valley	Pasoh
Aspect	-	-	-
Elevation	-	-	-
Topographic Position Index	-	-	-
Topographic Wetness Index	-	-	-
Topography PC1	-	-	-
Gap Fraction at 2 m	Natural log	Natural log	Natural log
Gap Fraction at 10 m	Natural log	Natural log	Natural log
Maximum Canopy Height	-	-	-
Canopy PC1	-	Natural log	Square-root
Canopy PC2	-	-	Square-root
Al	NA	NA	-
B	-	Natural log	NA
Ca	-	-	Natural log
Cr	NA	-	NA
Cu	-	NA	NA
Fe	-	-	-
K	NA	NA	-
Mg	NA	NA	-
Mn	-	-	-
NH_4	-	-	-
NO_3	-	-	-
Na	-	-	Natural log
Ni	NA	Natural log	NA
pH	NA	NA	-
PO_4	-	-	-
Bioavailable P	-	-	-
Soil PC1	-	Natural log	NA
Soil PC2	NA	-	NA

SI Figure 2.1: The proportion of species with a significant positive (black) or negative (grey) association to a range of environmental co-variates at each of the three study sites: (a) Pasoh (n = 221), (b) Danum Valley (n = 129), (c) Barro Colorado Island (n = 94). The same fifteen co-variates were included in the model structure at all sites (SI Methods equation 4) to allow direct comparison between sites. The white dotted line represents the proportion of species expected to be associated with each co-variate under a type I error rate of 0.0722.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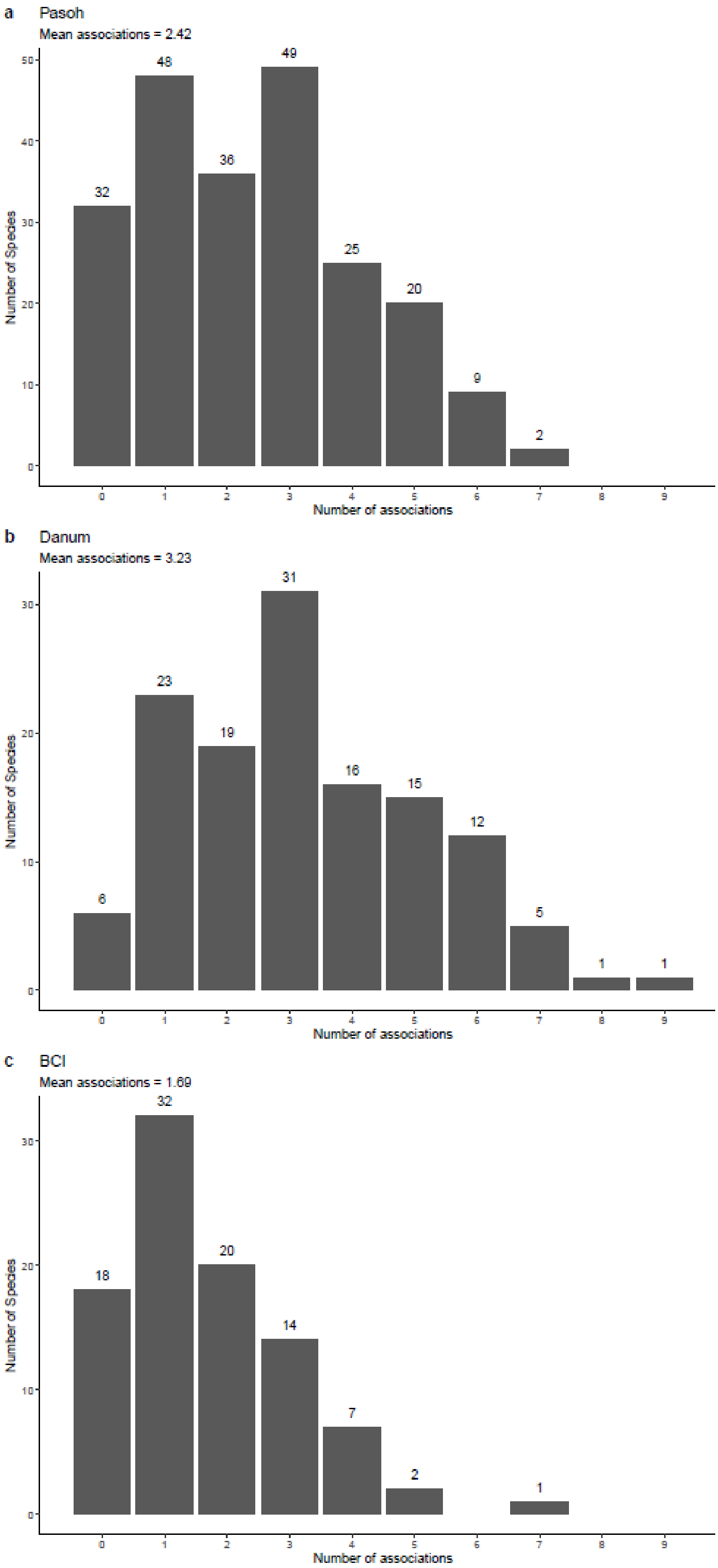
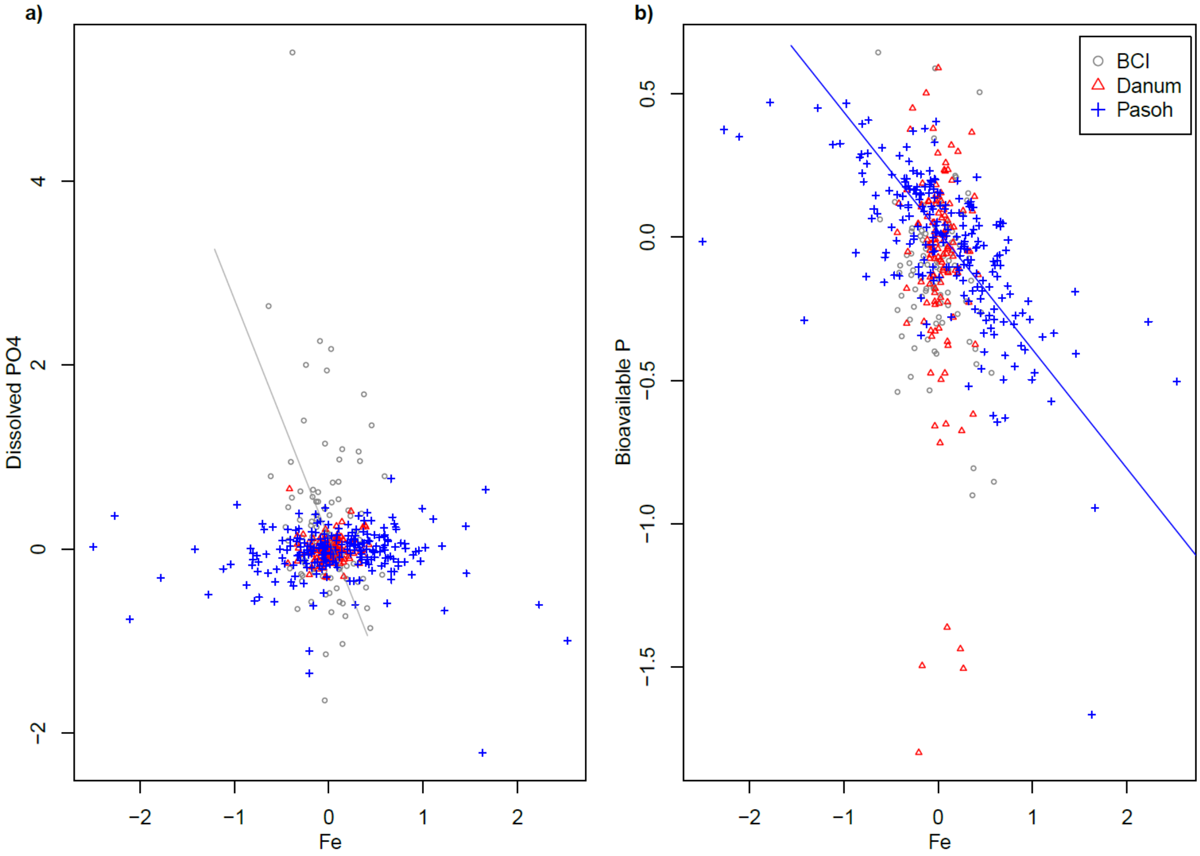
Canopy
Soil
Topography
Effect
+ve
−ve
None
Pasoh
GF 10
GF 2
H max
Fe
P
RB NH4
Mn
Ca
RB PO4
Na
RB NO3
Elevation
TPI
Aspect
TWI
0.00
0.25
0.50
0.75
1.00
Proportion
Danum
GF 2
GF 10
H max
Ca
Mn
Fe
RB NO3
P
Na
RB PO4
RB NH4
Elevation
Aspect
TWI
TPI
0.00
0.25
0.50
0.75
1.00
Proportion
BCI
H max
GF 2
GF 10
Fe
P
Mn
Ca
RB NH4
RB NO3
RB PO4
Na
TWI
TPI
Aspect
Elevation
0.00
0.25
0.50
0.75
1.00
Proportion

SI Figure 2.2: Histograms of the number of significant species-environment associations at the three sites (a) Pasoh, (b) Danum Valley and (c) Barro Colorado Island using the full model equations (SI Methods equations 1-3).

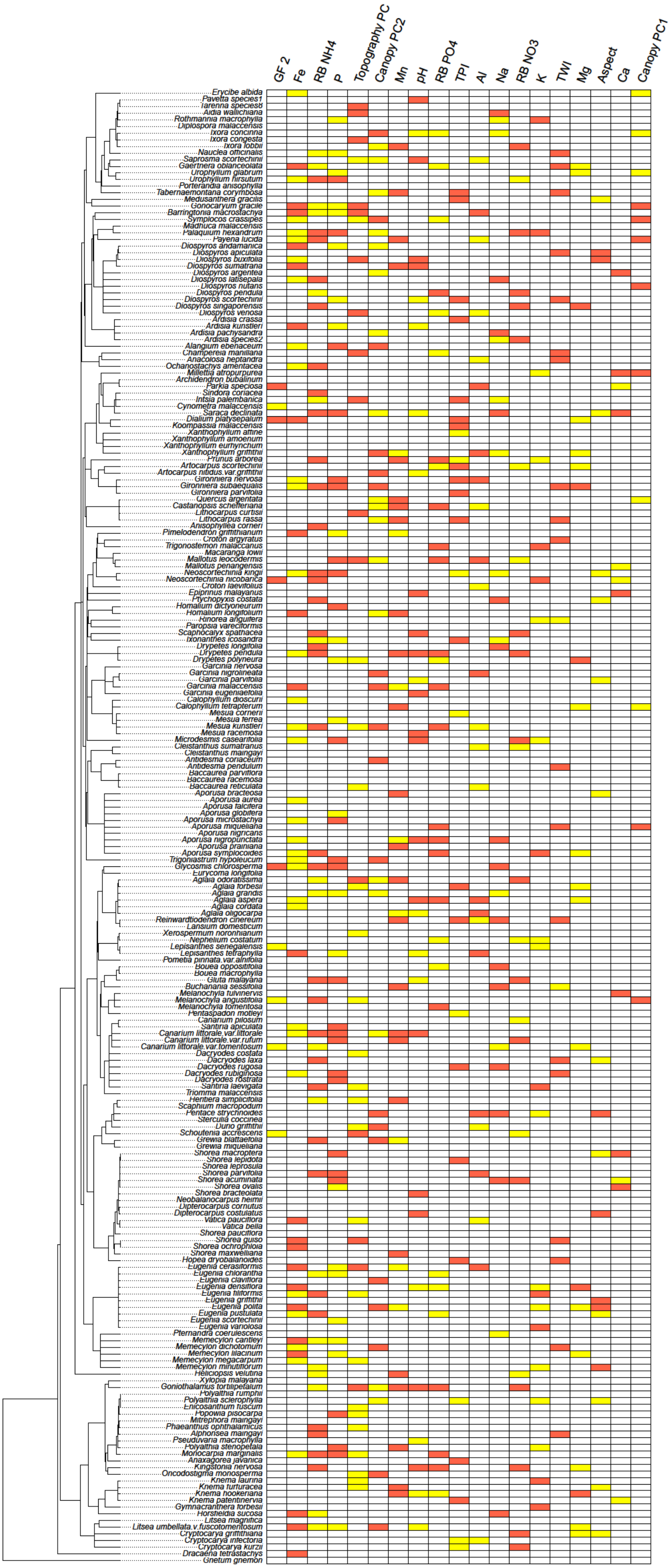


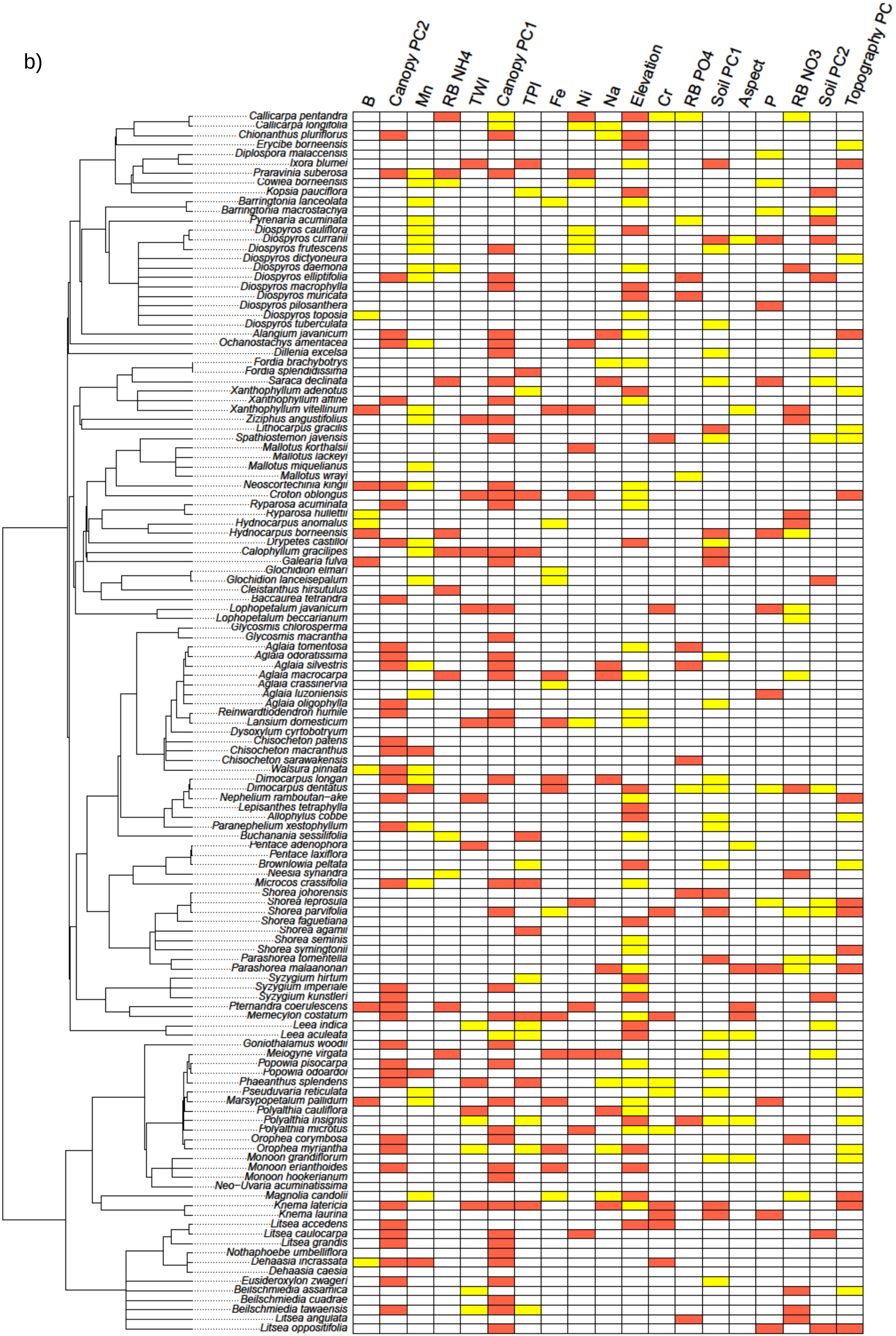
SI Figure 2.3: Standardised major axis regression between effect sizes of species associations to Fe and (a) dissolved PO_4 and (b) bioavailable P for each site: BCI – grey circles, Danum Valley – red triangles, Pasoh – blue crosses. Lines of significant regressions ($p < 0.05$) are presented. Effect sizes are taken from the models with the same 15 environmental co-variates shared by all sites.



SI Figure 2.4: Species associations plotted against a phylogenetic tree for (a) Pasoh, (b) Danum Valley and (c) Barro Colorado Island. Yellow boxes represent positive associations to an environmental co-variate, red boxes represent a negative association and white boxes represent no association.

a)


GF 2
Fe
RB NH4
P
Topography PC
Canopy PC2
Mn
pH
RB PO4
TPI
Al
Na
RB NO3
K
TWI
Mg
Aspect
Ca
Canopy PC1
Erycibe albida
Pavetta species1
Tarenna species8
Aidia wallichiana
Rothmannia macrophylla
Diplospora malaccensis
Ixora concinna
Ixora congesta
Ixora lobbii
Nauclea officinalis
Saprosma scortechinii
Gaertnera oblanceolata
Urophyllum glabrum
Urophyllum hirsutum
Porterandia anisophylla
Tabernaemontana corymbosa
Medusanthera gracilis
Gonocaryum gracile
Barringtonia macrostachya
Symplocos crassipes
Madhuca malaccensis
Palaquium hexandrum
Payena lucida
Diospyros andamanica
Diospyros apiculata
Diospyros buxifolia
Diospyros sumatrana
Diospyros argentea
Diospyros latisepala
Diospyros nutans
Diospyros pendula
Diospyros scortechinii
Diospyros singaporensis
Diospyros venosa
Ardisia crassa
Ardisia kunstleri
Ardisia pachysandra
Ardisia species2
Alangium ebenaceum
Champereia manillana
Anacolosa heptandra
Ochanostachys amentacea
Millettia atropurpurea
Archidendron bubalinum
Parkia speciosa
Sindora coriacea
Intsia palembanica
Cynometra malaccensis
Saraca declinata
Dialium platysepalum
Koompassia malaccensis
Xanthophyllum affine
Xanthophyllum amoenum
Xanthophyllum eurhynchum
Xanthophyllum griffithii
Prunus arborea
Artocarpus scortechinii
Artocarpus nitidus.var.griffithii
Gironniera nervosa
Gironniera subaequalis
Gironniera parvifolia
Quercus argentata
Castanopsis schefferiana
Lithocarpus curtisii
Lithocarpus rassa
Anisophyllea corneri
Pimelodendron griffithianum
Croton argyratus
Trigonostemon malaccanus
Macaranga lowii
Mallotus leocodermis
Mallotus penangensis
Neoscortechinia kingii
Neoscortechinia nicobarica
Croton laevifolius
Epiprinus malayanus
Ptychopyxis costata
Homalium dictyoneurum
Homalium longifolium
Rinorea anguifera
Paropsia vareciformis
Scaphocalyx spathacea
Ixonanthes icosandra
Drypetes longifolia
Drypetes pendula
Drypetes polyneura
Garcinia nervosa
Garcinia nigrolineata
Garcinia parvifolia
Garcinia malaccensis
Garcinia eugeniaefolia
Calophyllum dioscurii
Calophyllum tetrapterum
Mesua cornerii
Mesua ferrea
Mesua kunstleri
Mesua racemosa
Microdesmis caseariifolia
Cleistanthus sumatranus
Cleistanthus maingayi
Antidesma coriaceum
Antidesma pendulum
Baccaurea parviflora
Baccaurea racemosa
Baccaurea reticulata
Aporusa bracteosa
Aporusa aurea
Aporusa falcifera
Aporusa globifera
Aporusa microstachya
Aporusa miqueliana
Aporusa nigricans
Aporusa nigropunctata
Aporusa prainiana
Aporusa symplocoides
Trigoniastrum hypoleucum
Glycosmis chlorosperma
Eurycoma longifolia
Aglaia odoratissima
Aglaia forbesii
Aglaia grandis
Aglaia aspera
Aglaia cordata
Aglaia oligocarpa
Reinwardtiodendron cinereum
Lansium domesticum
Xerospermum noronhianum
Nephelium costatum
Lepisanthes senegalensis
Lepisanthes tetraphylla
Pometia pinnata.var.alnifolia
Bouea oppositifolia
Bouea macrophylla
Gluta malayana
Buchanania sessifolia
Melanochyla fulvinervis
Melanochyla angustifolia
Melanochyla tomentosa
Pentaspadon motleyi
Canarium pilosum
Santiria apiculata
Canarium littorale.var.littorale
Canarium littorale.var.rufum
Canarium littorale.var.tomentosum
Dacryodes costata
Dacryodes laxa
Dacryodes rugosa
Dacryodes rubiginosa
Dacryodes rostrata
Santiria laevigata
Triomma malaccensis
Heritiera simplicifolia
Scaphium macropodum
Pentace strychnoides
Sterculia coccinea
Durio griffithii
Schoutenia accrescens
Grewia blattaefolia
Grewia miqueliana
Shorea macroptera
Shorea lepidota
Shorea leprosula
Shorea parvifolia
Shorea acuminata
Shorea ovalis
Shorea bracteolata
Neobalanocarpus heimii
Dipterocarpus cornutus
Dipterocarpus costulatus
Vatica pauciflora
Vatica bella
Shorea pauciflora
Shorea guiso
Shorea ochrophloia
Shorea maxwelliana
Hopea dryobalanoides
Eugenia cerasiformis
Eugenia chlorantha
Eugenia claviflora
Eugenia densiflora
Eugenia filiformis
Eugenia griffithii
Eugenia polita
Eugenia pustulata
Eugenia scortechinii
Eugenia variolosa
Pternandra coerulescens
Memecylon cantleyi
Memecylon dichotomum
Memecylon lilacinum
Memecylon megacarpum
Memecylon minutiflorum
Heliciopsis velutina
Xylopia malayana
Goniothalamus tortilipetalum
Polyalthia rumphii
Polyalthia sclerophylla
Enicosanthum fuscum
Popowia pisocarpa
Mitrephora maingayi
Phaeanthus ophthalamicus
Alphonsea maingayi
Pseuduvaria macrophylla
Polyalthia stenopetala
Monocarpia marginalis
Anaxagorea javanica
Kingstonia nervosa
Oncodostigma monosperma
Knema laurina
Knema furfuracea
Knema hookeriana
Knema patentinervia
Gymnacranthera forbesii
Horsfieldia sucosa
Litsea magnifica
Litsea umbellata.v.fuscotomentosum
Cryptocarya griffithiana
Cryptocarya infectoria
Cryptocarya kurzii
Dracaena tetrastachys
Gnetum gnemon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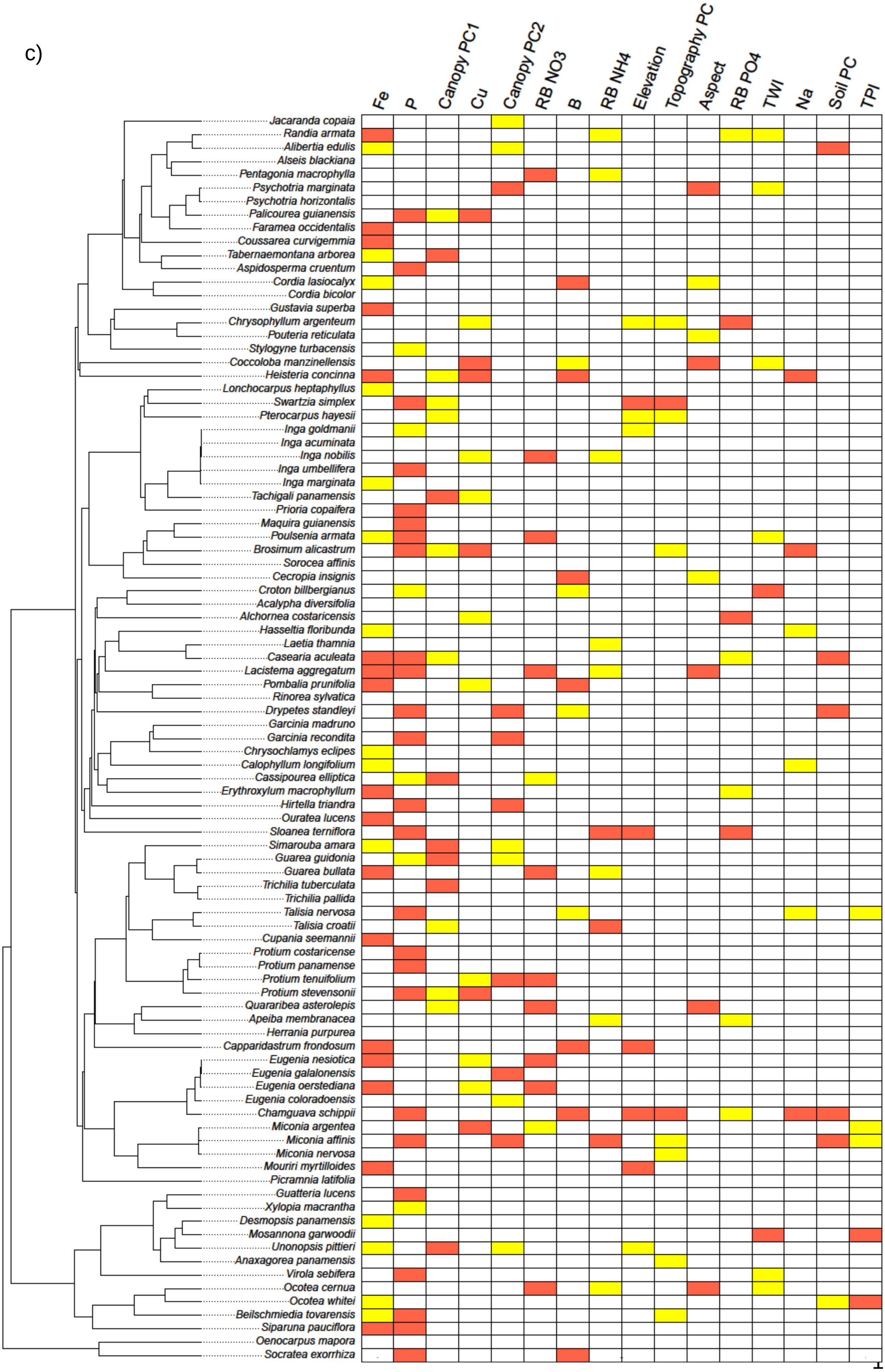
B
Canopy PC2
Mn
RB NH4
TWI
Canopy PC1
TPI
Fe
Ni
Na
Elevation
Cr
RB PO4
Soil PC1
Aspect
P
RB NO3
Soil PC2
Topography PC
Callicarpa pentandra
Callicarpa longifolia
Chionanthus pluriflorus
Erycibe borneensis
Diplospora malaccensis
Ixora blumei
Praravinia suberosa
Cowiea borneensis
Kopsia pauciflora
Barringtonia lanceolata
Barringtonia macrostachya
Pyrenaria acuminata
Diospyros cauliflora
Diospyros curranii
Diospyros frutescens
Diospyros dictyoneura
Diospyros daemona
Diospyros elliptifolia
Diospyros macrophylla
Diospyros muricata
Diospyros pilosanthera
Diospyros toposia
Diospyros tuberculata
Alangium javanicum
Ochanostachys amentacea
Dillenia excelsa
Fordia brachybotrys
Fordia splendidissima
Saraca declinata
Xanthophyllum adenotus
Xanthophyllum affine
Xanthophyllum vitellinum
Ziziphus angustifolius
Lithocarpus gracilis
Spathiostemon javensis
Mallotus korthalsii
Mallotus lackeyi
Mallotus miquelianus
Mallotus wrayi
Neoscortechinia kingii
Croton oblongus
Ryparosa acuminata
Ryparosa hullettii
Hydnocarpus anomalus
Hydnocarpus borneensis
Drypetes castilloi
Calophyllum gracilipes
Galearia fulva
Glochidion elmari
Glochidion lanceisepalum
Cleistanthus hirsutulus
Baccaurea tetrandra
Lophopetalum javanicum
Lophopetalum beccarianum
Glycosmis chlorosperma
Glycosmis macrantha
Aglaia tomentosa
Aglaia odoratissima
Aglaia silvestris
Aglaia macrocarpa
Aglaia crassinervia
Aglaia luzoniensis
Aglaia oligophylla
Reinwardtiodendron humile
Lansium domesticum
Dysoxylum cyrtobotryum
Chisocheton patens
Chisocheton macranthus
Chisocheton sarawakensis
Walsura pinnata
Dimocarpus longan
Dimocarpus dentatus
Nephelium ramboutan−ake
Lepisanthes tetraphylla
Allophylus cobbe
Paranephelium xestophyllum
Buchanania sessilifolia
Pentace adenophora
Pentace laxiflora
Brownlowia peltata
Neesia synandra
Microcos crassifolia
Shorea johorensis
Shorea leprosula
Shorea parvifolia
Shorea faguetiana
Shorea agamii
Shorea seminis
Shorea symingtonii
Parashorea tomentella
Parashorea malaanonan
Syzygium hirtum
Syzygium imperiale
Syzygium kunstleri
Pternandra coerulescens
Memecylon costatum
Leea indica
Leea aculeata
Goniothalamus woodii
Meiogyne virgata
Popowia pisocarpa
Popowia odoardoi
Phaeanthus splendens
Pseuduvaria reticulata
Marsypopetalum pallidum
Polyalthia cauliflora
Polyalthia insignis
Polyalthia microtus
Orophea corymbosa
Orophea myriantha
Monoon grandiflorum
Monoon erianthoides
Monoon hookerianum
Neo−Uvaria acuminatissima
Magnolia candolii
Knema latericia
Knema laurina
Litsea accedens
Litsea caulocarpa
Litsea grandis
Nothaphoebe umbelliflora
Dehaasia incrassata
Dehaasia caesia
Eusideroxylon zwageri
Beilschmiedia assamica
Beilschmiedia cuadrae
Beilschmiedia tawaensis
Litsea angulata
Litsea oppositifolia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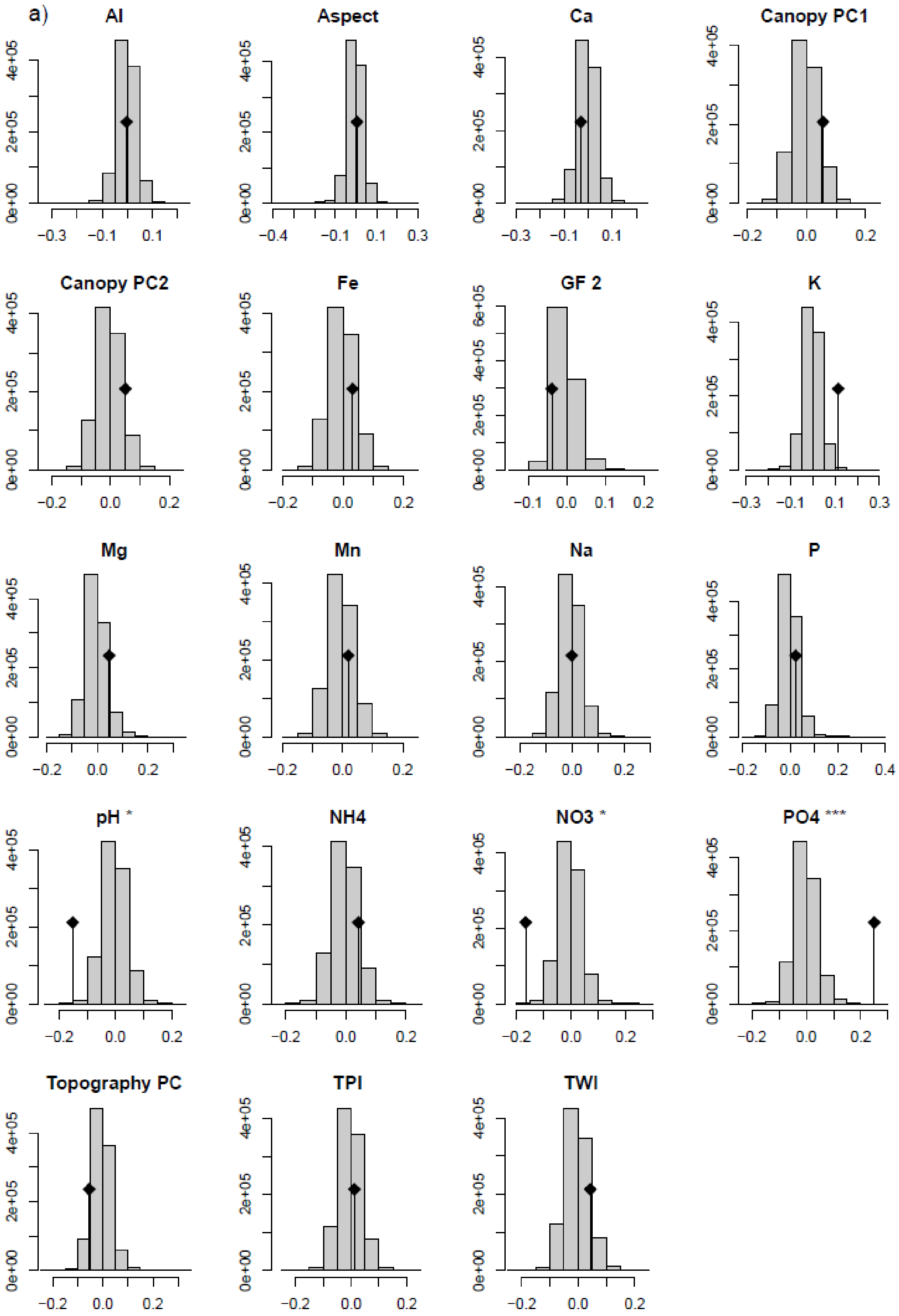
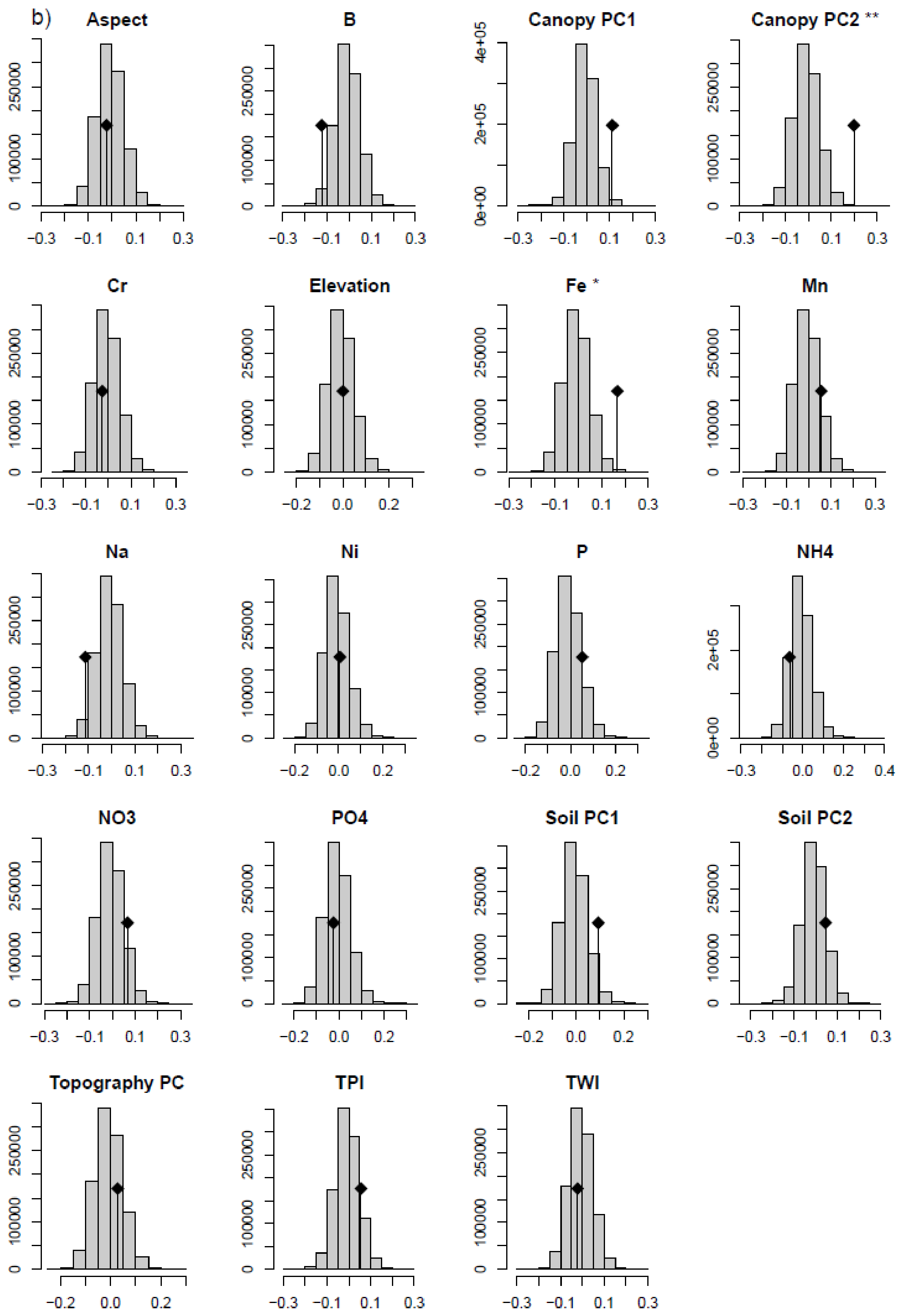
Fe
P
Canopy PC1
Cu
Canopy PC2
RB NO3
B
RB NH4
Elevation
Topography PC
Aspect
RB PO4
TWI
Na
Soil PC
TPI
Jacaranda copaia
Randia armata
Alibertia edulis
Alseis blackiana
Pentagonia macrophylla
Psychotria marginata
Psychotria horizontalis
Palicourea guianensis
Faramea occidentalis
Coussarea curvigemmia
Tabernaemontana arborea
Aspidosperma cruentum
Cordia lasiocalyx
Cordia bicolor
Gustavia superba
Chrysophyllum argenteum
Pouteria reticulata
Stylogyne turbacensis
Coccoloba manzinellensis
Heisteria concinna
Lonchocarpus heptaphyllus
Swartzia simplex
Pterocarpus hayesii
Inga goldmanii
Inga acuminata
Inga nobilis
Inga umbellifera
Inga marginata
Tachigali panamensis
Prioria copaifera
Maquira guianensis
Poulsenia armata
Brosimum alicastrum
Sorocea affinis
Cecropia insignis
Croton billbergianus
Acalypha diversifolia
Alchornea costaricensis
Hasseltia floribunda
Laetia thamnia
Casearia aculeata
Lacistema aggregatum
Pombalia prunifolia
Rinorea sylvatica
Drypetes standleyi
Garcinia madruno
Garcinia recondita
Chrysochlamys eclipes
Calophyllum longifolium
Cassipourea elliptica
Erythroxylum macrophyllum
Hirtella triandra
Ouratea lucens
Sloanea terniflora
Simarouba amara
Guarea guidonia
Guarea bullata
Trichilia tuberculata
Trichilia pallida
Talisia nervosa
Talisia croatii
Cupania seemannii
Protium costaricense
Protium panamense
Protium tenuifolium
Protium stevensonii
Quararibea asterolepis
Apeiba membranacea
Herrania purpurea
Capparidastrum frondosum
Eugenia nesiotica
Eugenia galalonensis
Eugenia oerstediana
Eugenia coloradoensis
Chamguava schippii
Miconia argentea
Miconia affinis
Miconia nervosa
Mouriri myrtilloides
Picramnia latifolia
Guatteria lucens
Xylopia macrantha
Desmopsis panamensis
Mosannona garwoodii
Unonopsis pittieri
Anaxagorea panamensis
Virola sebifera
Ocotea cernua
Ocotea whitei
Beilschmiedia tovarensis
Siparuna pauciflora
Oenocarpus mapora
Socratea exorrhiza

SI Figure 2.5: Phylogenetic autocorrelation of species-environment associations at each site: (a) Pasoh, (b) Danum Valley and (c) Barro Colorado Island. Grey histograms are presented for 1 million random permutations, with observed phylogenetic autocorrelation measured from a phylogenetic principal component analysis presented by the black diamond. Asterisks denote significance levels of Bonferroni correct p-values from an Abouheif-Moran test: * p < 0.05, ** p < 0.01, *** p < 0.001.




b)
Aspect
B
Canopy PC1
Canopy PC2 **
Cr
Elevation
Fe *
Mn
Na
Ni
P
NH4
NO3
PO4
Soil PC1
Soil PC2
Topography PC
TPI
TWI
0
100000
250000
0e+00
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−0.2
−0.1
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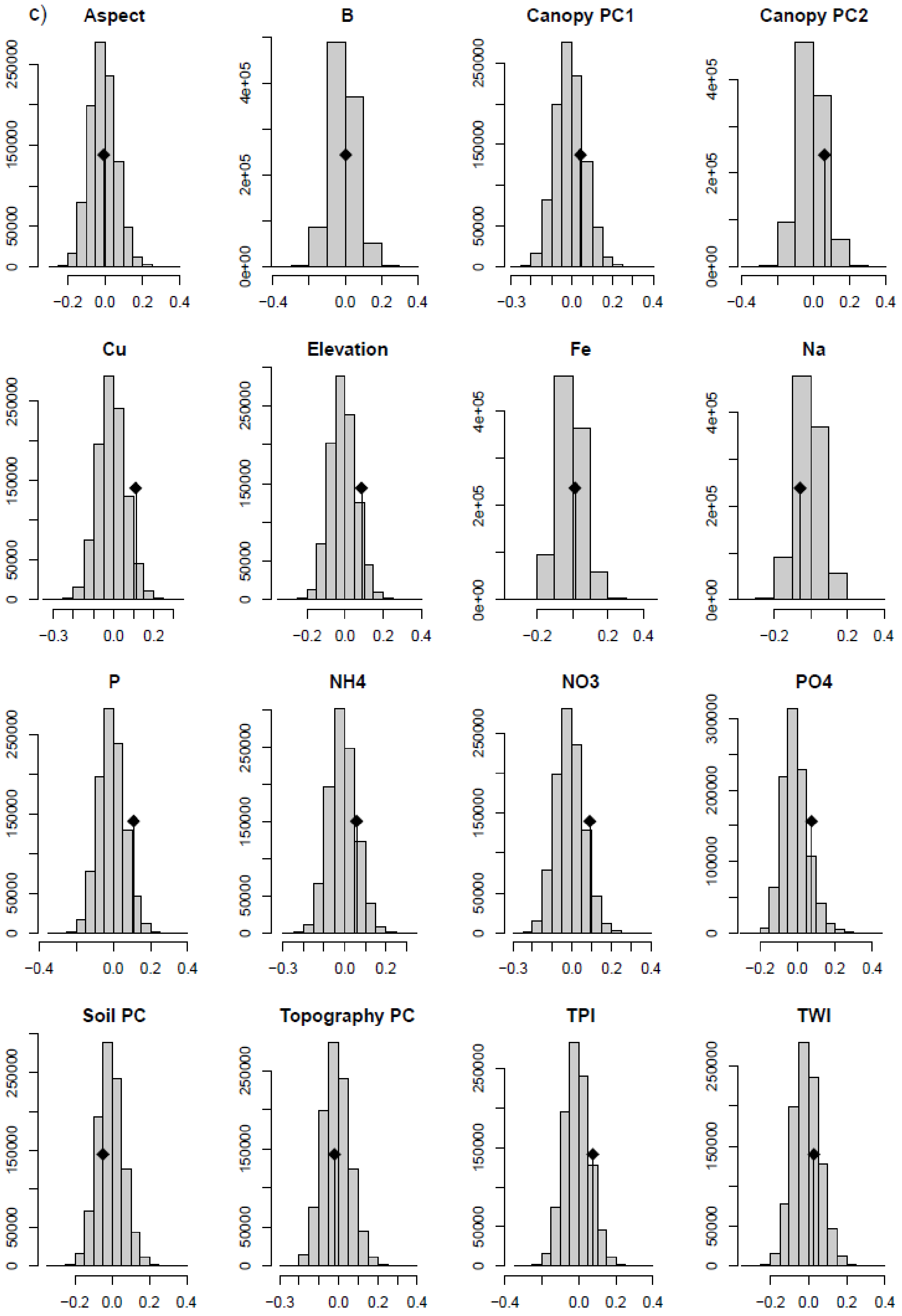
0.1
0.2
0.3
0.4


c)
Aspect
B
Canopy PC1
Canopy PC2
Cu
Elevation
Fe
Na
P
NH4
NO3
PO4
Soil PC
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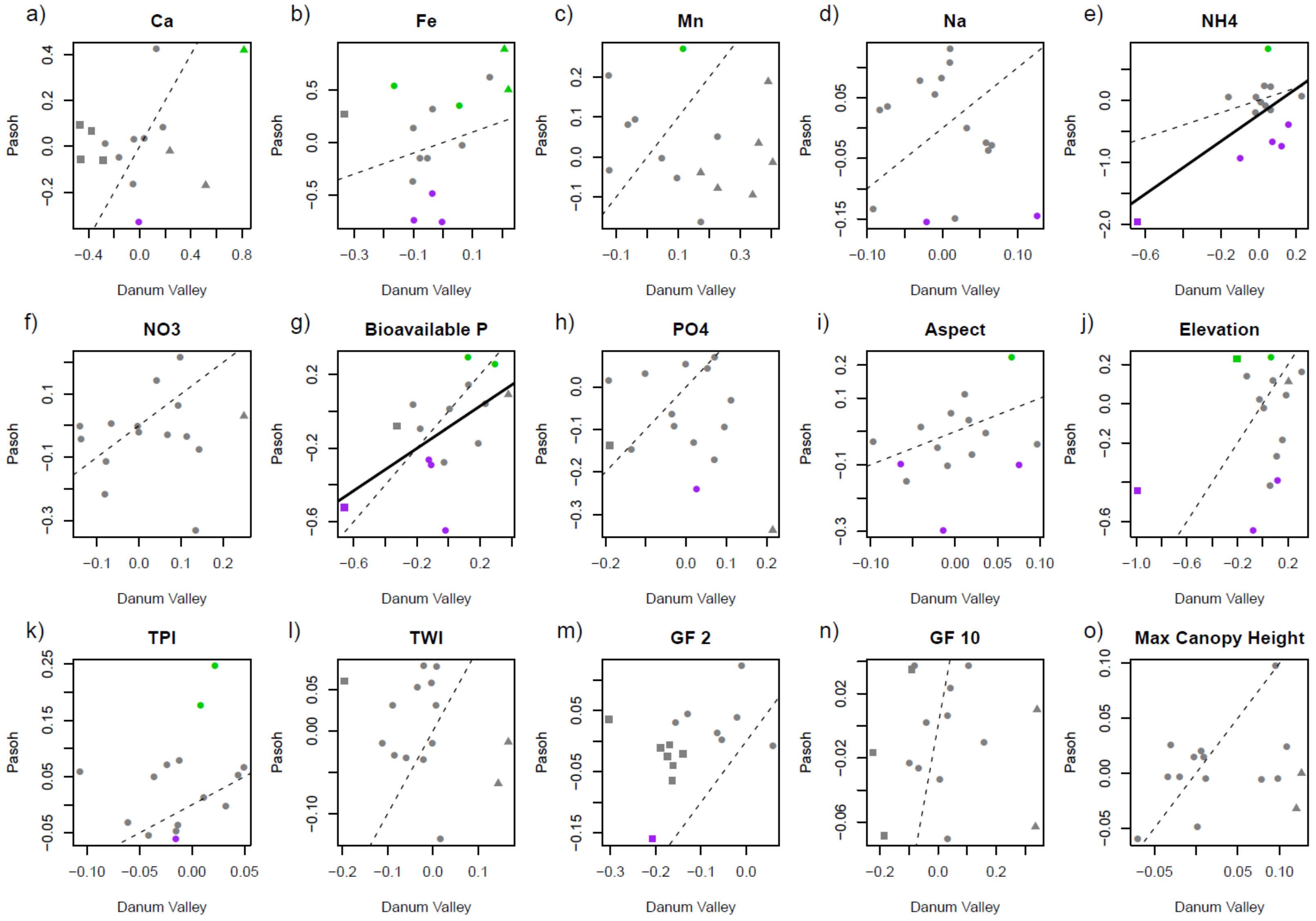
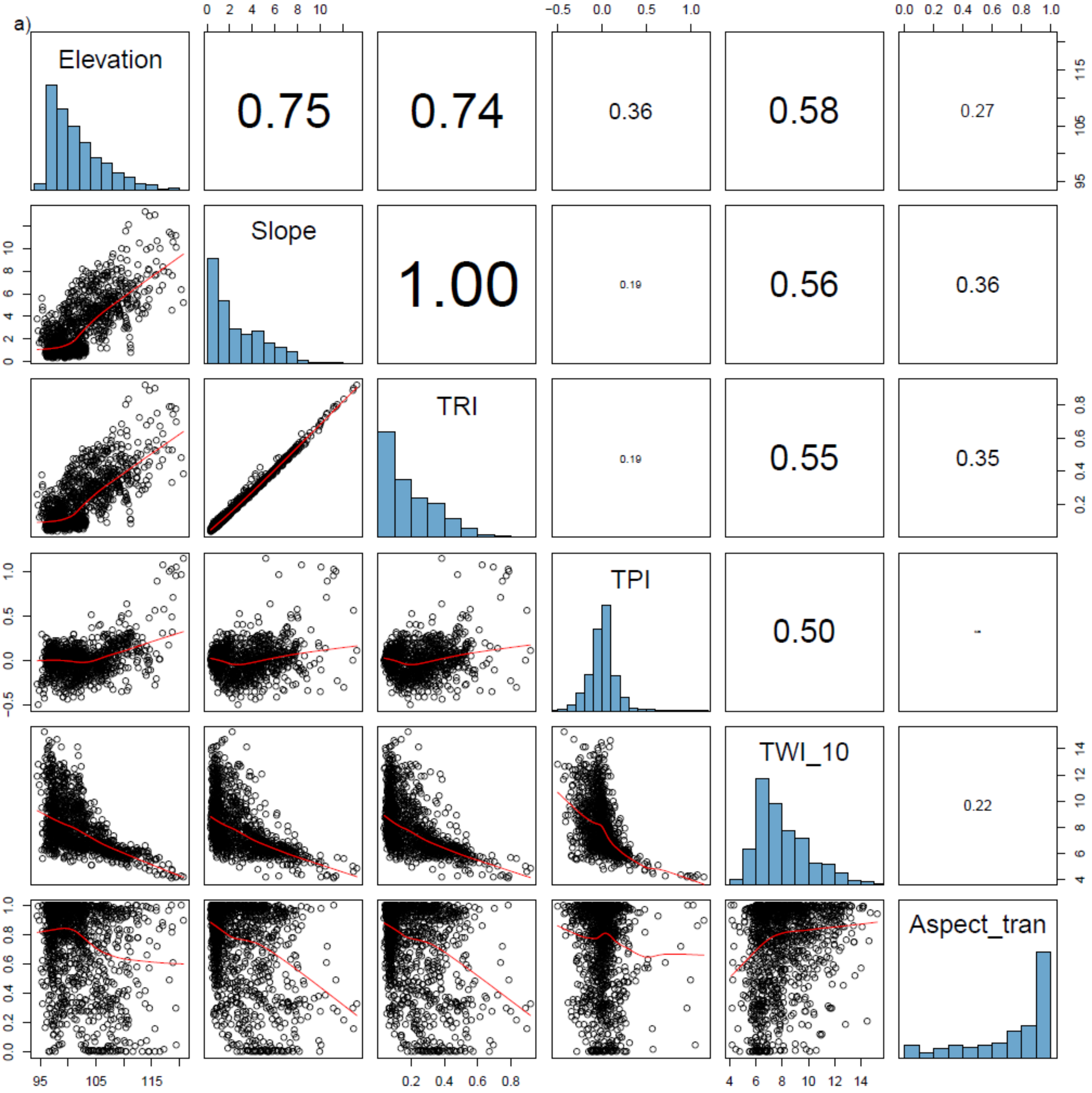
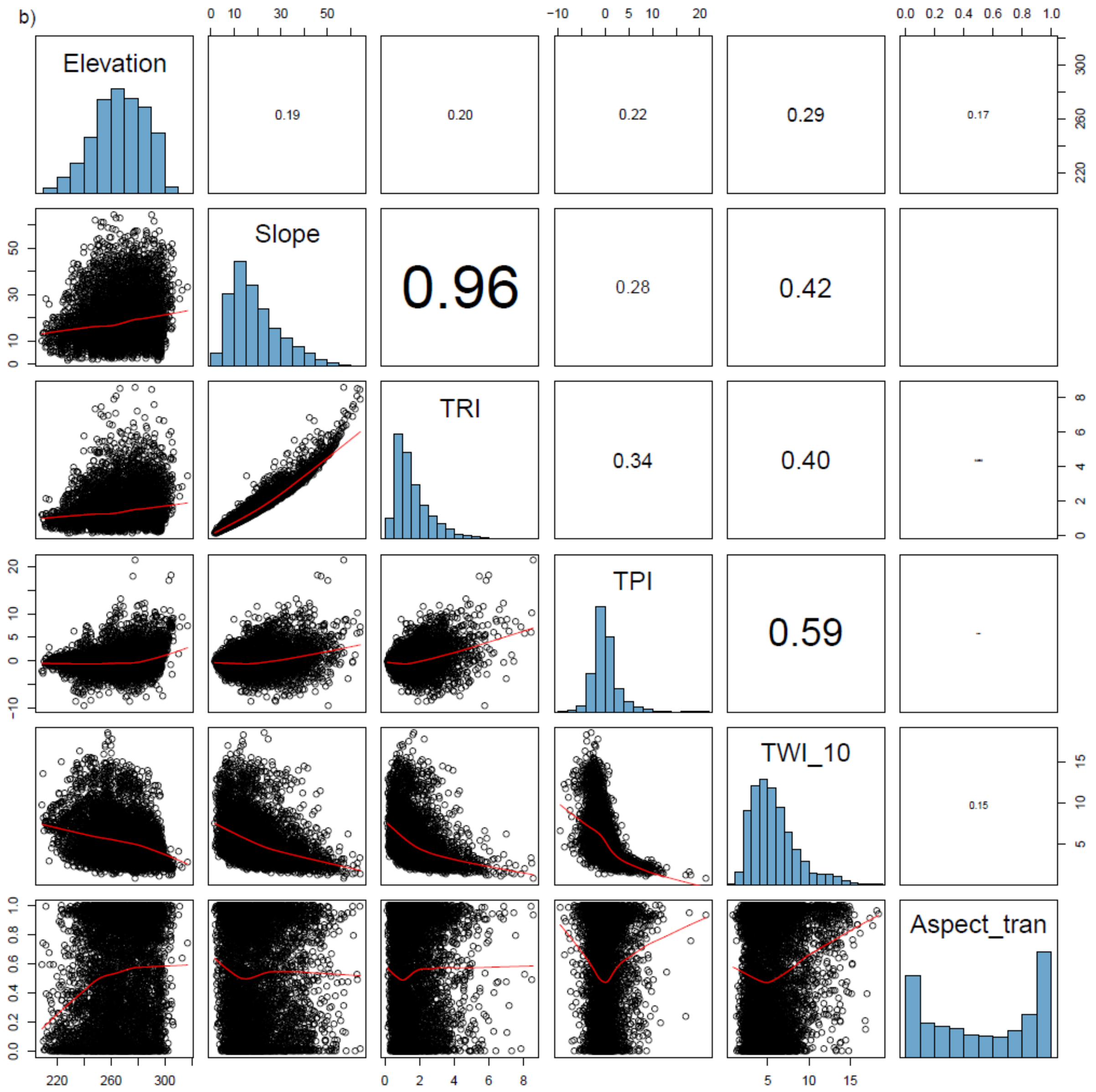
TWI
0
50000
150000
250000
300000
200000
100000
0e+00
2e+05
4e+05
−0.4
−0.3
−0.2
0.0
0.2
0.4

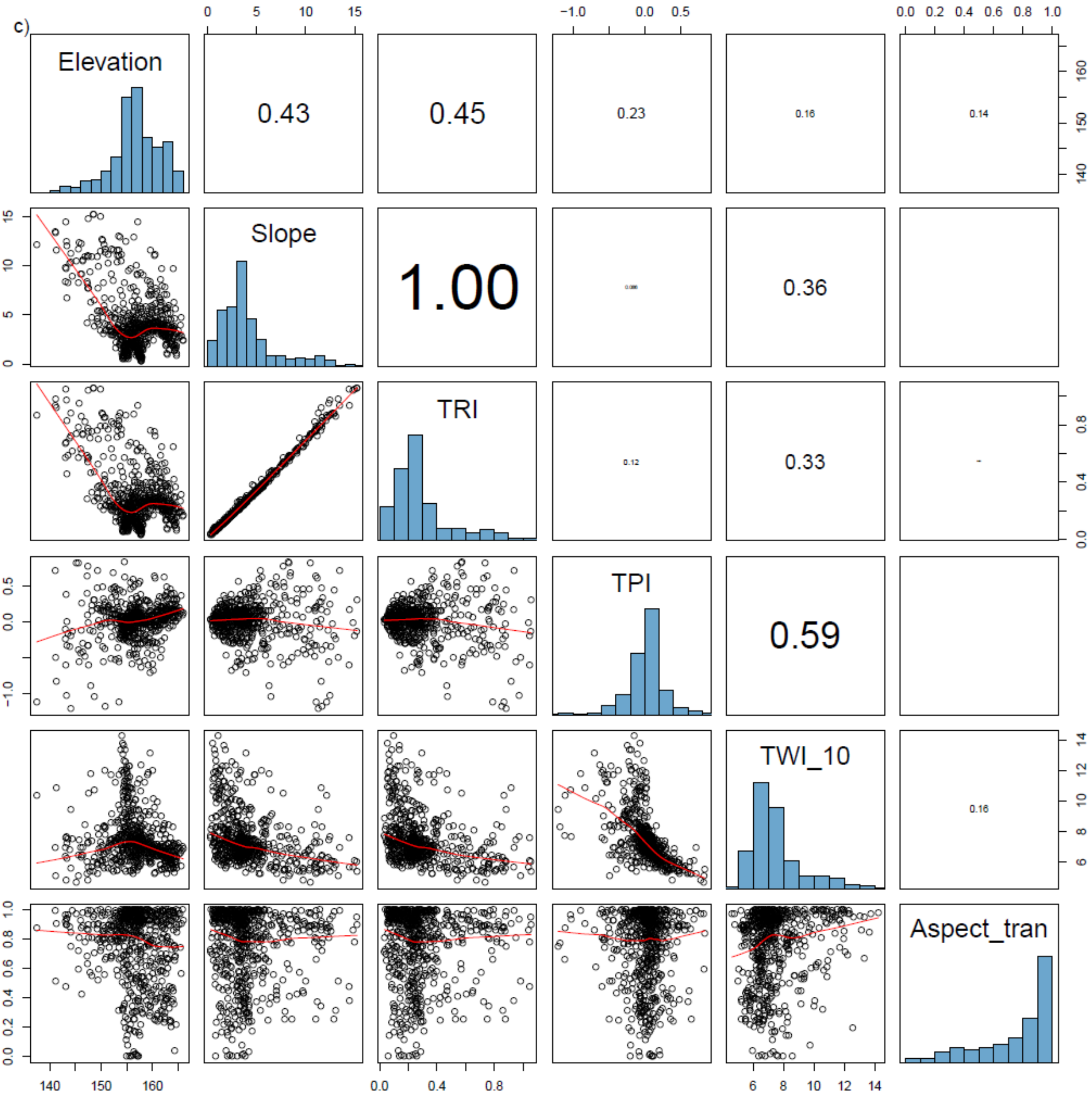
SI Figure 2.6: Effect sizes of species-environment associations to (a) calcium, (b) iron, (c) manganese, (d) sodium, (e) ammonium, (f) nitrates, (g) bioavailable phosphorus, (h) dissolved phosphates, (i) topographic aspect, (j) elevation, (k) topographic position index (l) topographic wetness index, (m) canopy gap fraction at 2m, (n) canopy gap fraction at 10 m and (o) maximum canopy height for the fifteen species found in both Danum Valley and Pasoh. Significant associations at Pasoh are indicated by colours (green: positive, purple: negative, grey: non-significant) and significant associations at Danum Valley are indicated by point shape (triangles: positive, squares: negative, dots: non-significant). The null expectation of identical associations is presented as a dashed line on the 1:1, whilst significant Pearson's correlations ($p < 0.05$) are presented as solid lines.



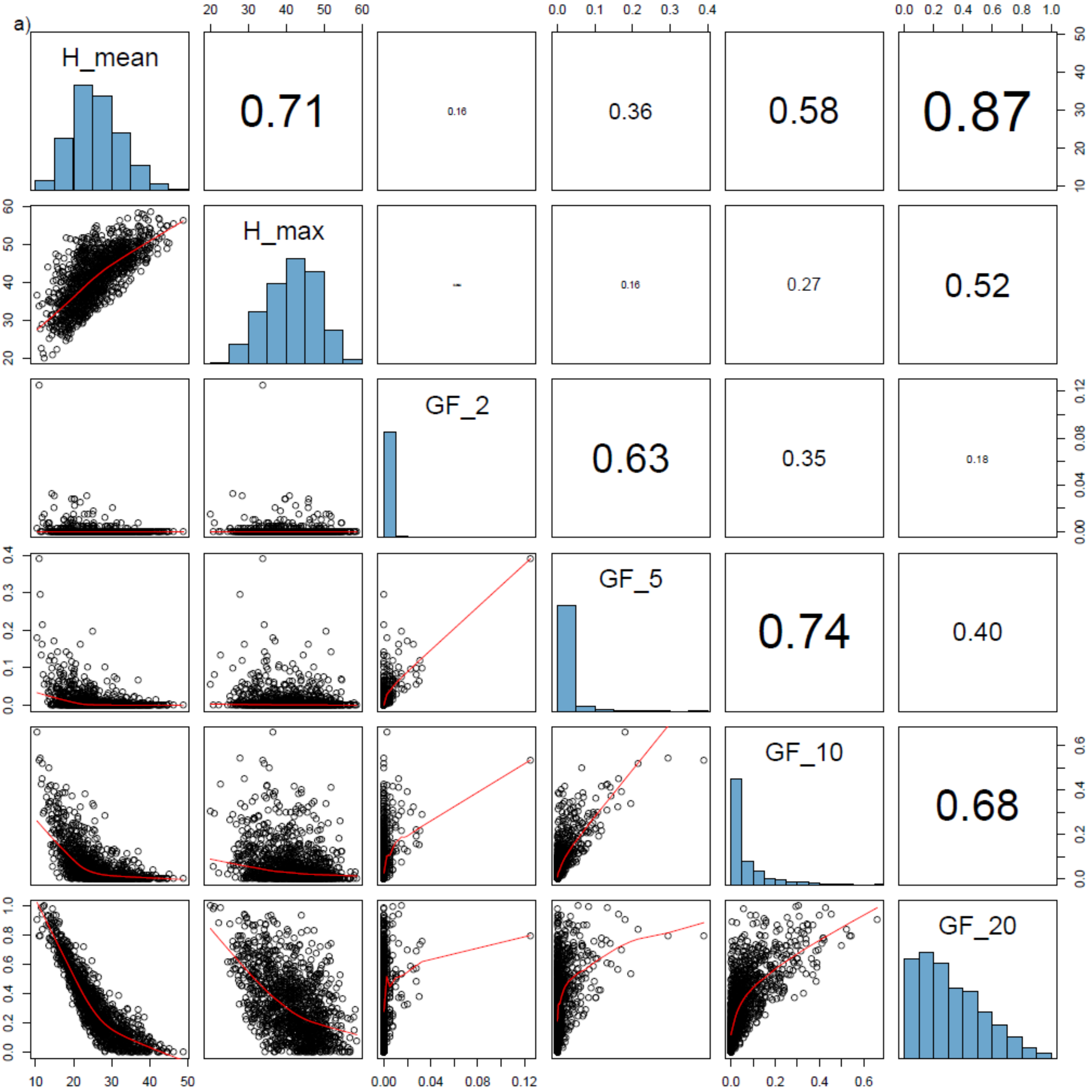
SI Figure 2.7: Auto-correlation between topographic co-variates measured for each 20 x 20 m square pixel at (a) Pasoh, (b) Danum Valley and (c) Barro Colorado Island. A histogram of each co-variate the bi-variate relationship of all co-variates and the correlation co-efficient scaled to the extent of correlation are presented. Co-variates with auto-correlation of r > 0.7 were condensed into principal components (Table 2.2). *Elevation: Elevation above sea level; Slope: Terrain slope angle; TRI: Terrain ruggedness index; TPI: Topographic position index; TWI: Mean terrain wetness index at 10 x 10 m resolution; Aspect_tran: Solar-radiation aspect index.*

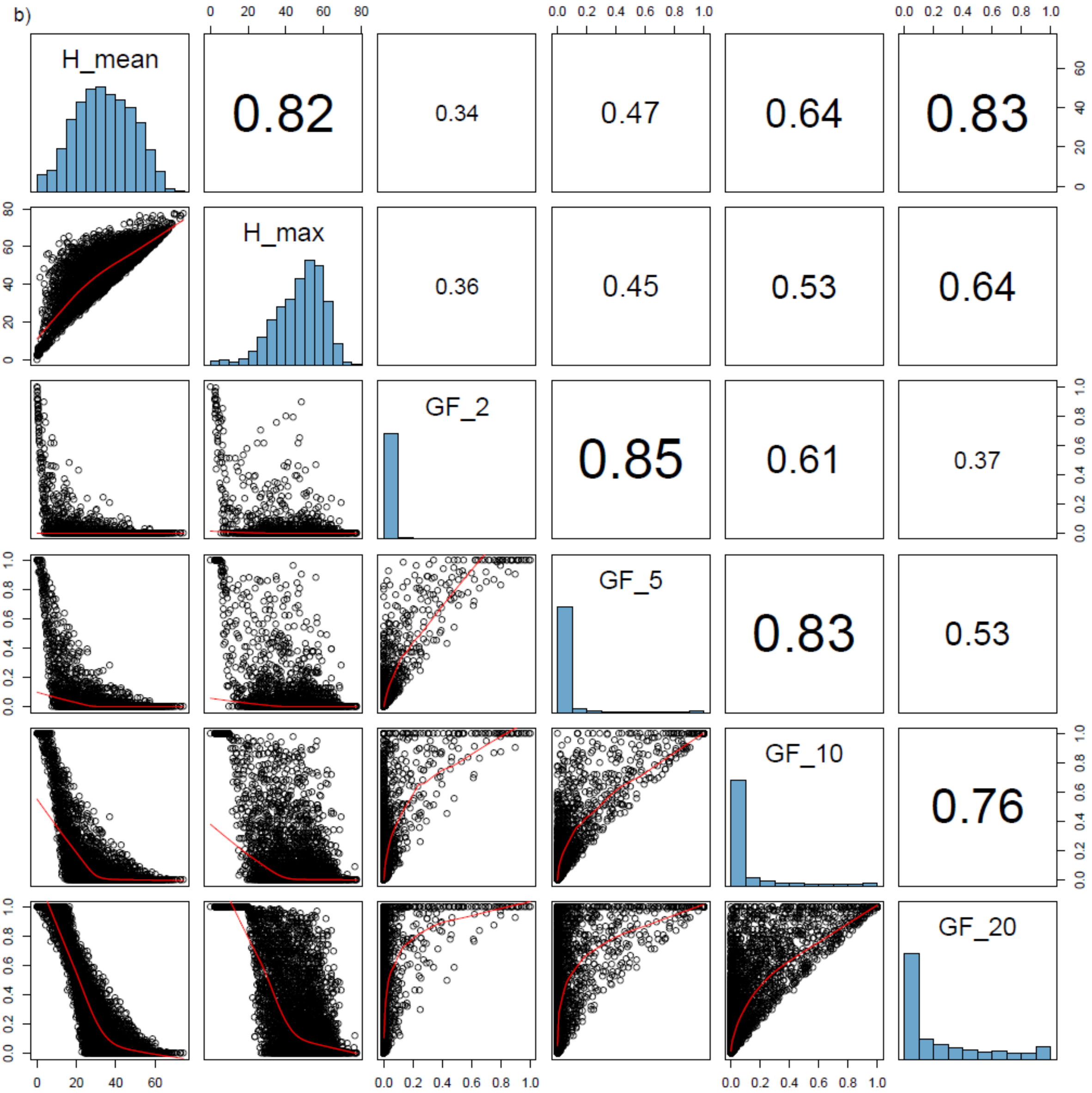


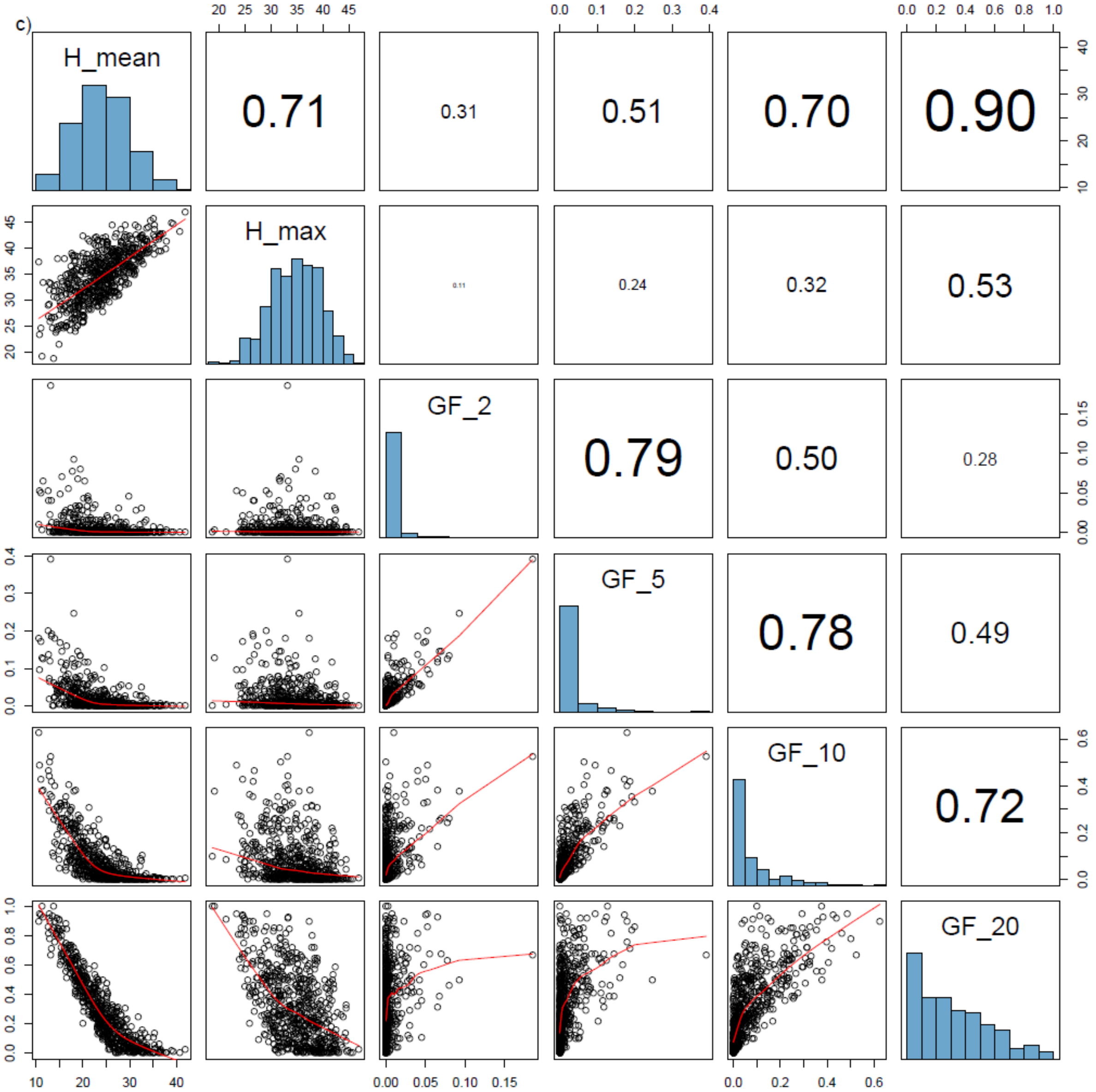

b)
Elevation
Slope
TRI
TPI
TWI_10
Aspect_tran
0.19
0.20
0.22
0.29
0.17
0.96
0.28
0.42
0.34
0.40
0.59
0.15
0 10 30 50
−10 0 5 10 20
0.0 0.2 0.4 0.6 0.8 1.0
300 260 220
8 6 4 2 0
15 10 5
50 30 10 0
20 10 5 0 −10
1.0 0.8 0.6 0.4 0.2 0.0
220 260 300
0 2 4 6 8
5 10 15


c)
Elevation
Slope
TRI
TPI
TWI_10
Aspect_tran
0.43
0.45
0.23
0.16
0.14
1.00
0.36
0.12
0.33
0.59
0.16
0 5 10 15
−1.0 0.0 0.5
0.0 0.2 0.4 0.6 0.8 1.0
140 150 160
0.0 0.4 0.8
6 8 10 12 14

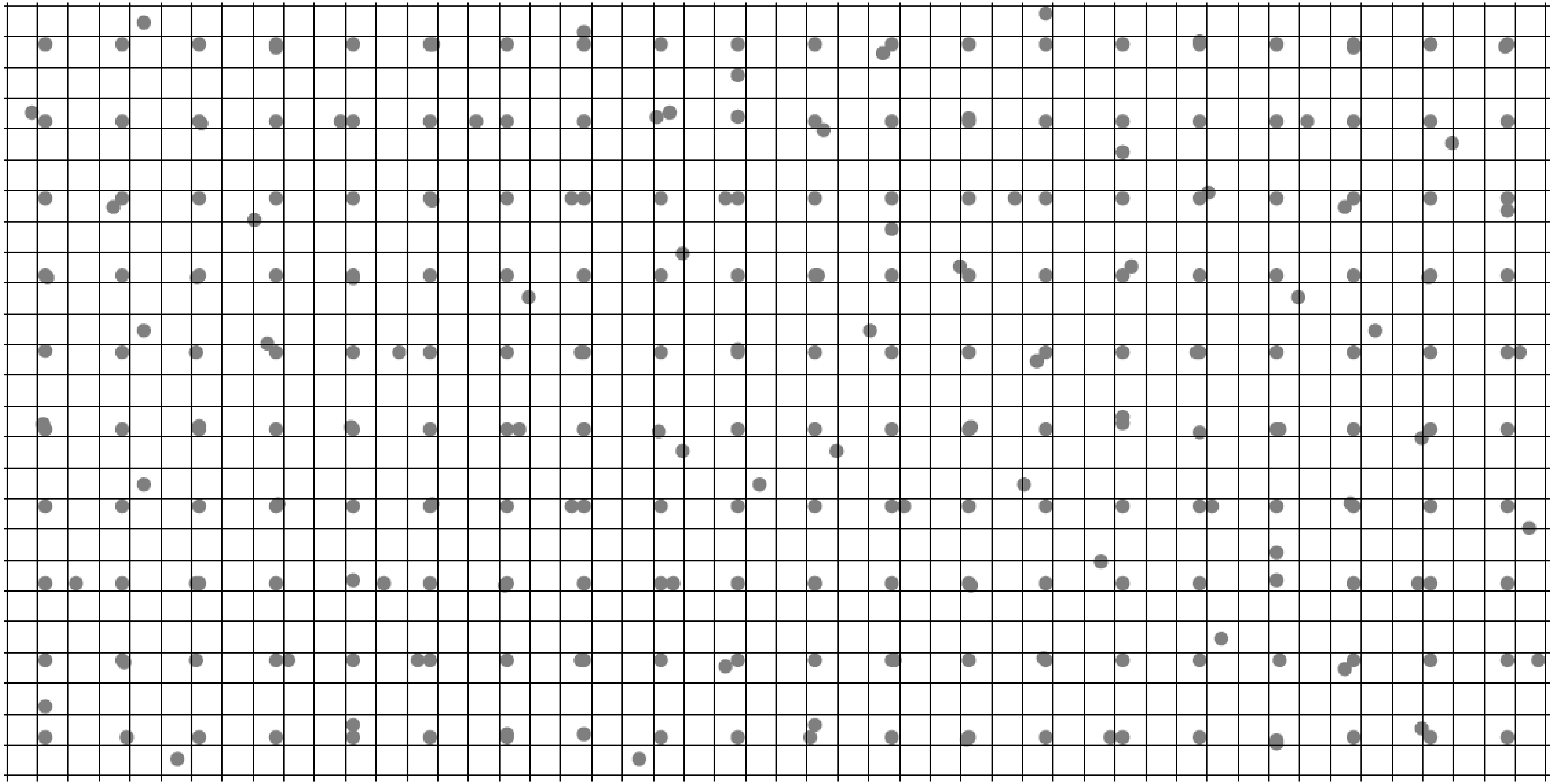
SI Figure 2.8: Auto-correlation between canopy structure co-variates measured for each 20 x 20 m square pixel at (a) Pasoh, (b) Danum Valley and (c) Barro Colorado Island. A histogram of each co-variate the bi-variate relationship of all co-variates and the correlation co-efficient scaled to the extent of correlation are presented. Co-variates with auto-correlation of r > 0.7 were condensed into principal components (Table 2.2). Additional co-variates were added to the principal components if auto-correlation between the principal components and remaining co-variates produced auto-correlation issues. *H_mean: Mean canopy height; H_max: Maximum canopy height; GF_2: Gap fraction at 2 m; GF_5: Gap fraction at 5 m; GF_10: Gap fraction at 10 m; GF_20: Gap fraction at 20 m.*



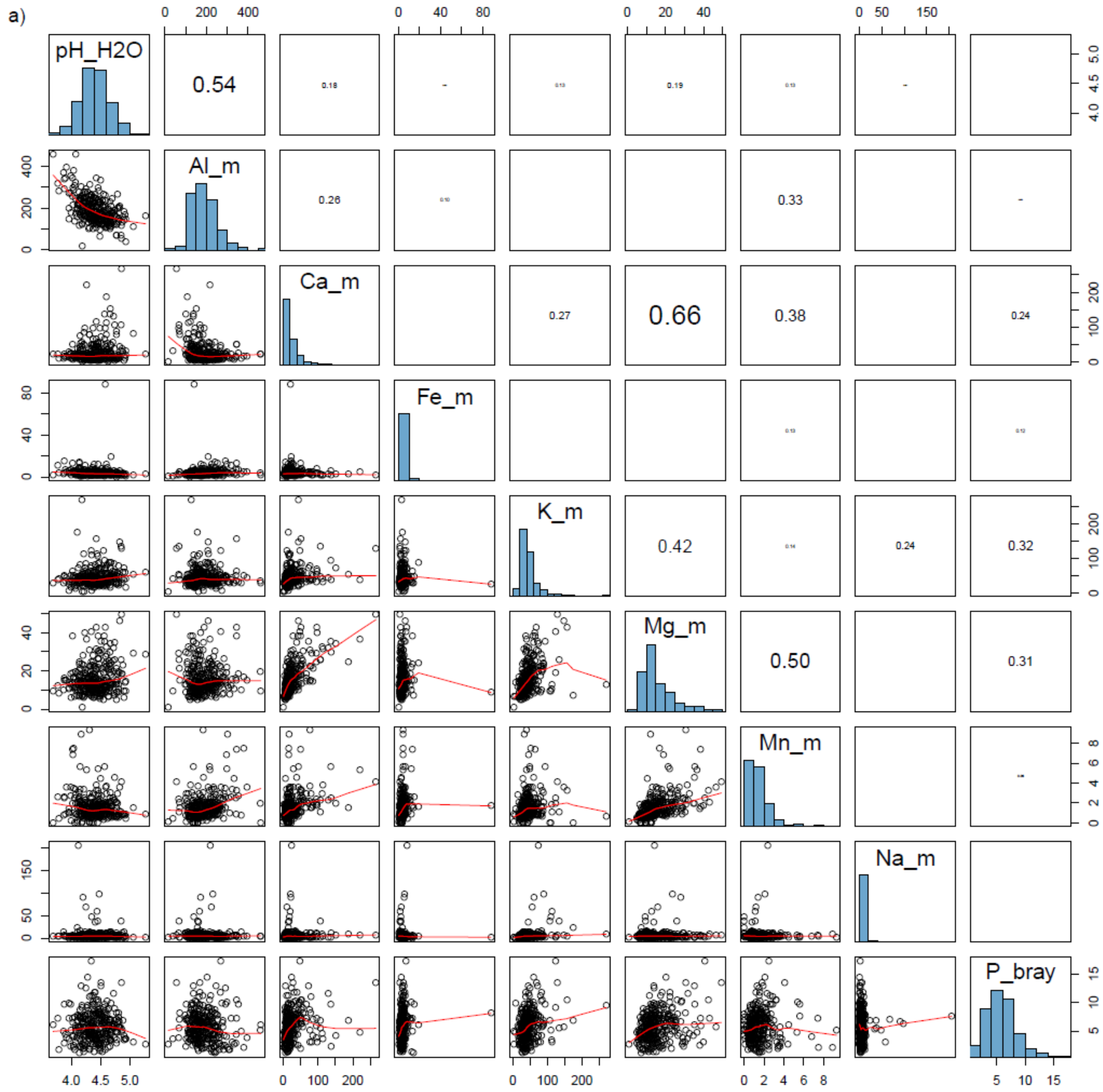

b)
H_mean
H_max
GF_2
GF_5
GF_10
GF_20
0.82
0.34
0.47
0.64
0.83
0.36
0.45
0.53
0.64
0.85
0.61
0.37
0.83
0.53
0.76
0 20 40 60 80
0.0 0.2 0.4 0.6 0.8 1.0
0 20 40 60


c)
H_mean
H_max
GF_2
GF_5
GF_10
GF_20
0.71
0.31
0.51
0.70
0.90
0.11
0.24
0.32
0.53
0.79
0.50
0.28
0.78
0.49
0.72

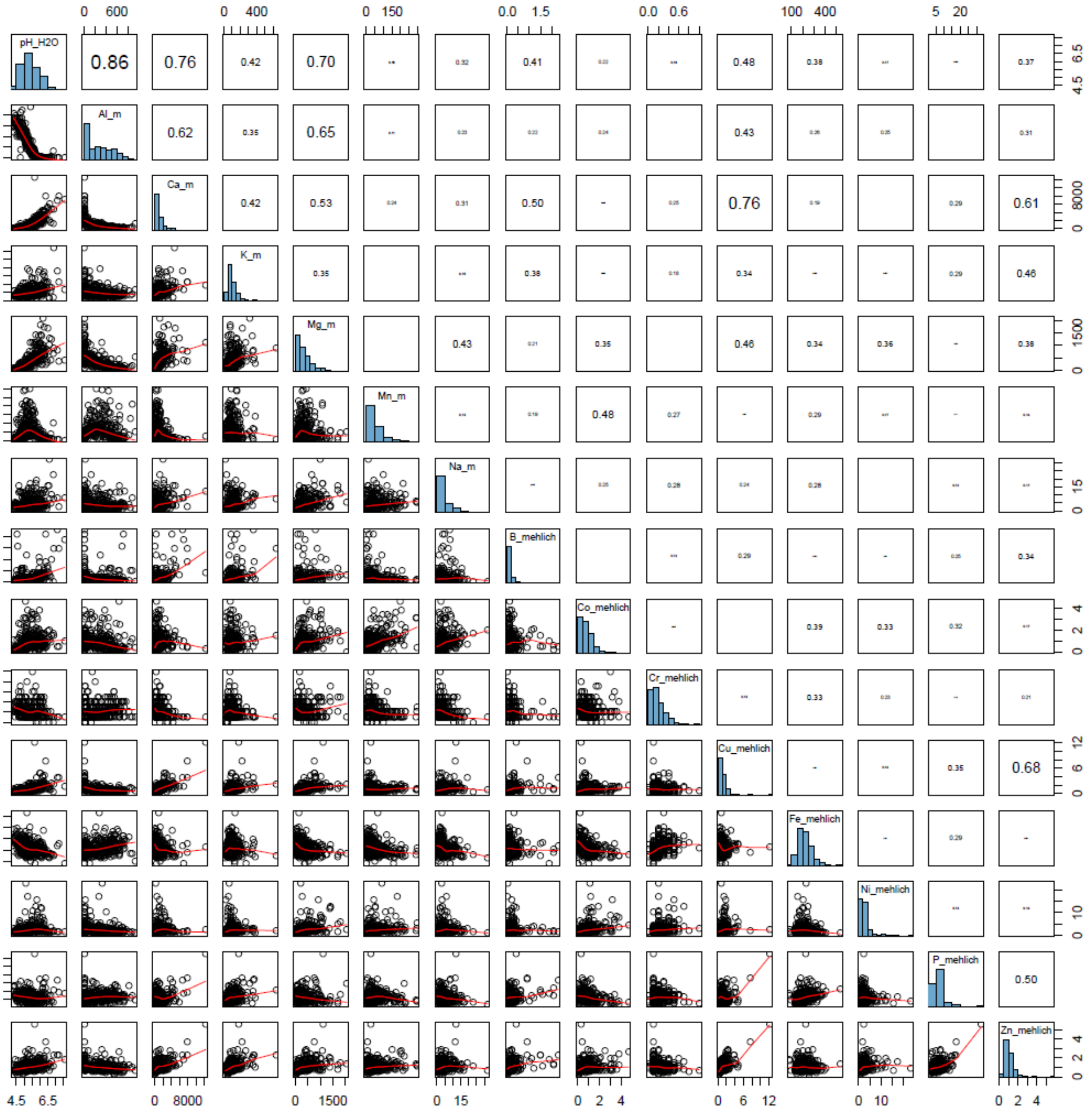
SI Figure 2.9: Sampling design for soil samples at the Pasoh 50 ha plot. Dots represent sampling locations, whilst squares represent the 20 x 20 m quadrats used in this study. Samples were collected in a gridded pattern with additional samples used to capture finer scale variations. Soil nutrient availability data were geospatially kriged to get an estimate for each quadrat. See Methods for more details. Equivalent sampling designs were used at all study sites.



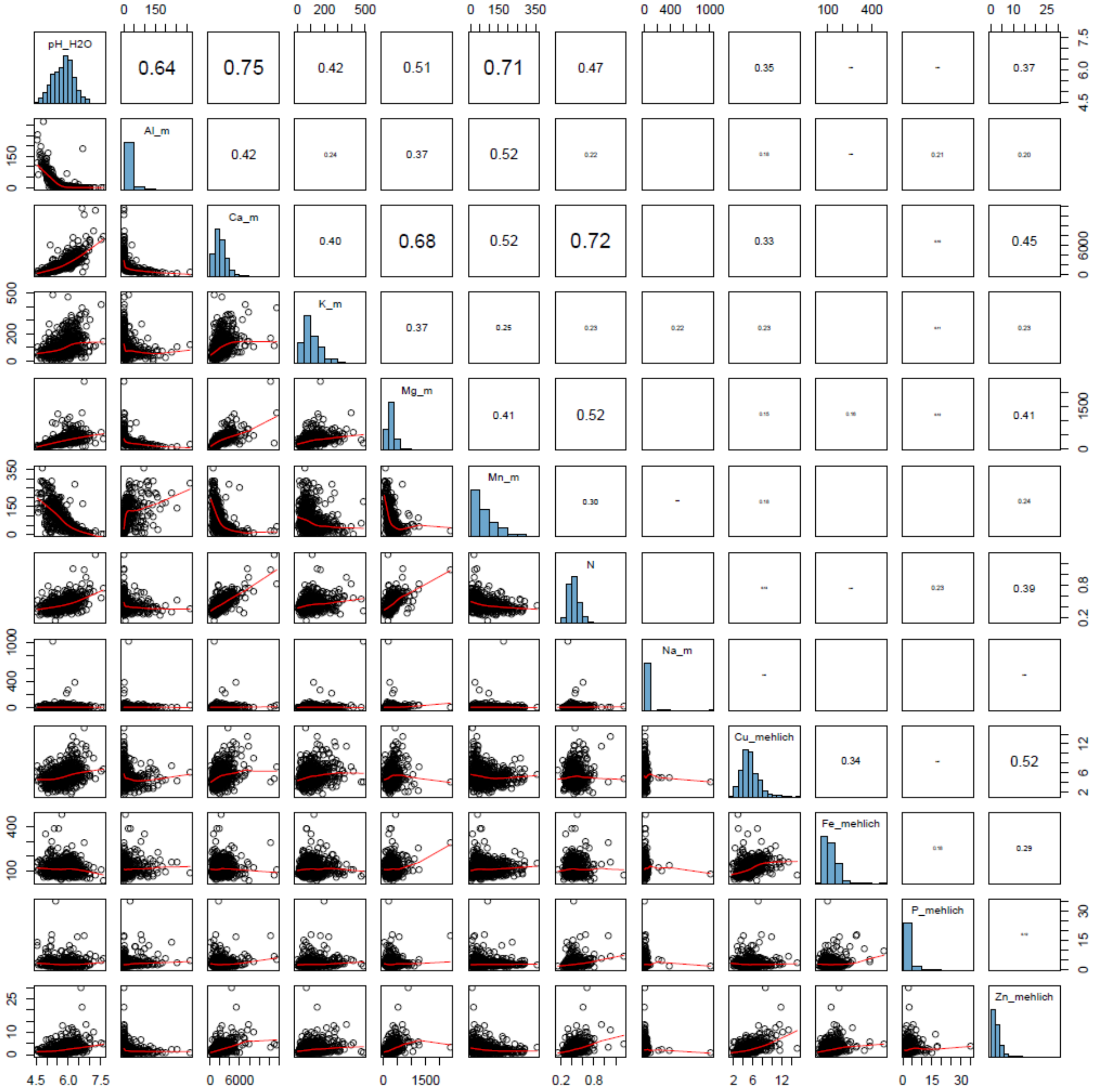
SI Figure 2.10 – Auto-correlation between soil co-variates at (a) Pasoh, (b) Danum Valley and (c) Barro Colorado Island. A histogram of each co-variate the bi-variate relationship of all co-variates and the correlation co-efficient scaled to the extent of correlation are presented. Co-variates with auto-correlation of r > 0.7 were condensed into principal components prior to geo-spatial kriging (Table 2.2). Additional co-variates were added to the principal components if auto-correlation between the soil principal components and remaining soil-co-variates produced auto-correlation issues after geo-spatial kriging. *pH_H2O: pH in water; Al_m: BaCl₂ extracted aluminium; Ca_m: BaCl₂ extracted calcium; Fe_m: BaCl₂ extracted iron; K_m: BaCl₂ extracted potassium; Mg_m: BaCl₂ extracted magnesium; Mn_m: BaCl₂ extracted manganese; N: BaCl₂ extracted nitrogen; Na_m: BaCl₂ extracted sodium; P_bray: Bray extracted phosphorus; B_mehlich: Mehlich extracted boron; Co_mehlich: Mehlich extracted cobalt; Cr_mehlich: Mehlich extracted chromium; Cu_mehlich: Mehlich extracted copper; Fe_mehlich: Mehlich extracted iron; Ni_mehlich: Mehlich extracted nickel; P_mehlich: Mehlich extracted phosphorus; Zn_mehlich: Mehlich extracted zinc.*



b)


pH_H2O
Al_m
Ca_m
K_m
Mg_m
Mn_m
Na_m
B_mehlich
Co_mehlich
Cr_mehlich
Cu_mehlich
Fe_mehlich
Ni_mehlich
P_mehlich
Zn_mehlich
0.86
0.76
0.42
0.70
0.32
0.41
0.48
0.38
0.37
0.62
0.35
0.65
0.43
0.31
0.42
0.53
0.31
0.50
0.76
0.29
0.61
0.35
0.38
0.34
0.29
0.46
0.43
0.35
0.46
0.34
0.36
0.38
0.48
0.27
0.29
0.28
0.28
0.29
0.34
0.39
0.33
0.32
0.33
0.35
0.68
0.29
0.50
0 600
0 400
0 150
0.0 1.5
0.0 0.6
100 400
5 20
4.5 6.5
0 8000
0 1500
0 15
0 2 4
0 6 12
0 10

c)


pH_H2O
Al_m
Ca_m
K_m
Mg_m
Mn_m
N
Na_m
Cu_mehlich
Fe_mehlich
P_mehlich
Zn_mehlich
0.64
0.75
0.42
0.51
0.71
0.47
0.35
0.37
0.42
0.37
0.52
0.40
0.68
0.52
0.72
0.33
0.45
0.37
0.41
0.52
0.41
0.30
0.39
0.34
0.52
4.5
6.0
7.5
0
150
0
6000
0
200
500
0
1500
0
150
350
0.2
0.8
0
400
1000
2
6
12
100
400
0
15
30
0
10
25

Appendix 3: Supporting Information of Chapter 3

Supplementary Methods

Branch sampling

Leaves were sampled to make the following measures: maximum photosynthetic capacity (V_{cmax}), leaf dark respiration (R_{leaf}), abaxial leaf conductance after 30 minutes of dark adaptation (g_{dark}), leaf mass per area (LMA), leaf thickness and leaf nutrient concentrations ($[N]_{leaf}$, $[P]_{leaf}$, $[Ca]_{leaf}$, $[K]_{leaf}$, $[Mg]_{leaf}$), as elaborated in the following sections. For each tree, we collected a sunlit branch, or a branch from the top of the crown for understory trees, of approximately 1-2 m length and 1-2 cm diameter. All trees, or neighbouring trees, were climbed using single and double rope climbing techniques to access the canopy. Branches were cut between 9:00 h and 14:00 h, except when logistical challenges associated with tree climbing delayed branch harvesting. Following branch harvesting, the branch was trimmed to a length of approximately 1 m for gas exchange measurements, placed in water and cut twice underwater to restore water supply to the leaves (Domingues *et al.*, 2010). For leaf mass per area (LMA) estimates, an additional branch of 60-80 cm length was collected, placed in a large, black plastic bag with wet tissue paper and transported back to the Forest Research Centre, Sepilok, for further processing on the day of collection.

Gas exchange measurements

We measured V_{cmax} and R_{leaf} on non-senescing, fully formed leaves using two cross-calibrated portable photosynthesis systems (LI-6400XT and LI-6800, LI-COR, Nebraska, USA). For measurements of V_{cmax}, leaves were allowed to stabilise for a minimum of 20 minutes in full sunlight before being placed within the leaf chamber of the LI-6800 (Verryckt *et al.*, 2020). Inside the leaf chamber, a CO_2 concentration of 400 ppm, photosynthetically active radiation (*PAR*) of 1500 µmol m^{-2} s^{-1}, a temperature of 28 ˚C and relative humidity of 60-70% was set. We measured net photosynthetic assimilation under these conditions to estimate photosynthesis under saturating light (A_{sat}) and used the one-point method to estimate maximum rates of rubisco carboxylation (V_{cmax}) standardised to 25 ˚C following the equations of De Kauwe *et al.* (2016), using measured R_{leaf} values (see below). In order to maintain data quality, photosynthesis measurements were only taken if stomatal conductance exceeded 0.05 mol m^{-2} s^{-1} (Rowland *et al.*, 2015b).

R_{leaf} was measured on a leaf adjacent to that used to measure photosynthetic capacity using a LI-6400XT. We wrapped these leaves inside aluminium foil for a minimum of 30 minutes to adapt them to the dark before placing them inside the leaf chamber. R_{leaf} measurements were taken directly after photosynthesis measurements. Leaf chamber conditions were maintained at 400 ppm CO_2, 0 μmol m^{-2} s^{-1} *PAR*, 28 ˚C and 60-70% relative humidity. Five measurements of R_{leaf} were recorded at 5 second intervals, and subsequently standardised to 25 ˚C following Rowland *et al.* (2015b), and the mean calculated. We use the stomatal conductance from the R_{leaf} measurement as a measure of g_{dark}, with lower values an indicator of greater resource conservation. Steady state conditions within the leaf chamber were reached before all gas exchange measurements were recorded.

Leaf morphological traits

Once leaf gas exchange measurements were complete, we removed both the photosynthesis and respiration leaves and placed them in an airtight ziplock bag. Moist cotton wool was used to maintain humidity inside the bag and prevent water loss from the leaves. Leaves were weighed immediately on return to the lab and scanned using a flatbed scanner (CanoScan LiDE 120, Canon Inc., Tokyo, Japan). Leaf area was calculated using ImageJ software (Schneider *et al.*, 2012). Leaf thickness was measured at three points on both the V_{cmax} and R_{leaf} leaves using precision digital callipers avoiding major veins. A mean of means was calculated to generate an estimate of branch level leaf thickness. Leaves were subsequently placed in an oven at 50 ˚C and dried to a constant mass for 48-72 hours, before being re-weighed. LMA for the V_{cmax} and R_{leaf} leaves was calculated by dividing dry leaf mass by leaf area, allowing gas exchange measurements to be expressed on both an area and mass basis. To generate a branch level estimate of LMA, we removed all the leaves from the additional adjacent branch and followed the same protocol used for the V_{cmax} and R_{leaf} leaves.

Leaf nutrient analyses

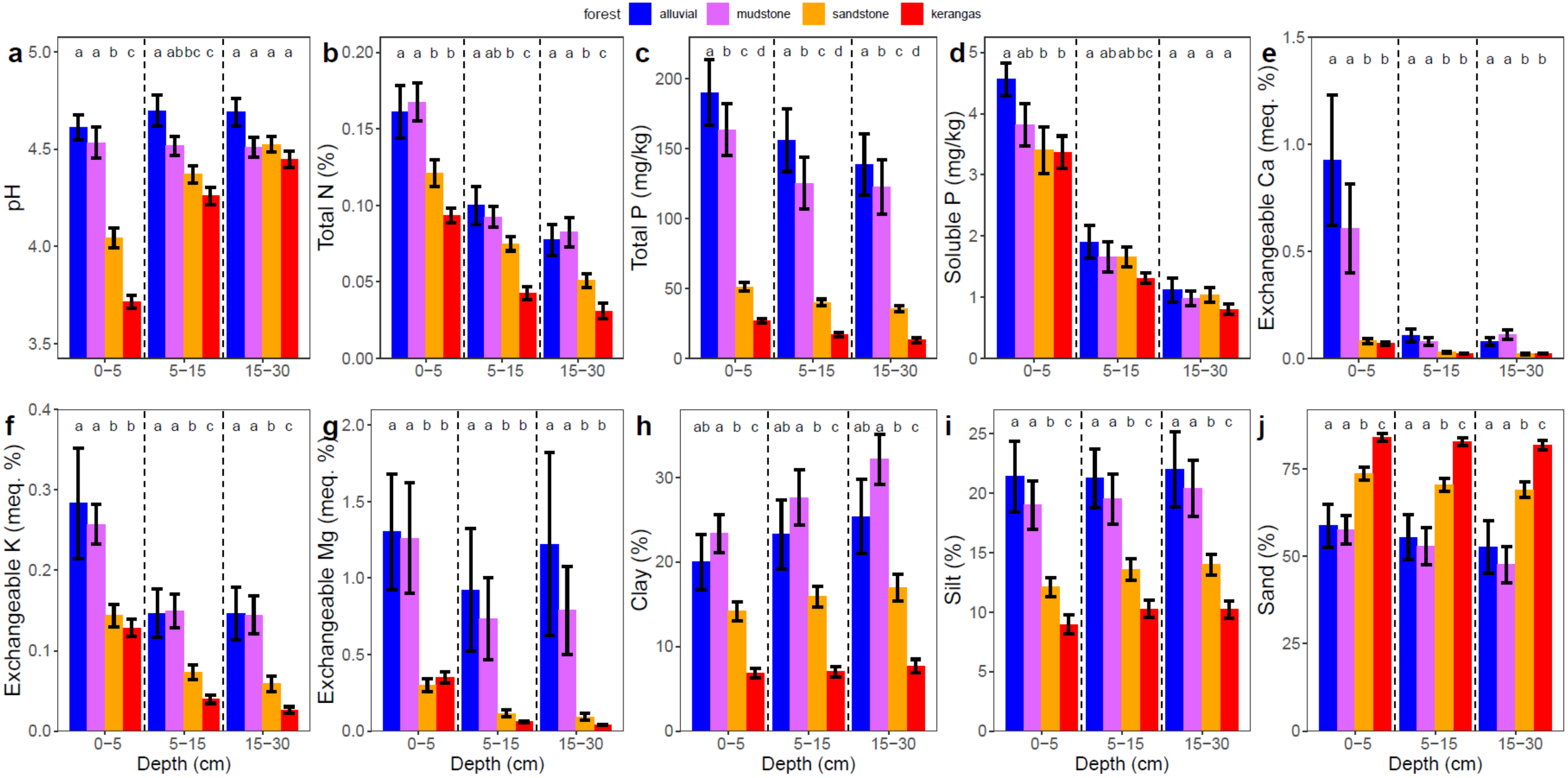
The leaves used to estimate branch level LMA were analysed to quantify $[N]_{\text{leaf}}$, $[P]_{\text{leaf}}$, $[Ca]_{\text{leaf}}$, $[K]_{\text{leaf}}$ and $[Mg]_{\text{leaf}}$ concentrations. Leaves were dried in a lab oven to constant weight and then ground using a Wiley Mill ED-5 (Thomas Scientific, USA) to pass a 2-mm sieve. A portion of each sample was further dried at 105˚C to determine the moisture content, which was used to convert all data (based on air-dry values) to oven-dry values. Subsamples of the ground leaves were analysed for total N, P, Ca, K, and Mg concentrations. Leaves were digested following the Kjeldahl method using concentrated sulphuric acid (Anderson & Ingram, 1993) and $[N]_{leaf}$ was measured using a micro-SFA (Astoria2 Analyzer, Astoria Pacific, Oregon, USA). For the determination of $[P]_{leaf}$, $[Ca]_{leaf}$, $[K]_{leaf}$, and $[Mg]_{leaf}$, the ground samples were digested using the sulphuric acid-hydrogen peroxide method (Allen, 1989). $[P]_{leaf}$ was determined colorimetrically using the molybdenum-blue method (Anderson & Ingram, 1993) by measuring the absorbance at 880 nm on a Spectrophotometer (Hitachi U-2900 UV/Vis , Tokyo, Japan). $[Ca]_{leaf}$, $[K]_{leaf}$ and $[Mg]_{leaf}$ were measured spectrophotometrically on a Spectro Arcos ICP-OES (Spectro Analytical Instruments, Kleve, Germany).

Soil nutrient analyses

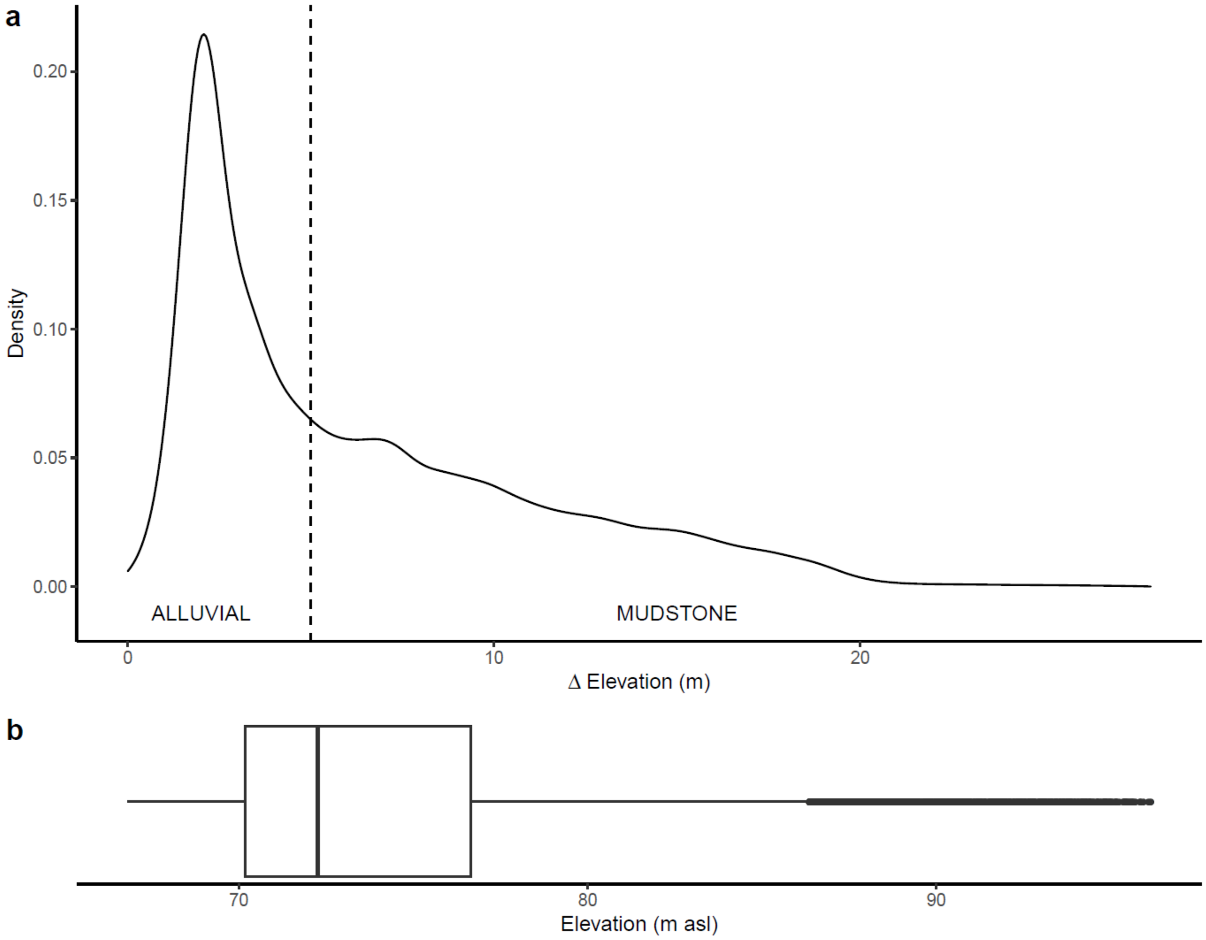
Soil samples collected across the four forest types were analysed for concentrations of total N, total P, soluble P, exchangeable Ca, K and Mg, pH and granulometry. Ten samples were collected across each of the six permanent 4 ha forest plots, across two elevational gradients per plot (five samples per elevation gradient; SI Figure 3.11) and at three depths: 0-5 cm, 5-15 cm, 15-30 cm. Samples were categorised as mudstone hill or alluvial floodplain within the alluvial 4 ha plots, according the same elevation thresholds for tree selection, with the sample located closest to the elevational threshold (73 m a.s.l.; see above) excluded. The transects ranged from approx. 50 to 200 m in length and were designed to maximise spatial and elevational coverage within each plot. Three local samples were collected 5 m apart at each sampling location and combined for 0-5 cm depth, whilst one single sample was collected at 5-15 cm and 15-30 cm depths at each location using a soil auger. Soil samples were brought back to the laboratory on the day of collection and airdried for two weeks. Soils were further dried at 40 ˚C in a lab oven for 3-4 days before being passed through a 2 mm sieve. Total N samples were digested using concentrated sulphuric acid following the Kjeldahl method (Anderson & Ingram, 1993), before being measured using a micro-SFA (Astoria2 Analyzer, Astoria Pacific, Oregon, USA). For total P determination, ground soils were digested following the sulphuric acid-hydrogen peroxide method (Allen, 1989), whilst soluble P was extracted following the method of Bray and Kurtz (1945). P concentrations were determined colorimetrically using the molybdenum blue method (Anderson & Ingram, 1993) by measuring absorbance at

880 nm on a Hitachi U-2900 UV/Vis Spectrophotometer (Tokyo, Japan). Concentrations of exchangeable base cations (Ca^{2+}, K^{+}, Mg^{2+}) were determined by first leaching the soil with 1M ammonium acetate (Thomas, 1982; Gillman *et al.*, 2008), and subsequently measuring the leachate for Ca, K and Mg using a Spectro Arcos ICP-OES Spectrophotometer (Spectro Analytical Instruments, Kleve, Germany). Soil pH was determined by analysing the soil in distilled water (1:2.5) using a Mettler Toledo pH electrode (Greifensee, Switzerland) connected to a Corning pH meter 240 (Corning Life Sciences, Texas, USA), according to Peech (1965). Soil granulometry was determined using the pipette method (Day, 1965). A sub-sample was dried at 105 ˚C to constant mass to adjust sample dry mass measurements. All foliar and soil lab analyses were undertaken in the Chemistry lab at the Forest Research Centre, Sepilok, and all analyses were quality-controlled using laboratory standards.

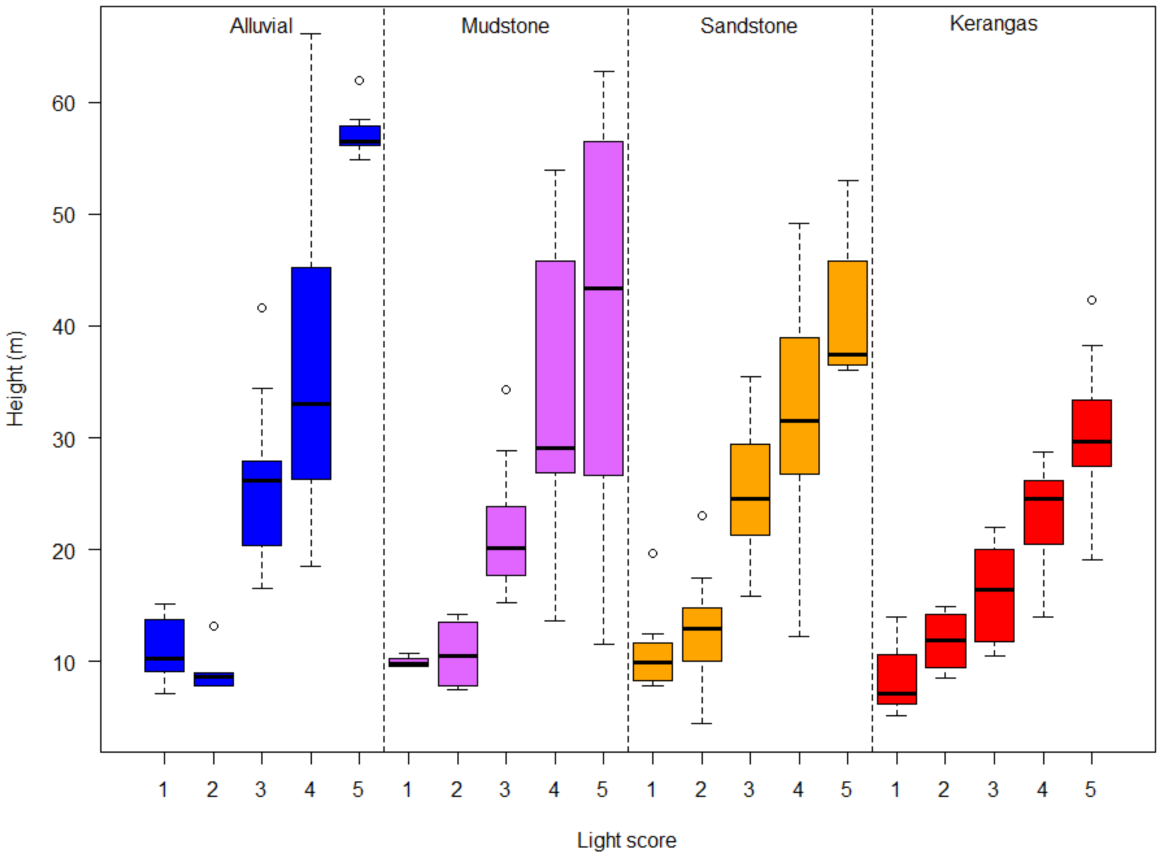
SI Figure 3.1: Soil conditions across the four forest types in Sepilok at three depths: 0-5 cm, 5-15 cm and 15-30 cm. Data on pH (a), total N and P concentration (b-c), available P (d), exchangeable Ca, K, Mg (e-g) and granulometry (h-j) are presented. Bars represent the mean values for sampling locations in each forest (see methods; n = 42), with error bars representing the mean ± standard error. Identical letters represent categories where there is no significant difference between forests for each soil depth from linear models (p > 0.05). For details of soil sampling and nutrient analysis, see supplementary methods.



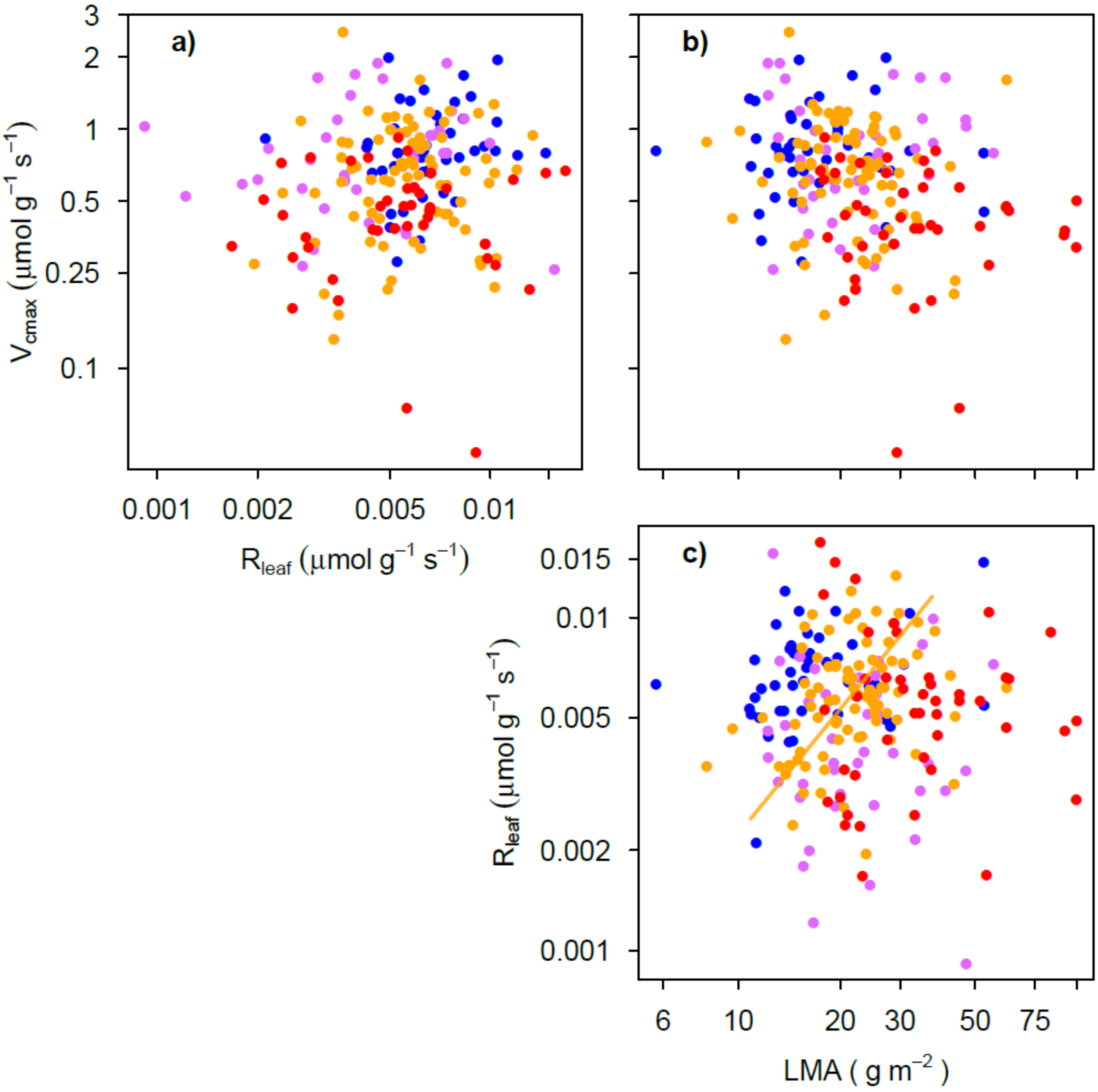
SI Figure 3.2: The distribution of relative elevation (a) and absolute elevation (b) within the two 4 ha alluvial plots. Individual 1x1m pixels of ground elevation within the forest plots were estimated from an airborne laser scanning generated digital elevation model (see Jucker *et al.* (2018b) for more details). Relative elevation was calculated by subtracting the lowest elevation within each 4 ha plot from absolute elevation. A clear difference in topographic structure between the flat lowland areas, here defined as alluvial, and hill areas, here defined as mudstone, exists. Within this study, a relative elevation threshold of 5m was used to separate areas of alluvial and mudstone forest within the plots, which approximately equates to 73m asl.



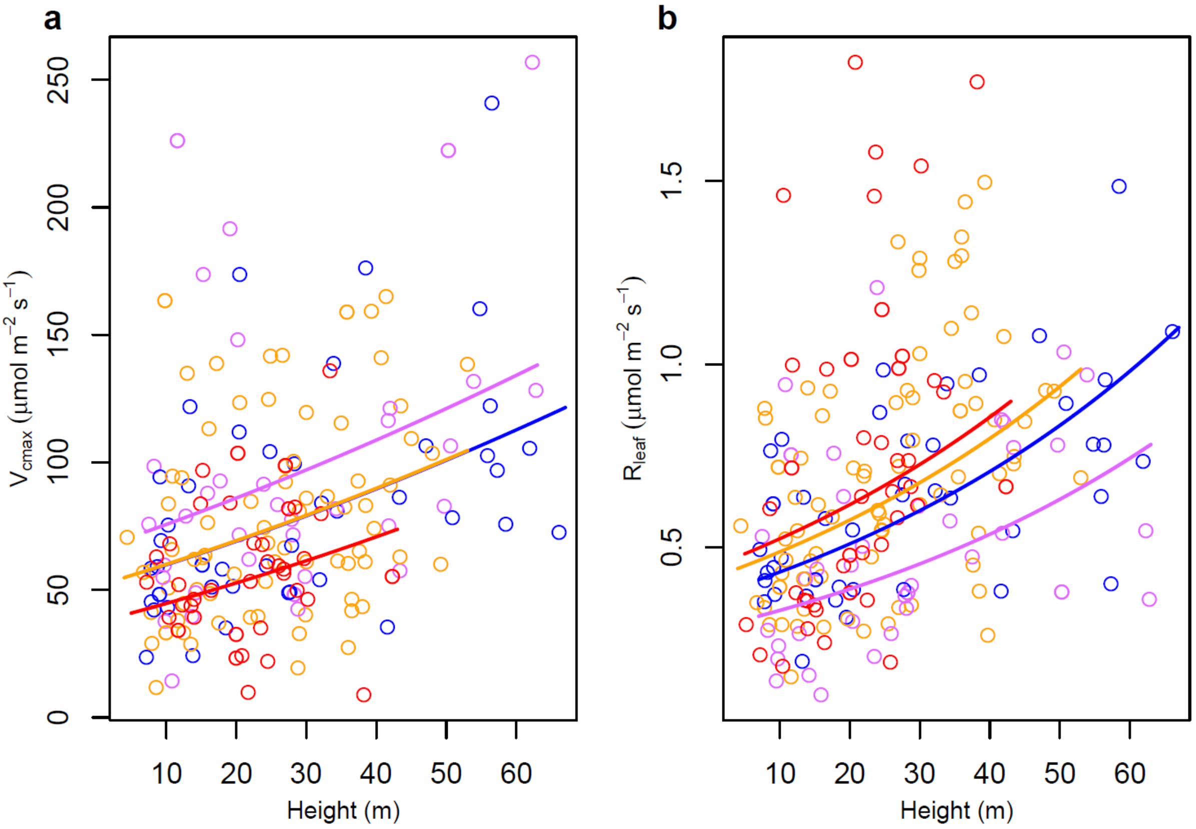
SI Figure 3.3: Variation in light availability with tree height across the four forest types (alluvial, mudstone, sandstone, kerangas). Each tree was assigned a light availability score following Keeling and Phillips (2007), whereby: 1 = Fully shaded tree, receiving no direct incoming sunlight; 2 = Mostly shaded tree with a minority of leaves receiving direct sunlight; 3 = Tree receiving direct sunlight to the upper branches, but still has a large number of shaded leaves; 4 = Fully sunlit tree with only lateral shading; 5 = Tree receiving full crown illumination for the whole of the day.



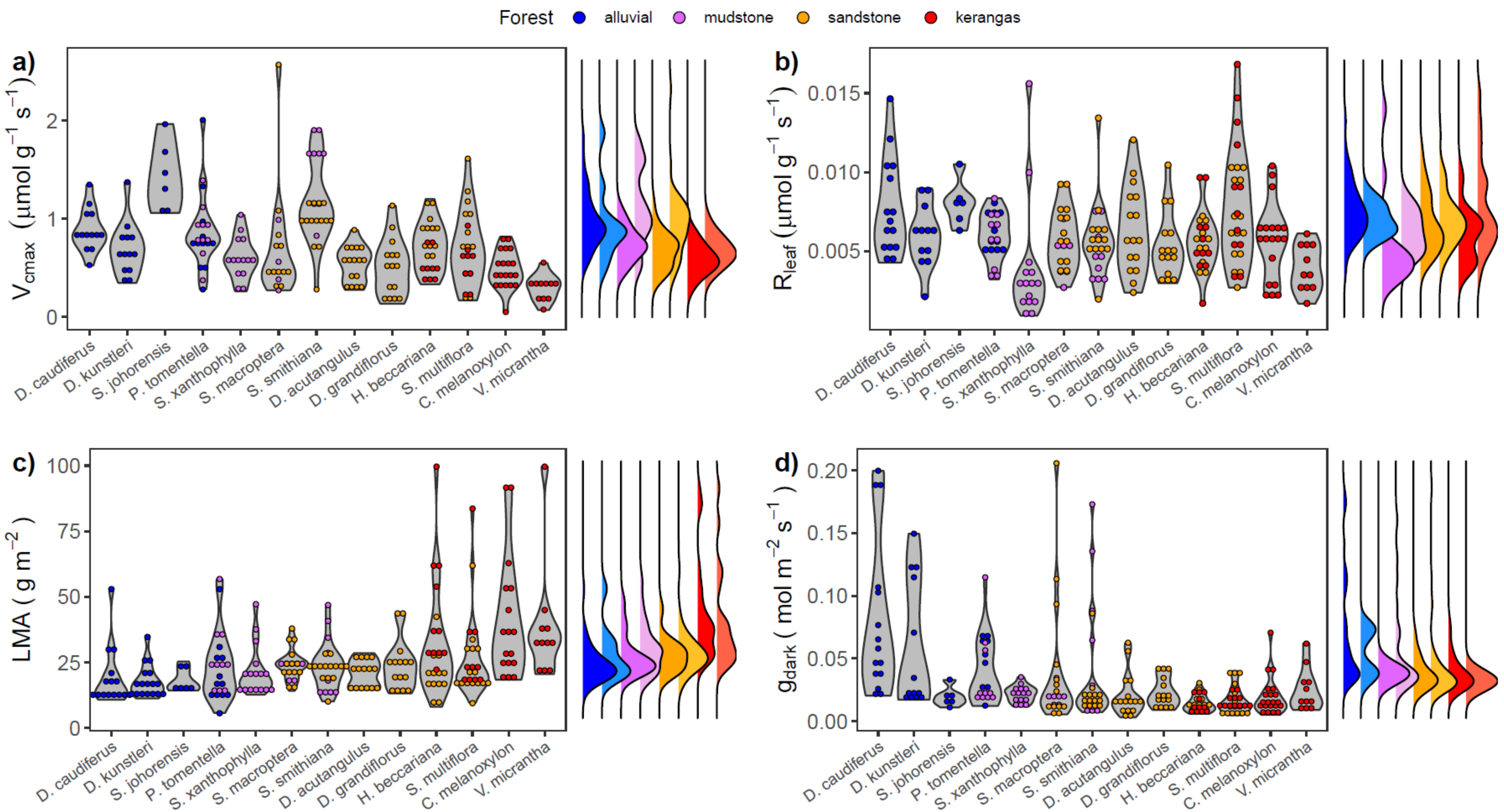
SI Figure 3.4: Standardised major axis regressions (SMAs) for bivariate trait relationships between V_{cmax}, R_{leaf} and leaf mass per area (LMA). Colours represent the different forests (blue – alluvial, purple – mudstone, orange – sandstone, red – kerangas). Lines are plotted only for significant SMA relationships ($p < 0.05$), with their degree of transparency scaled to the degree of significance (greater opacity represents greater significance). Note that data and axes are natural log transformed.



SI Figure 3.5: Scatterplots showing how *V*cmax (a), and *R*leaf (b) expressed on an area basis 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 3.1).

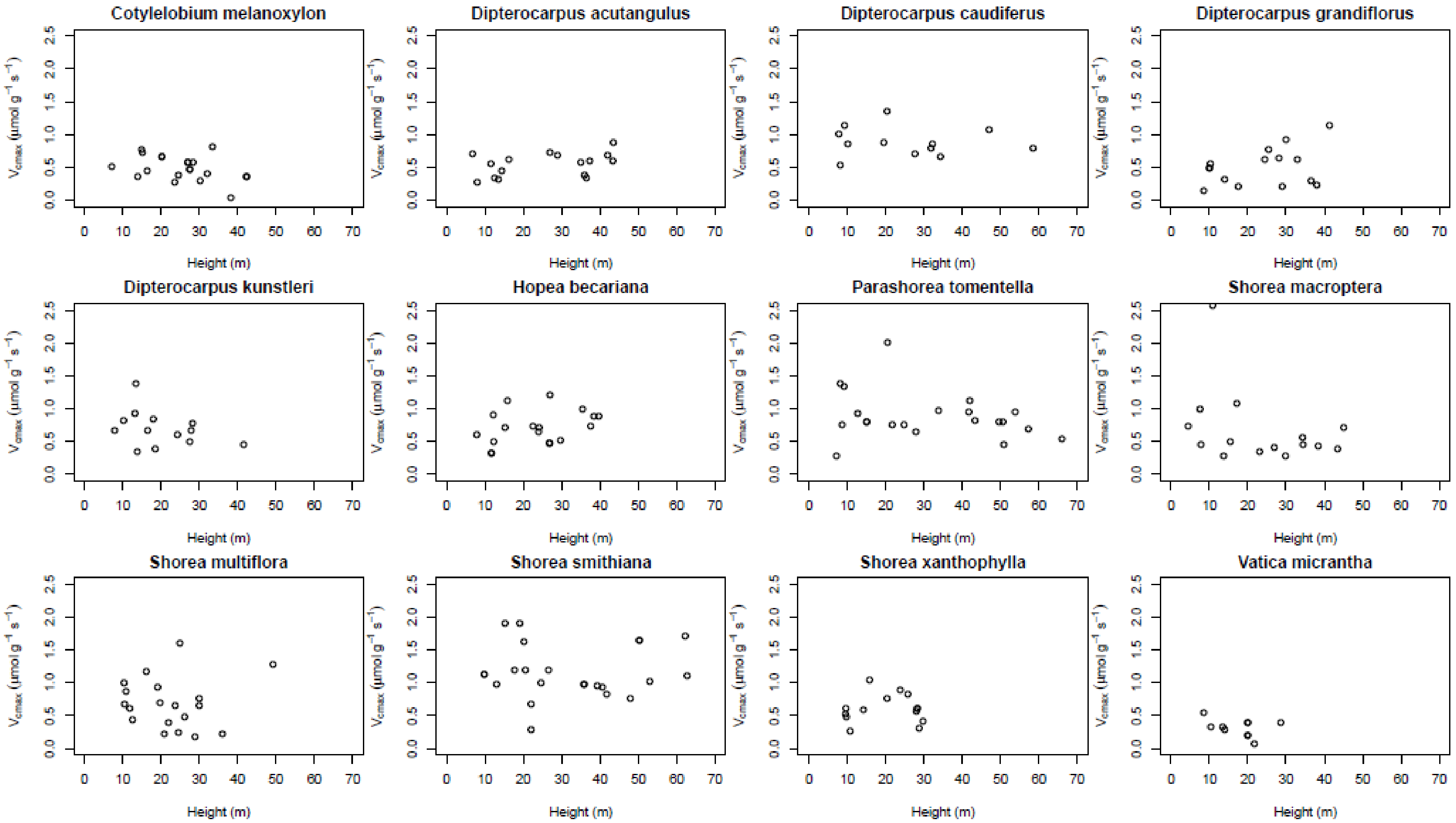


SI Figure 3.6: Violin plots showing intraspecific variation in *V*cmax (a), *R*leaf (b), leaf mass per area (LMA; c) and dark-adapted stomatal conductance (*g*dark; d) for the 13 species studied. Dots represent individual binned data points with colours representing the forest (blue – alluvial, purple – mudstone, orange – sandstone, red – kerangas). Associated density ridge plots represent the overall distribution of the data for specialist (darker colours) and generalist (paler colours) species for each forest type with corresponding colours.

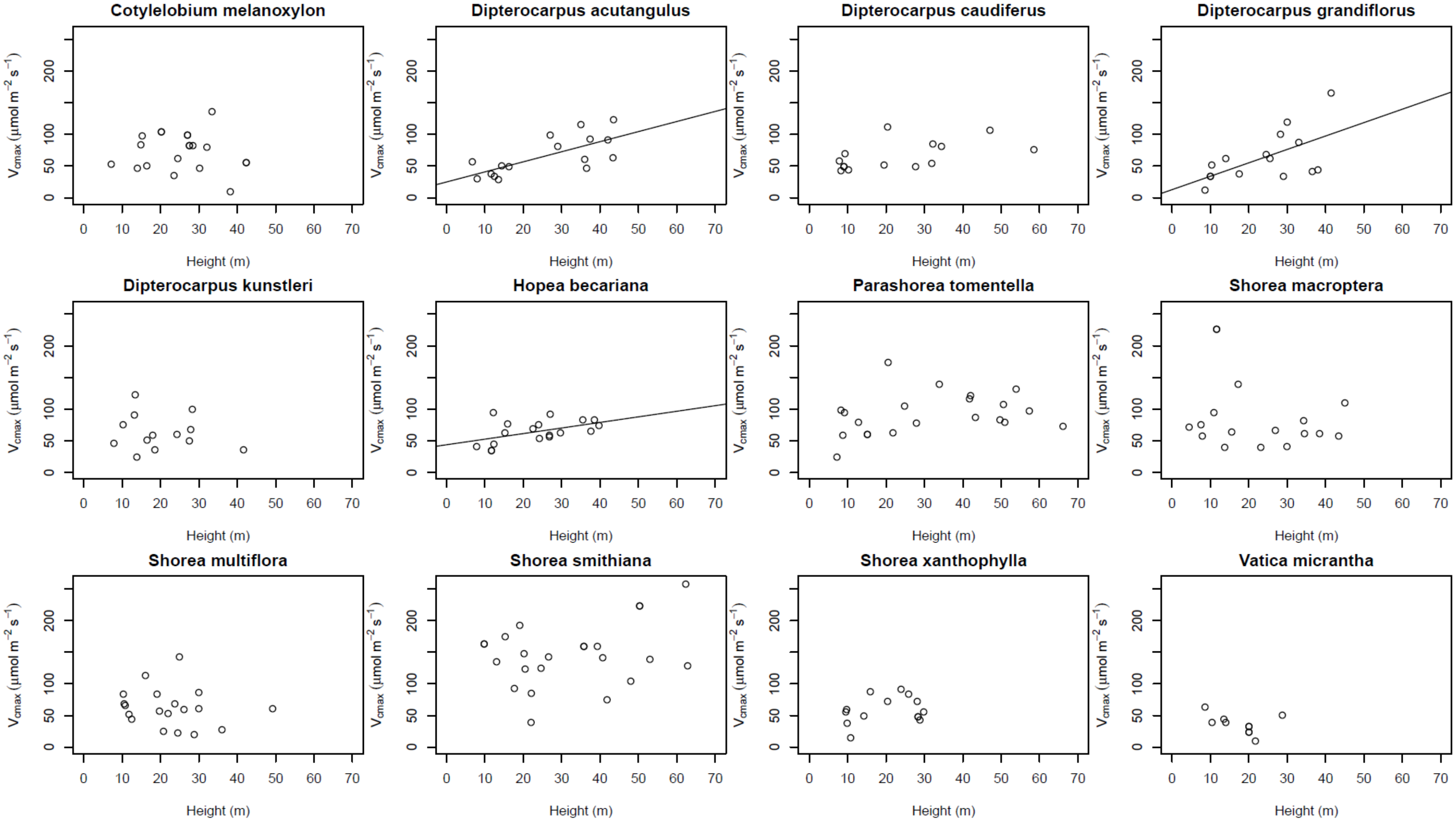

Forest
● alluvial
● mudstone
● sandstone
● kerangas
a)
V_{cmax} (µmol g^{-1} s^{-1})
0
1
2
b)
R_{leaf} (µmol g^{-1} s^{-1})
0.005
0.010
0.015
c)
LMA (g m^{-2})
0
25
50
75
100
d)
g_{dark} (mol m^{-2} s^{-1})
0.00
0.05
0.10
0.15
0.20
D. caudiferus
D. kunstleri
S. johorensis
P. tomentella
S. xanthophylla
S. macroptera
S. smithiana
D. acutangulus
D. grandiflorus
H. beccariana
S. multiflora
C. melanoxylon
V. micrantha

SI Figure 3.7: Height-trait relationships for each of the study species for (a) V_{cmax} (mass-basis), (b) V_{cmax} (area-basis), (c) R_{leaf} (mass-basis), (d) R_{leaf} (area-basis), (e) leaf mass per area (LMA), (f) leaf thickness, (g) g_{dark}, (h) $[N]_{leaf}$, (i) $[P]_{leaf}$, (j) $[Ca]_{leaf}$, (k) $[K]_{leaf}$ and (l) $[Mg]_{leaf}$. Lines are plotted when the linear model with height included as a fixed effect was significantly better than the null model ($p > 0.05$) for each species. *Shorea johorensis* is not plotted as only large trees were sampled in this study for this species.

a)



b)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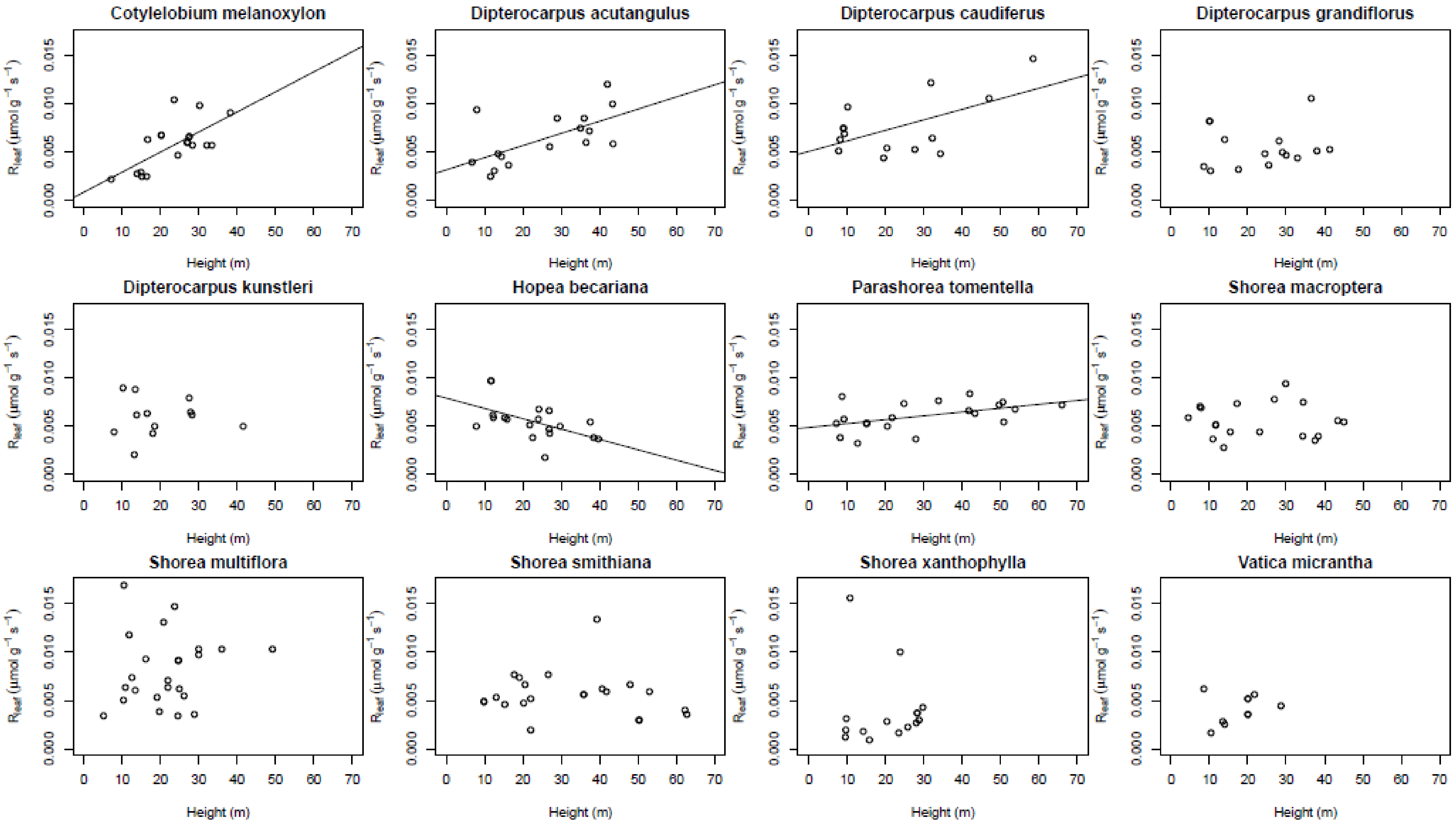
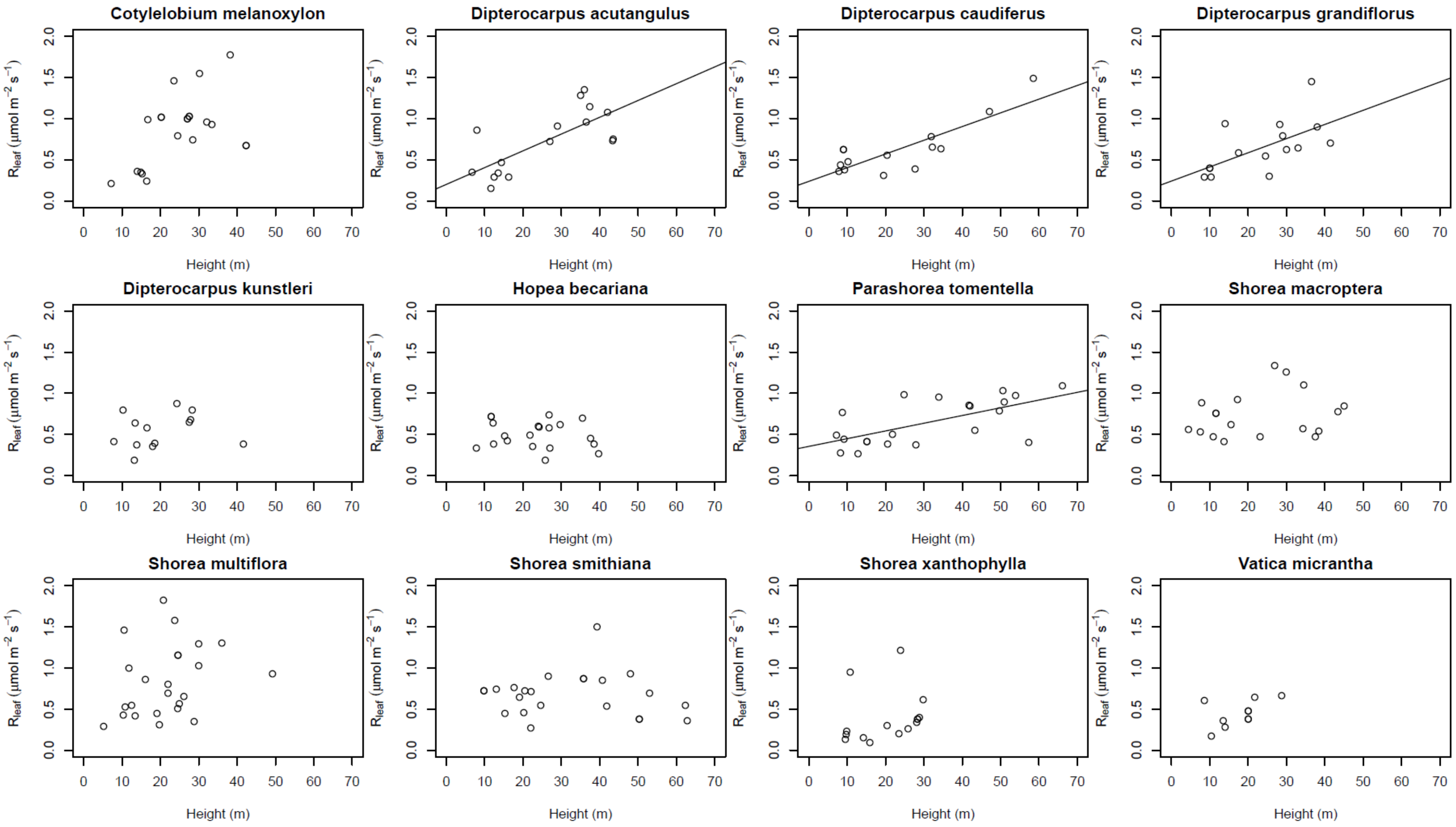
Dipterocarpus acutangulus
Dipterocarpus caudiferus
Dipterocarpus grandiflorus
Dipterocarpus kunstleri
Hopea becariana
Parashorea tomentella
Shorea macroptera
Shorea multiflora
Shorea smithiana
Shorea xanthophylla
Vatica micrantha
V_{cmax} (µmol m^{-2} s^{-1})
0
50
100
200
Height (m)
0
10
20
30
40
50
60
70

c)


Cotylelobium melanoxylon
Dipterocarpus acutangulus
Dipterocarpus caudiferus
Dipterocarpus grandiflorus
Dipterocarpus kunstleri
Hopea becariana
Parashorea tomentella
Shorea macroptera
Shorea multiflora
Shorea smithiana
Shorea xanthophylla
Vatica micrantha
R_{leaf} (μmol g^{-1} s^{-1})
0.000
0.005
0.010
0.015
Height (m)
0
10
20
30
40
50
60
70

d)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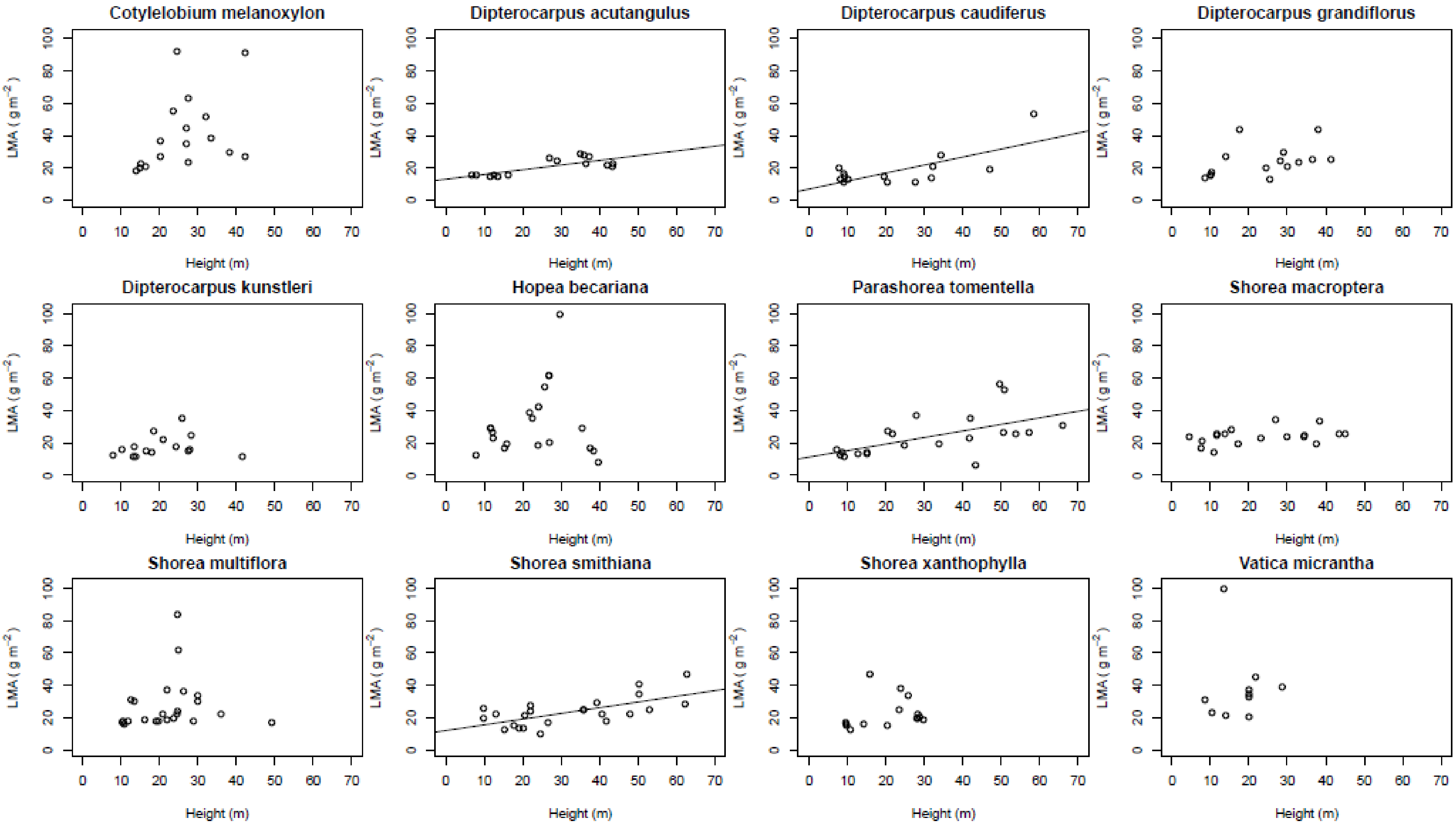
Dipterocarpus acutangulus
Dipterocarpus caudiferus
Dipterocarpus grandiflorus
Dipterocarpus kunstleri
Hopea becariana
Parashorea tomentella
Shorea macroptera
Shorea multiflora
Shorea smithiana
Shorea xanthophylla
Vatica micrantha
R_{leaf} (μmol m^{-2} s^{-1})
0.0
0.5
1.0
1.5
2.0
0
10
20
30
40
50
60
70
Height (m)

e)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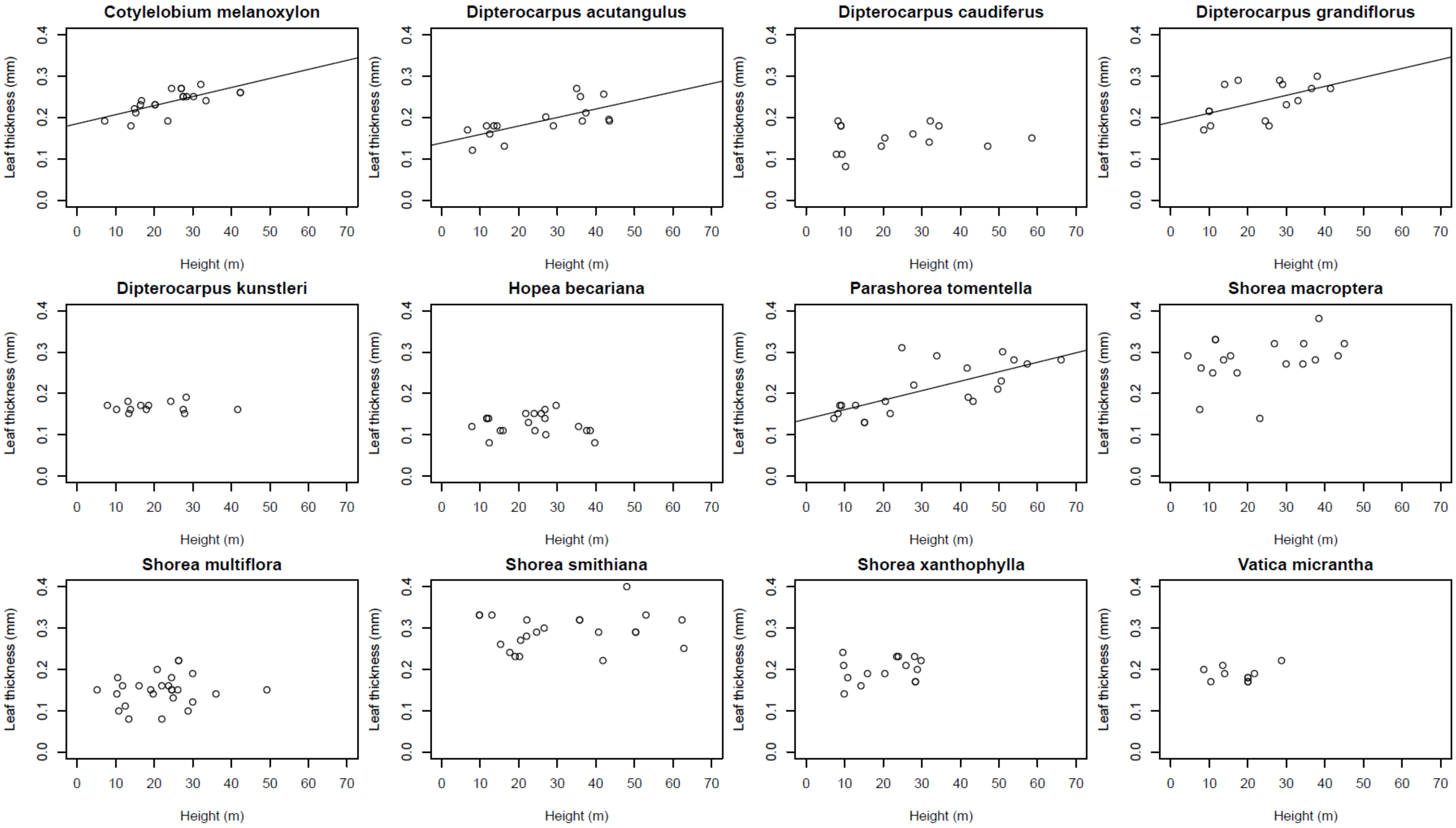
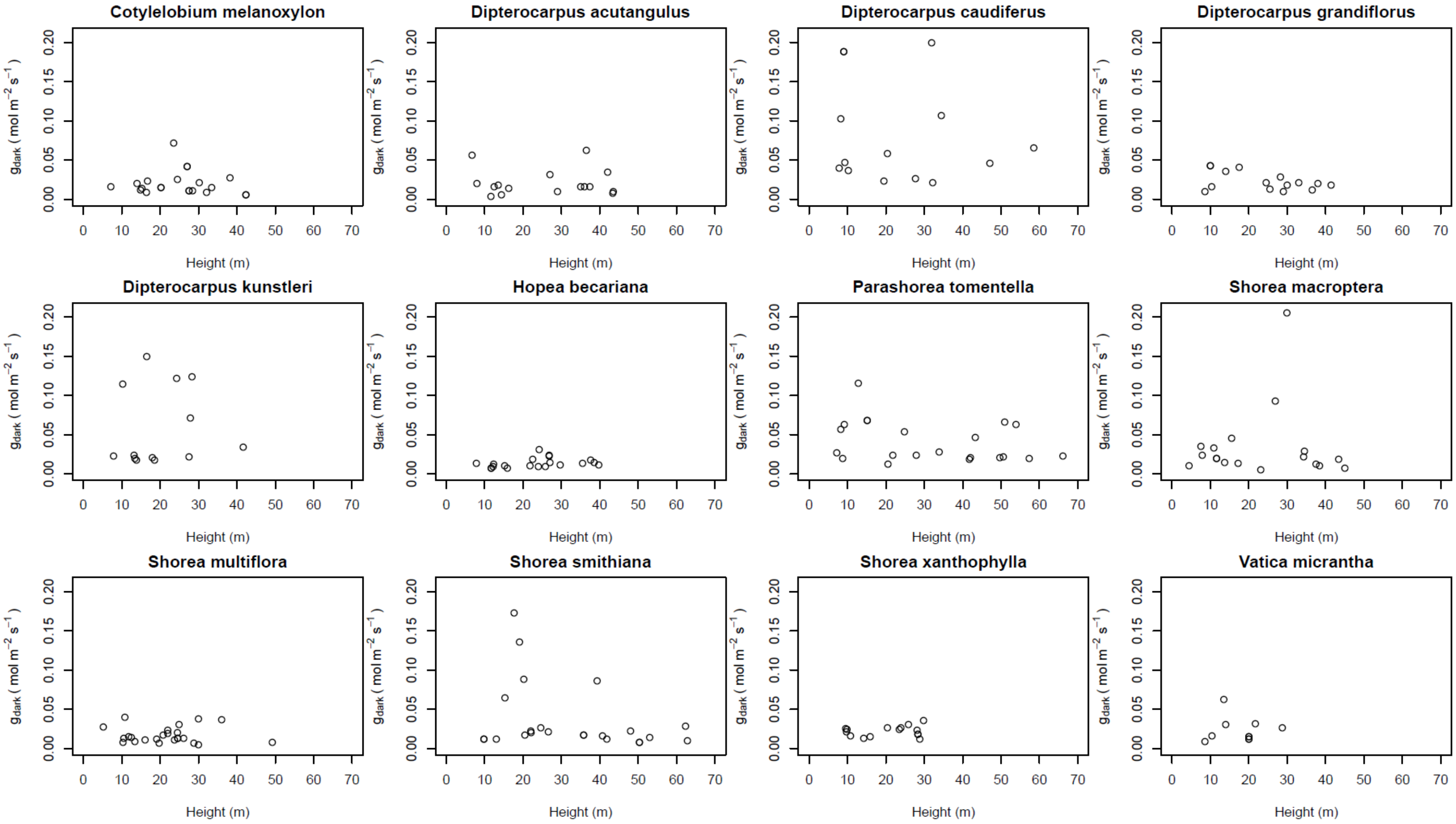
Dipterocarpus grandiflorus
Dipterocarpus kunstleri
Hopea becariana
Parashorea tomentella
Shorea macroptera
Shorea multiflora
Shorea smithiana
Shorea xanthophylla
Vatica micrantha
LMA (g m^{-2})
0 20 40 60 80 100
Height (m)
0 10 20 30 40 50 60 70

f)


Cotylelobium melanoxylon
Dipterocarpus acutangulus
Dipterocarpus caudiferus
Dipterocarpus grandiflorus
Dipterocarpus kunstleri
Hopea becariana
Parashorea tomentella
Shorea macroptera
Shorea multiflora
Shorea smithiana
Shorea xanthophylla
Vatica micrantha
Leaf thickness (mm)
0.0
0.1
0.2
0.3
0.4
Height (m)
0
10
20
30
40
50
60
70

g)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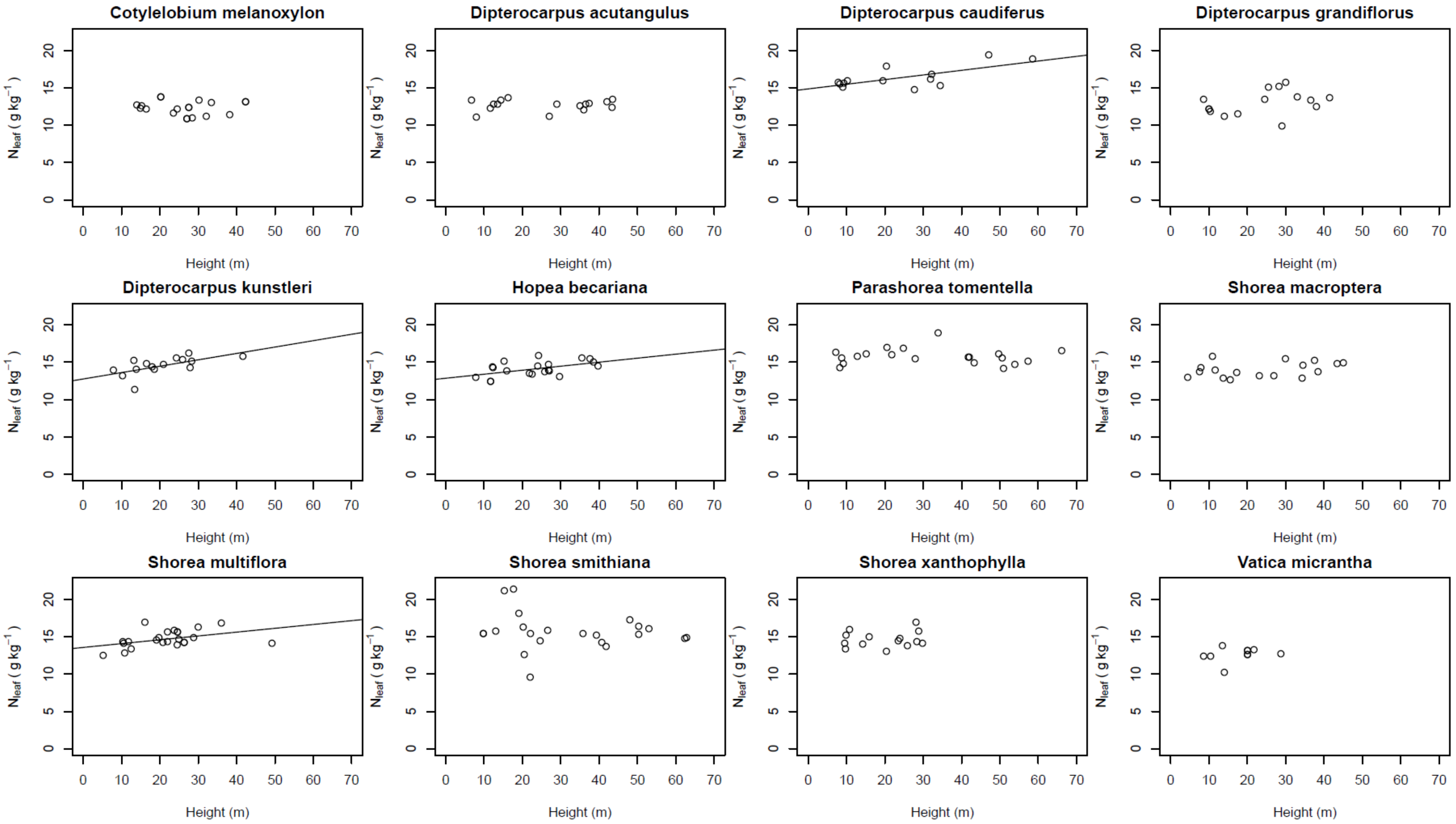
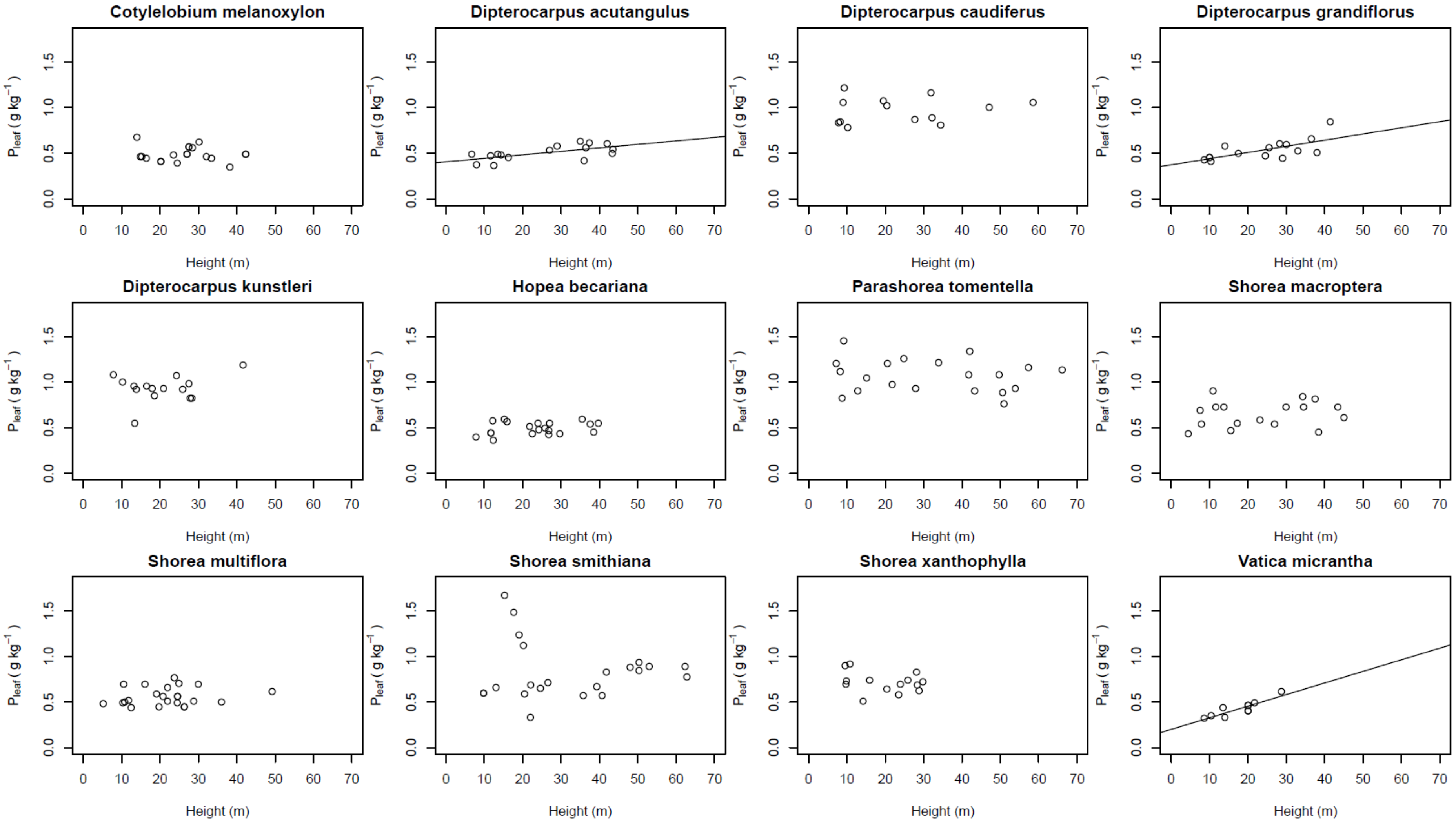
Dipterocarpus acutangulus
Dipterocarpus caudiferus
Dipterocarpus grandiflorus
Dipterocarpus kunstleri
Hopea becariana
Parashorea tomentella
Shorea macroptera
Shorea multiflora
Shorea smithiana
Shorea xanthophylla
Vatica micrantha
g_{dark} (mol m^{-2} s^{-1})
0.00
0.05
0.10
0.15
0.20
Height (m)
0
10
20
30
40
50
60
70

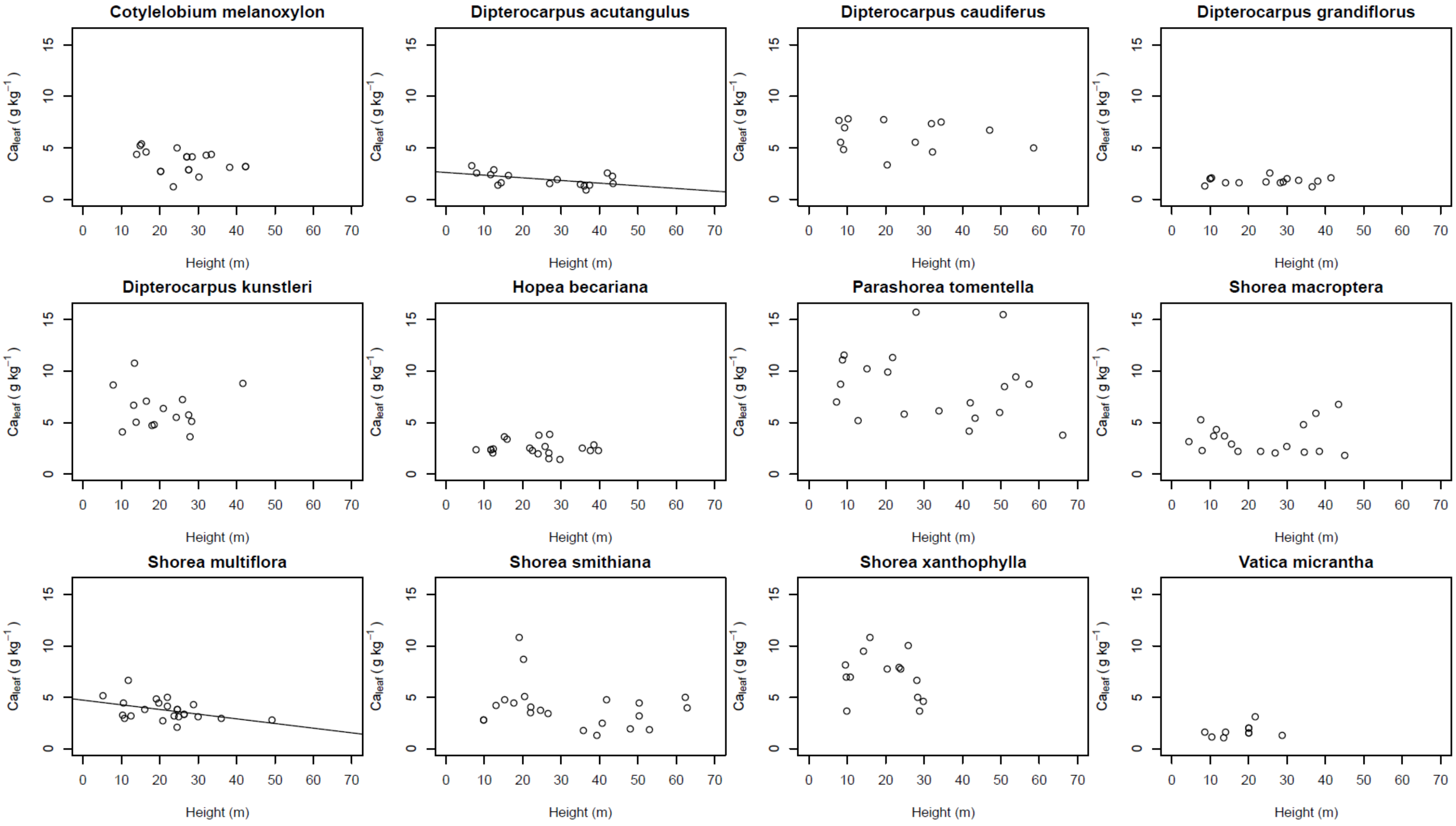
h)


Cotylelobium melanoxylon
Dipterocarpus acutangulus
Dipterocarpus caudiferus
Dipterocarpus grandiflorus
Dipterocarpus kunstleri
Hopea becariana
Parashorea tomentella
Shorea macroptera
Shorea multiflora
Shorea smithiana
Shorea xanthophylla
Vatica micrantha
N_{leaf} (g kg^{-1})
0
5
10
15
20
Height (m)
0
10
20
30
40
50
60
70

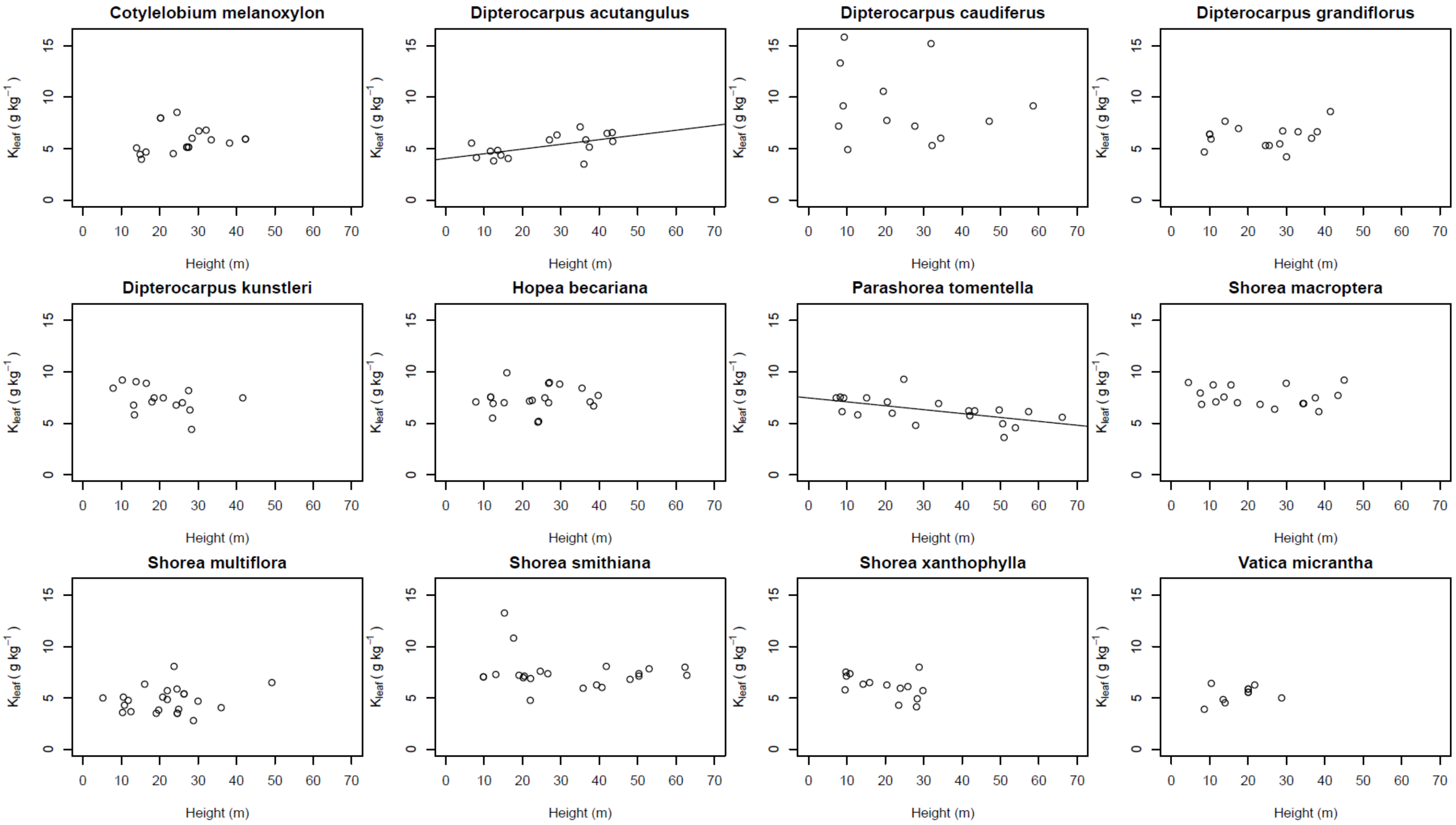
i)


Cotylelobium melanoxylon
Dipterocarpus acutangulus
Dipterocarpus caudiferus
Dipterocarpus grandiflorus
Dipterocarpus kunstleri
Hopea becariana
Parashorea tomentella
Shorea macroptera
Shorea multiflora
Shorea smithiana
Shorea xanthophylla
Vatica micrantha
P_{leaf} (g kg^{-1})
0.0
0.5
1.0
1.5
Height (m)
0
10
20
30
40
50
60
70

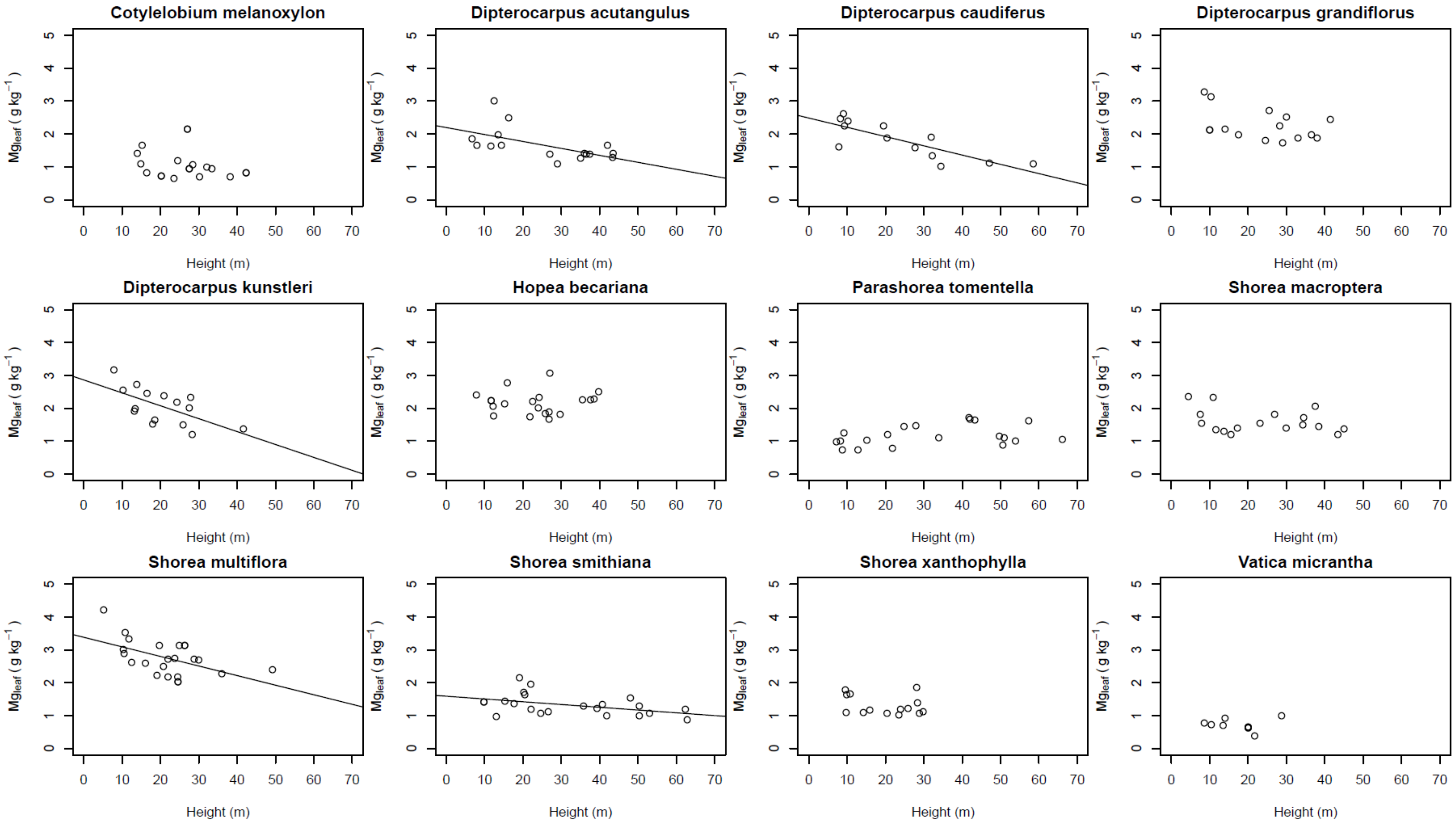
j)


Cotylelobium melanoxylon
Dipterocarpus acutangulus
Dipterocarpus caudiferus
Dipterocarpus grandiflorus
Dipterocarpus kunstleri
Hopea becariana
Parashorea tomentella
Shorea macroptera
Shorea multiflora
Shorea smithiana
Shorea xanthophylla
Vatica micrantha
Ca$_{leaf}$ (g kg^{-1})
0
5
10
15
Height (m)
0
10
20
30
40
50
60
70

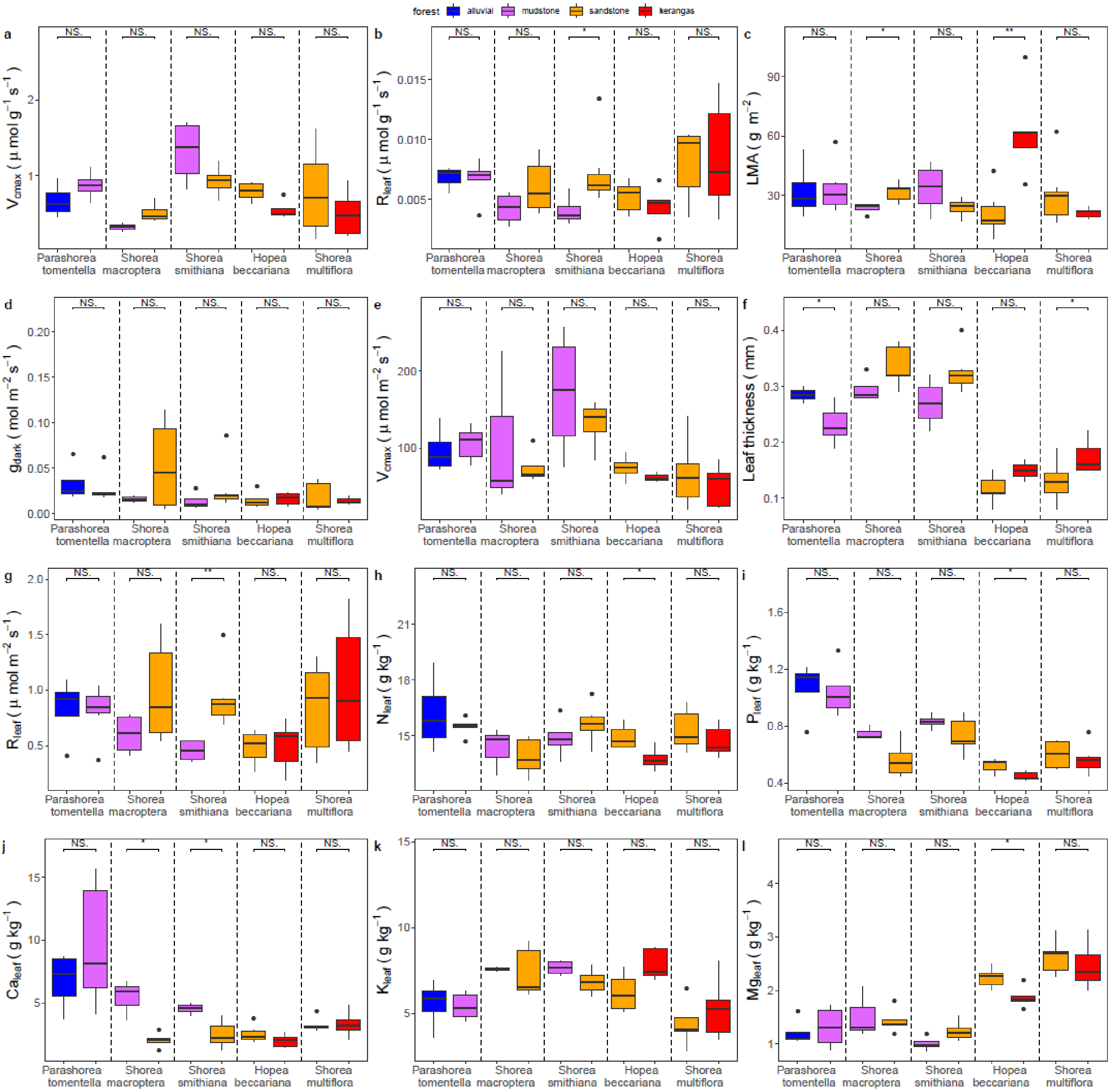
k)


Cotylelobium melanoxylon
Dipterocarpus acutangulus
Dipterocarpus caudiferus
Dipterocarpus grandiflorus
Dipterocarpus kunstleri
Hopea becariana
Parashorea tomentella
Shorea macroptera
Shorea multiflora
Shorea smithiana
Shorea xanthophylla
Vatica micrantha
K_{leaf} (g kg^{-1})
0
5
10
15
Height (m)
0
10
20
30
40
50
60
70

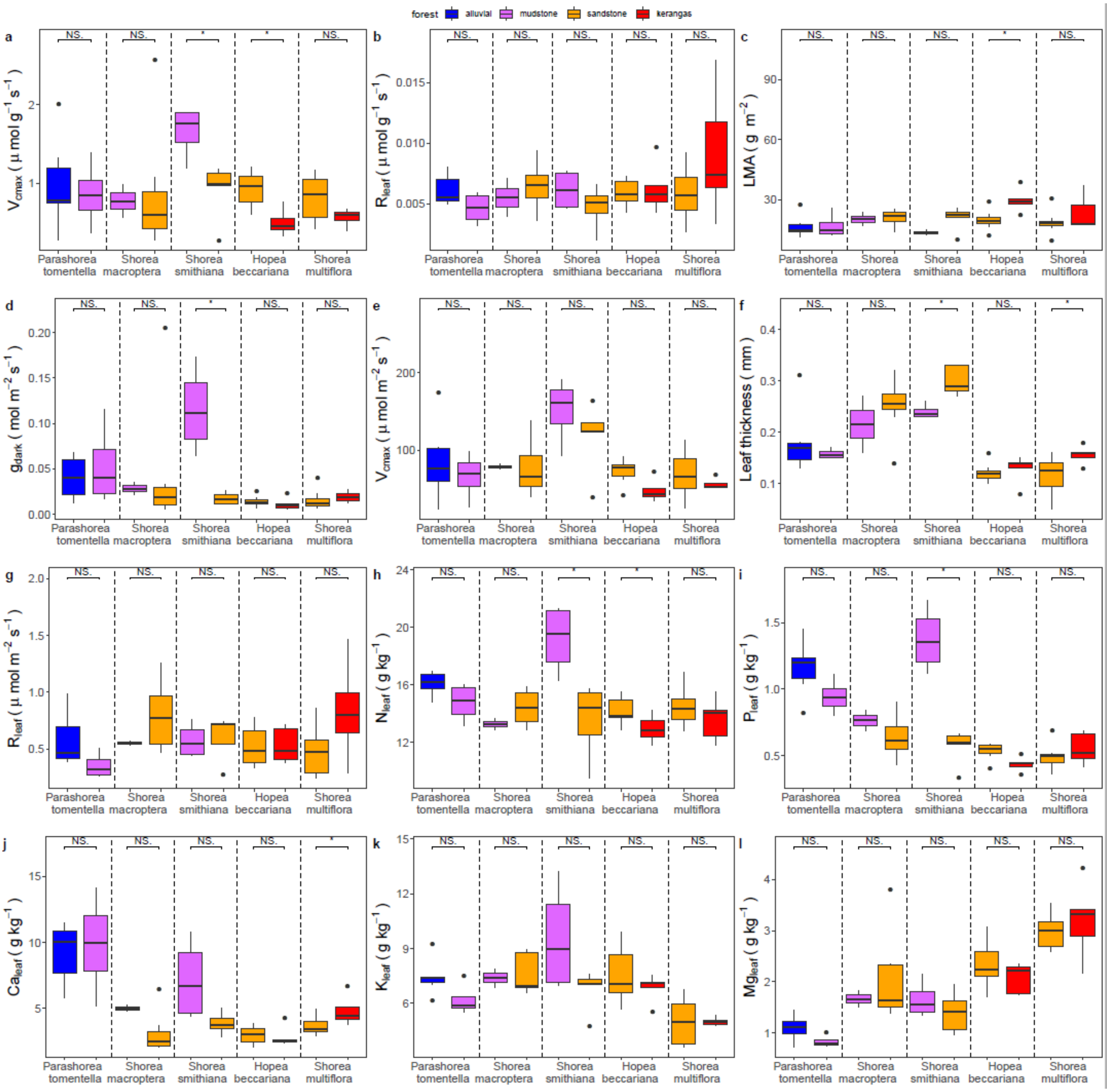
l)


Cotylelobium melanoxylon
Dipterocarpus acutangulus
Dipterocarpus caudiferus
Dipterocarpus grandiflorus
Dipterocarpus kunstleri
Hopea becariana
Parashorea tomentella
Shorea macroptera
Shorea multiflora
Shorea smithiana
Shorea xanthophylla
Vatica micrantha
Mg_{leaf} (g kg^{-1})
0
1
2
3
4
5
Height (m)
0
10
20
30
40
50
60
70

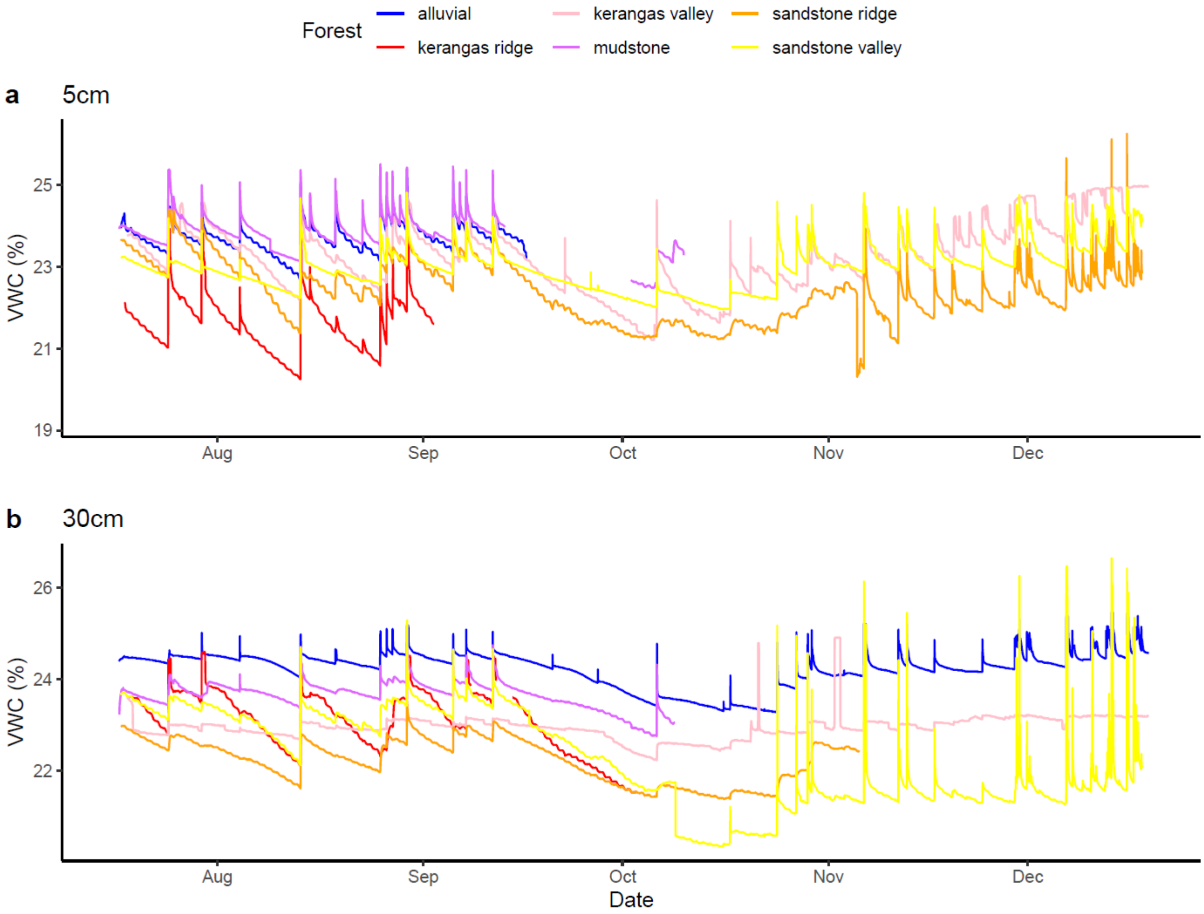
SI Figure 3.8: Boxplots showing intraspecific differences in V_{cmax_mass} (a), R_{leaf_mass} (b), leaf mass per area (LMA; c), minimum stomatal conductance (g_{dark}; d), V_{cmax_area} (e), leaf thickness (f), R_{leaf_area} (g), $[N]_{leaf}$ (h), $[P]_{leaf}$ (i), $[Ca]_{leaf}$ (j), $[K]_{leaf}$ (k) and $[Mg]_{leaf}$ (l) between forests (alluvial – blue, mudstone – purple, sandstone – orange, kerangas – red) for fully sunlit trees from five generalist species. Species were classified according to stem density across the forests (see methods for details). Pairwise comparisons between forests were made for each species using Wilcoxon signed rank tests. Asterisks represent significance levels: NS – $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. 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 1.5*interquartile range. Comparisons of traits for all trees can be seen in Figures 3.5 and SI Figure 3.12.


forest
alluvial
mudstone
sandstone
kerangas
a
V_cmax (µ mol g⁻¹ s⁻¹)
1
2
b
R_leaf (µ mol g⁻¹ s⁻¹)
0.005
0.010
0.015
c
LMA (g m⁻²)
30
60
90
d
g_dark (mol m⁻² s⁻¹)
0.00
0.05
0.10
0.15
0.20
e
V_cmax (µ mol m⁻² s⁻¹)
100
200
f
Leaf thickness (mm)
0.1
0.2
0.3
0.4
g
R_leaf (µ mol m⁻² s⁻¹)
0.5
1.0
1.5
2.0
h
N_leaf (g kg⁻¹)
15
18
21
i
P_leaf (g kg⁻¹)
0.4
0.8
1.2
1.6
j
Ca_leaf (g kg⁻¹)
5
10
15
k
K_leaf (g kg⁻¹)
5
10
15
l
Mg_leaf (g kg⁻¹)
1
2
3
4
NS.
*
**
Parashorea tomentella
Shorea macroptera
Shorea smithiana
Hopea beccariana
Shorea multiflora

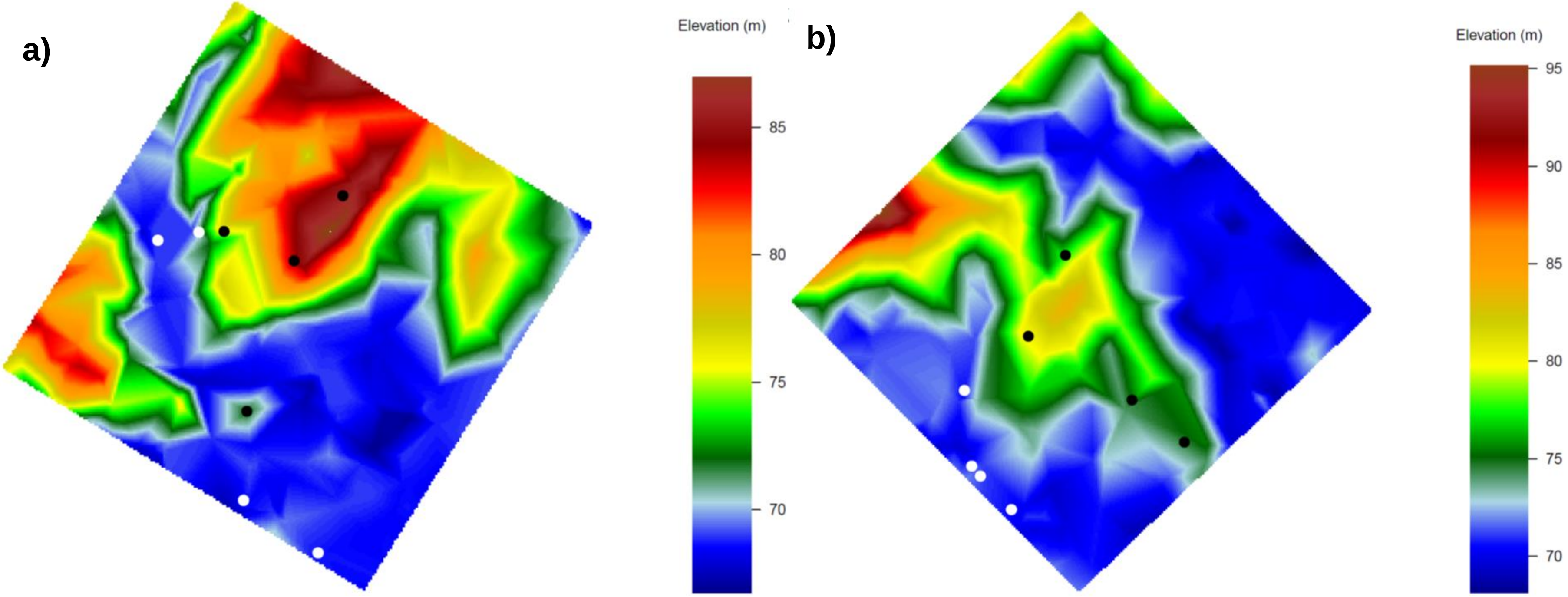
SI Figure 3.9: Boxplots showing intraspecific differences in $V_{\text{cmax\_mass}}$ (a), $R_{\text{leaf\_mass}}$ (b), leaf mass per area (LMA; c), minimum stomatal conductance (g_{dark}; d), $V_{\text{cmax\_area}}$ (e), leaf thickness (f), $R_{\text{leaf\_area}}$ (g), $[\mathrm{N}]_{\text{leaf}}$ (h), $[P]_{\text{leaf}}$ (i), $[Ca]_{\text{leaf}}$ (j), $[K]_{\text{leaf}}$ (k) and $[Mg]_{\text{leaf}}$ (l) between forests (alluvial – blue, mudstone – purple, sandstone – orange, kerangas – red) for shaded trees from five generalist species. Species were classified according to stem density across the forests (see methods for details). Pairwise comparisons between forests were made for each species using Wilcoxon signed rank tests. Asterisks represent significance levels: NS – $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. 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 1.5*interquartile range.

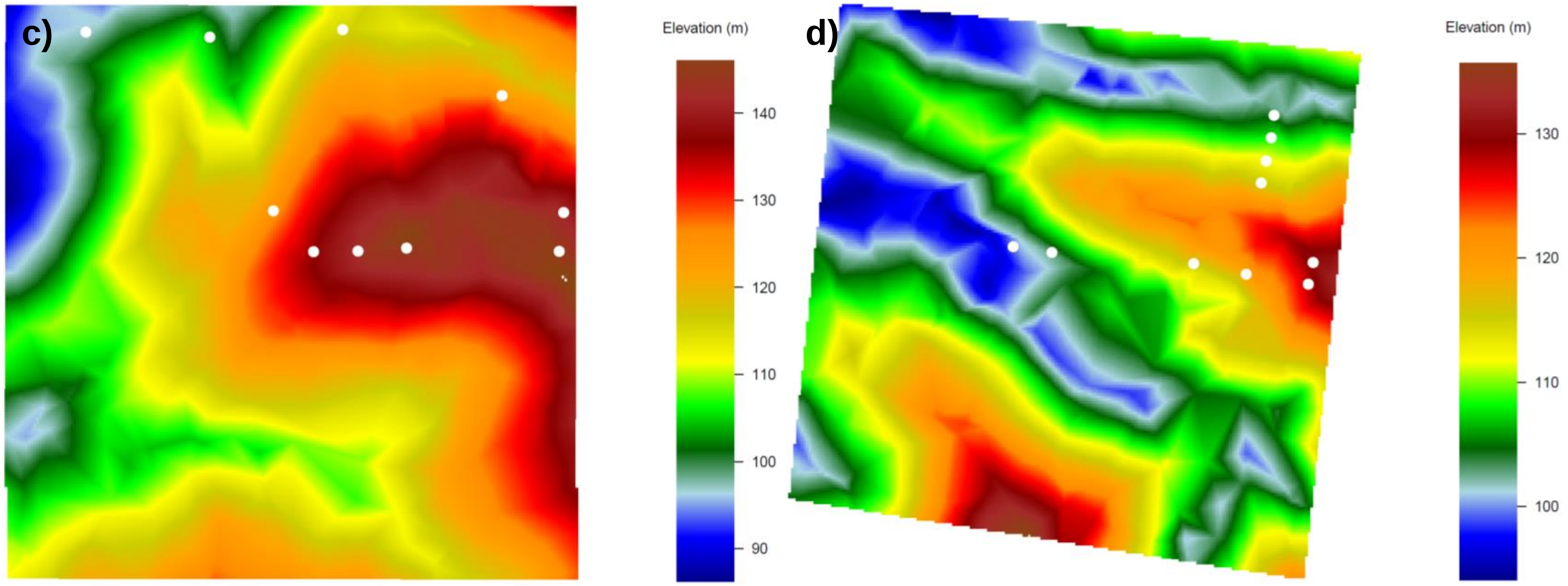

forest alluvial mudstone sandstone kerangas
a
b
c
d
e
f
g
h
i
j
k
l
V_{cmax} (μ mol g^{-1} s^{-1})
R_{leaf} (μ mol g^{-1} s^{-1})
LMA (g m^{-2})
g_{dark} (mol m^{-2} s^{-1})
V_{cmax} (μ mol m^{-2} s^{-1})
Leaf thickness (mm)
R_{leaf} (μ mol m^{-2} s^{-1})
N_{leaf} (g kg^{-1})
P_{leaf} (g kg^{-1})
Ca_{leaf} (g kg^{-1})
K_{leaf} (g kg^{-1})
Mg_{leaf} (g kg^{-1})
NS.
*
Parashorea tomentella
Shorea macroptera
Shorea smithiana
Hopea beccariana
Shorea multiflora

SI Figure 3.10 – Patterns in volumetric water content (VWC) for soil at 5 cm (a) and 30 cm (b) depth within each forest. A single delta-T SM150T soil moisture sensor (Delta-T Devices Ltd, Cambridge, UK) was installed at 5cm and 30cm depth in six different locations across the study site: an alluvial valley (blue), a mudstone hill (purple), a sandstone ridge (orange) and valley (yellow), and a kerangas ridge (red) and valley (pink). Measurements were recorded every 15 minutes from 17th July 2019 to 17th December 2019. Voltage output readings were converted to VWC using mineral soil calibration coefficients. Breaks in the lines represent data gaps resulting from sensor or logger failure caused by damage by wildlife or flooding.

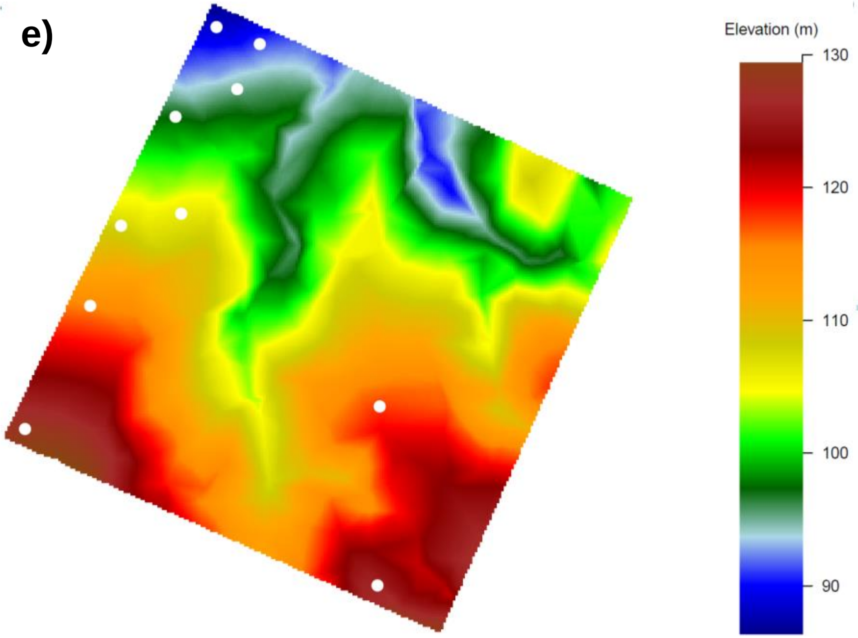


SI Figure 3.11 - Maps showing the ground elevation and locations for soil samples across the nine permanent 4 ha plots in Sepilok: (a-b) alluvial/mudstone forest; (c-d) sandstone; (e-f) kerangas. Sampling locations are shown in white dots for all forests, except for alluvial/mudstone plots where mudstone forests are distinguished by black dots.

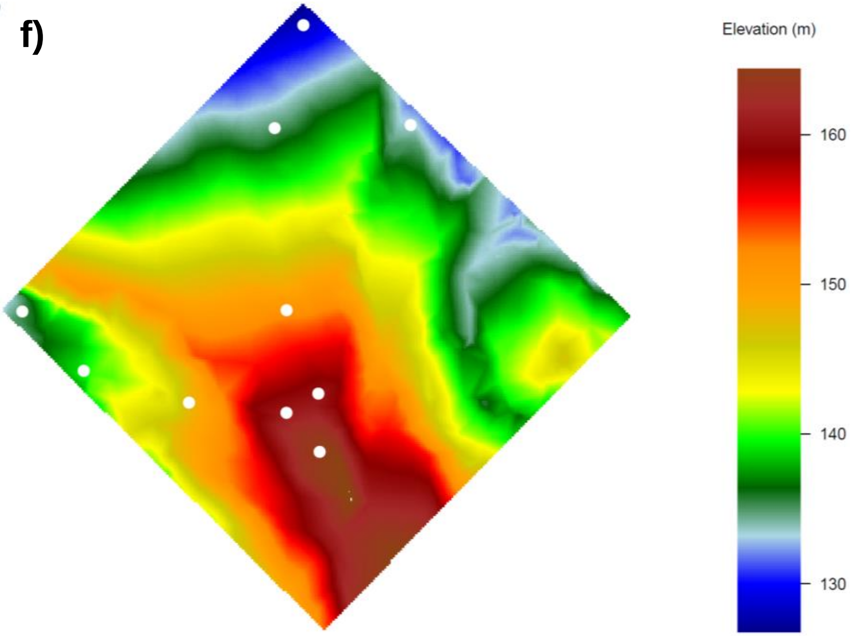



c)
Elevation (m)
140
130
120
110
100
90
d)
Elevation (m)
130
120
110
100

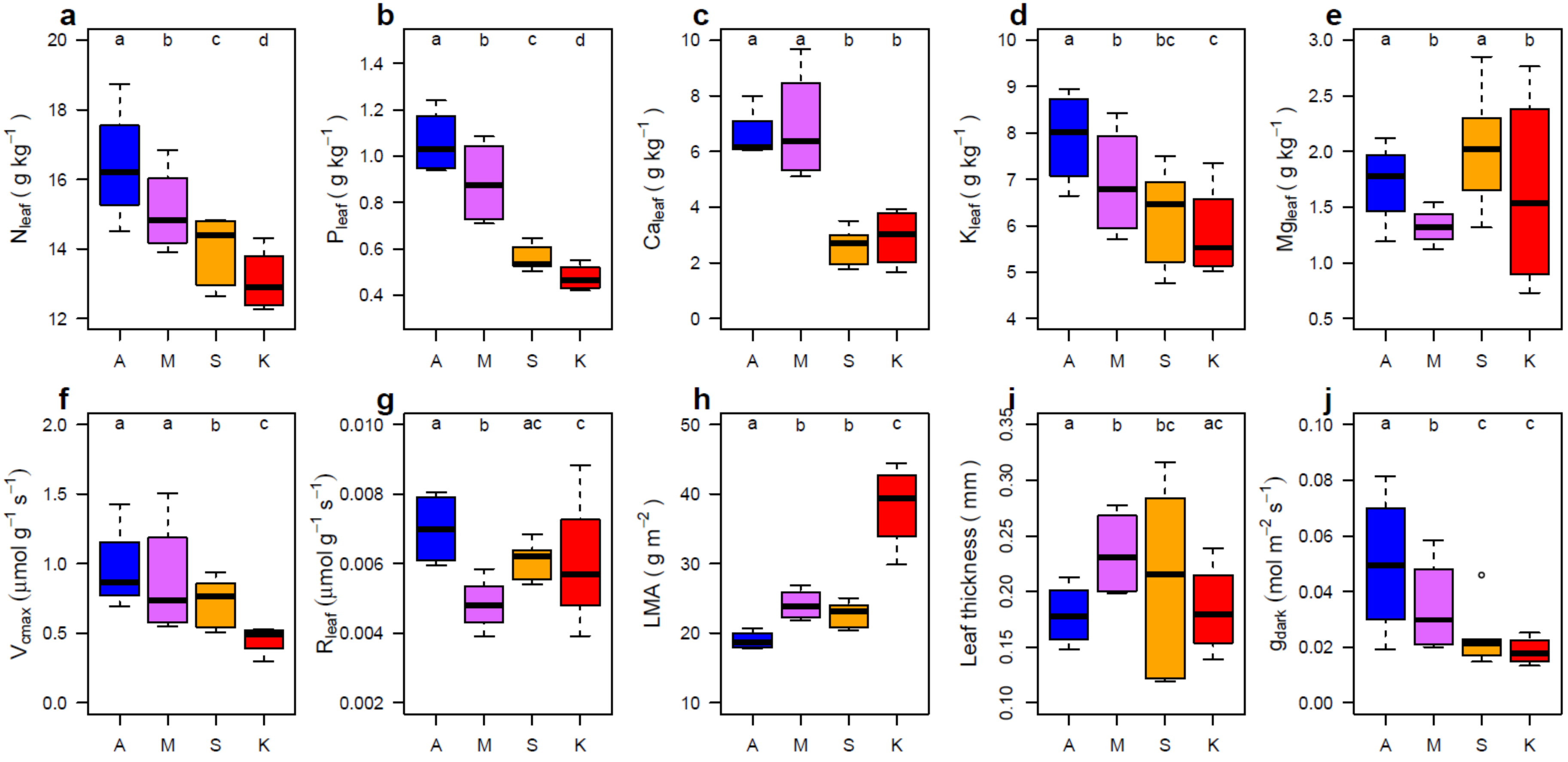
e)



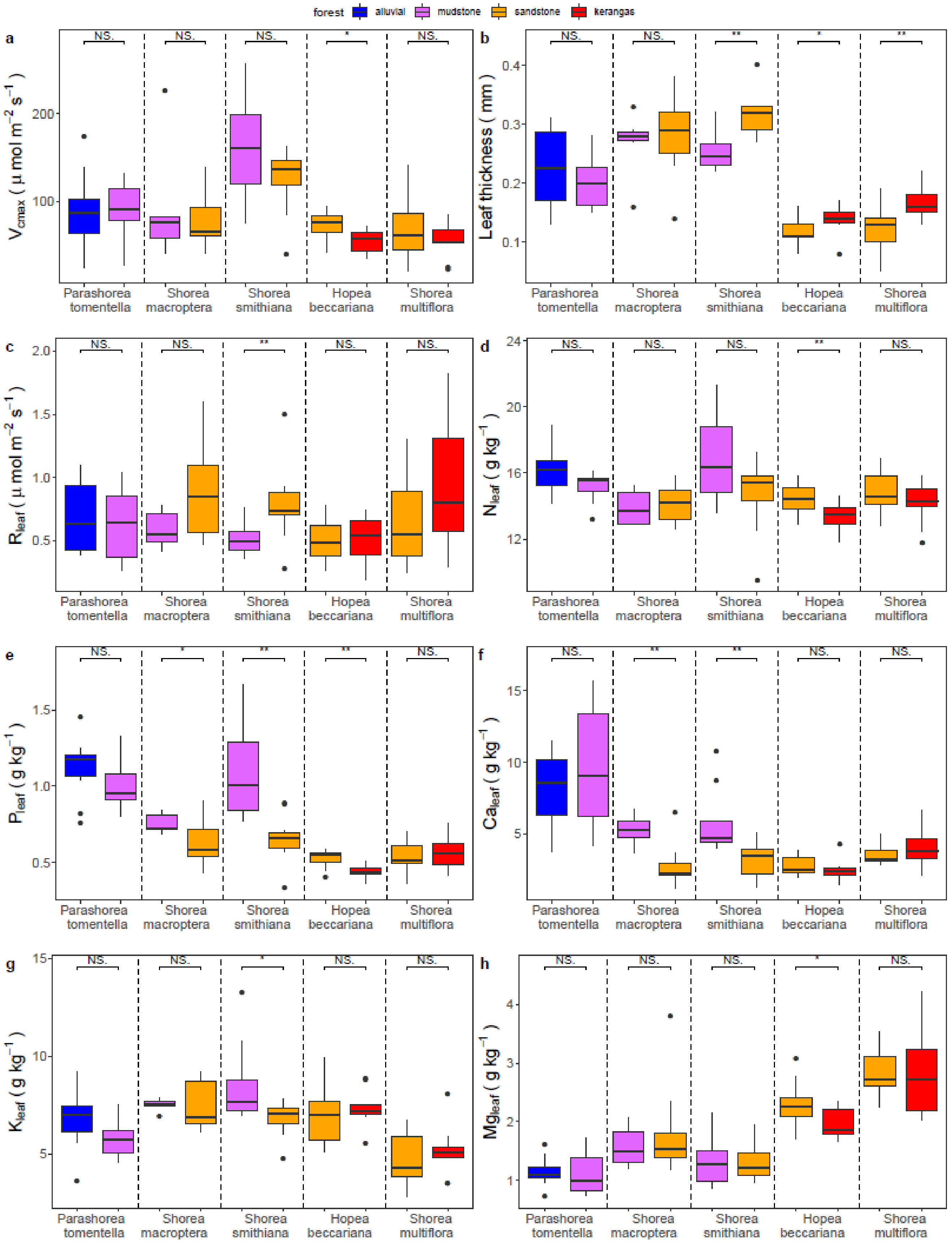
f)



SI Figure 3.12: Boxplots showing how leaf nutrient concentrations (a-e), V_{cmax} (f), R_{leaf} (g), leaf mass per area (LMA; h), leaf thickness (i) and dark-adapted stomatal conductance (g_{dark}; j) change between the four forests (alluvial (A) – blue, mudstone (M) – purple, sandstone (S) – orange, kerangas (K) – red). Data presented represent species-mean trait values (see Figure 3.1 for presentation at the individual-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 1.5*interquartile range.



SI Figure 3.13: Boxplots showing intraspecific differences in V_{cmax_area} (a), leaf thickness (b), R_{leaf_area} (c), $[N]_{leaf}$ (d), $[P]_{leaf}$ (e), $[Ca]_{leaf}$ (f), $[K]_{leaf}$ (g) and $[Mg]_{leaf}$ (h) between forests (alluvial – blue, mudstone – purple, sandstone – orange, kerangas – red) for five generalist species. Species were classified according to stem density across the forests (see methods for details). Pairwise comparisons between forests were made for each species using Wilcoxon signed rank tests. Asterisks represent significance levels: NS – $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. 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 1.5*interquartile range.


forest
alluvial
mudstone
sandstone
kerangas
a
V_{cmax} (µ mol m^{-2} s^{-1})
100
200
NS.
NS.
NS.
*
NS.
b
Leaf thickness (mm)
0.1
0.2
0.3
0.4
NS.
NS.
**
*
**
c
R_{leaf} (µ mol m^{-2} s^{-1})
0.5
1.0
1.5
2.0
NS.
NS.
**
NS.
NS.
d
N_{leaf} (g kg^{-1})
12
16
20
24
NS.
NS.
NS.
**
NS.
e
P_{leaf} (g kg^{-1})
0.5
1.0
1.5
NS.
*
**
**
NS.
f
Ca_{leaf} (g kg^{-1})
5
10
15
NS.
**
**
NS.
NS.
g
K_{leaf} (g kg^{-1})
5
10
15
NS.
NS.
*
NS.
NS.
h
Mg_{leaf} (g kg^{-1})
1
2
3
4
NS.
NS.
NS.
*
NS.
Parashorea tomentella
Shorea macroptera
Shorea smithiana
Hopea beccariana
Shorea multiflora

SI Table 3.1: Summary of tree abundance and basal area for study species across six (two per forest type) permanent 4 ha plots established in the Sepilok Forest Reserve. Data presented is the total across 8 ha for each forest habitat and was collected in 2013. Note, alluvial forest plots were divided into two forest classifications - alluvial floodplains and mudstone hills - for analysis of eco-physiological data in this study, but here are presented as combined alluvial forest as Nilus (2004) and Jucker *et al.* (2018b).

Species	**Abundance**				**Basal Area (m^2)**			
	Alluvial	**Mudstone**	**Sandstone**	**Kerangas**	**Alluvial**	**Mudstone**	**Sandstone**	**Kerangas**
Cotylelobium melanoxylon	0	0	13	815	0	0	0.381	26.508
Dipterocarpus acutangulus	5	0	339	0	0.012	0	22.627	0
Dipterocarpus caudiferus	64	21	0	0	8.795	1.127	0	0
Dipterocarpus grandiflorus	0	0	76	0	0	0	2.900	0
Dipterocarpus kunstleri	286	86	0	0	7.734	2.027	0	0
Hopea beccariana	0	0	184	141	0	0	8.220	1.841
Parashorea tomentella	98	115	0	0	17.610	22.023	0	0
Shorea johorensis	57	6	0	0	17.187	2.701	0	0
Shorea macroptera	21	12	152	0	0.946	1.623	3.897	0
Shorea multiflora	0	0	743	1851	0	0	28.141	50.005
Shorea smithiana	7	12	44	0	1.751	4.874	5.474	0
Shorea xanthophylla	394	495	0	0	6.163	8.462	0	0
Vatica micrantha	0	0	155	364	0	0	1.746	4.638

SI Table 3.2: Species habitat associations, degree of specialism and sample sizes (n) for study species. The range of height and diameter of each species in each forest is provided. For more details, see Methods.

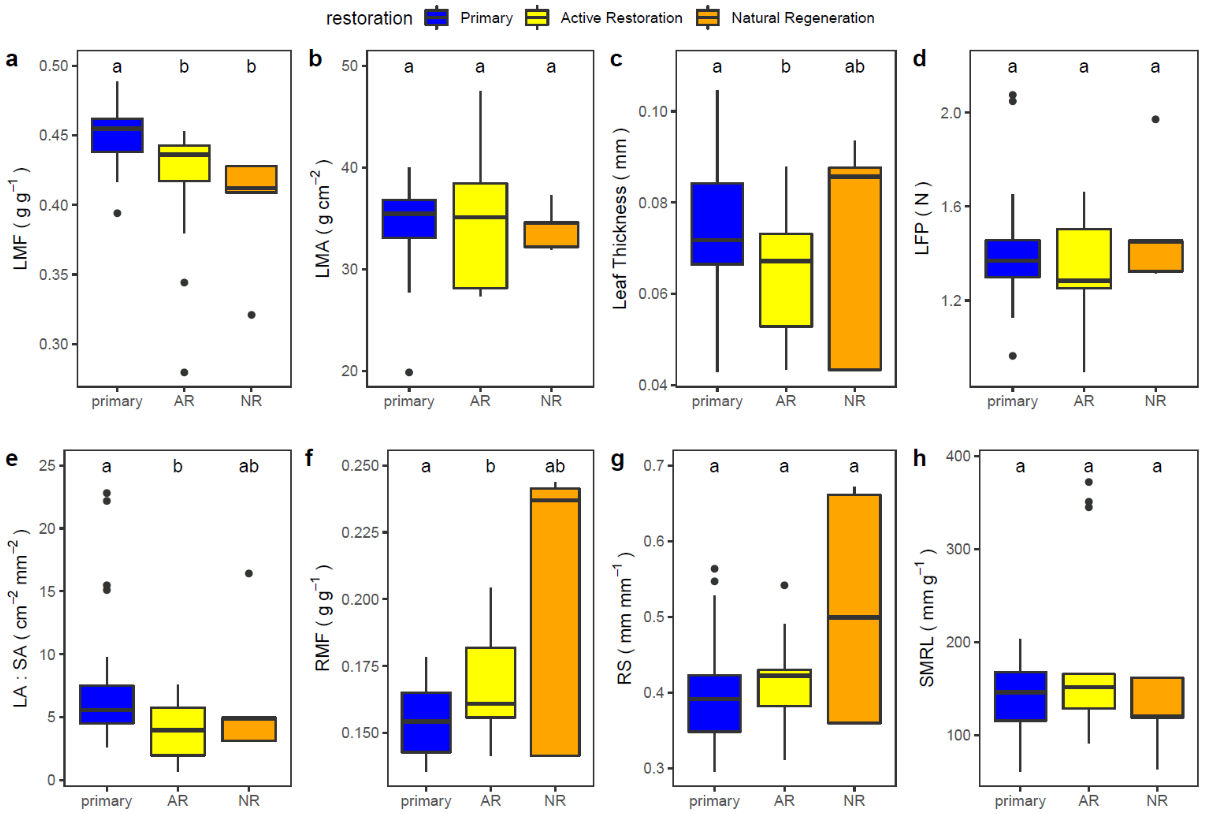
Species	Specialist or Generalist	Habitat association	n	Height (m)		DBH (cm)	
				min.	max.	min.	max.
Cotylelobium melanoxylon	Specialist	Kerangas	21	7.2	42.3	5.7	52.7
Dipterocarpus acutangulus	Specialist	Sandstone	16	6.7	43.5	7.2	108.5
Dipterocarpus caudiferus	Specialist	Alluvial	15	7.8	58.5	5.7	137.3
Dipterocarpus grandiflorus	Specialist	Sandstone	15	8.6	41.4	7.3	97.1
Dipterocarpus kunstleri	Specialist	Alluvial	17	7.9	41.6	6.0	51.9
Hopea beccariana	Generalist	Sandstone	13	7.8	39.7	5.7	60.8
		Kerangas	11	11.7	29.7	7.3	38.8
Parashorea tomentella	Generalist	Alluvial	12	7.2	66.1	6.7	104.4
		Mudstone	10	8.3	53.9	6.7	102.5
Shorea johorensis	Specialist	Alluvial	6	38.5	61.9	57.6	137.8
Shorea macroptera	Generalist	Mudstone	7	7.5	43.4	6.7	87.9
		Sandstone	13	4.4	45.0	5.7	60.5
Shorea multiflora	Generalist	Sandstone	15	10.3	49.2	6.0	89.1
		Kerangas	14	5.2	26.3	6.0	82.8
Shorea smithiana	Generalist	Mudstone	9	15.3	62.8	16.9	89.1
		Sandstone	14	9.8	53.0	7.96	98.4
Shorea xanthophylla	Specialist	Mudstone	16	9.5	29.8	8.0	94.3
Vatica micrantha	Specialist	Kerangas	11	8.6	28.7	6.4	37.6

SI Table 3.3: Summary of the forest plots from which leaves were sampled, including information on the number of stems, basal area and elevation range of the plot.

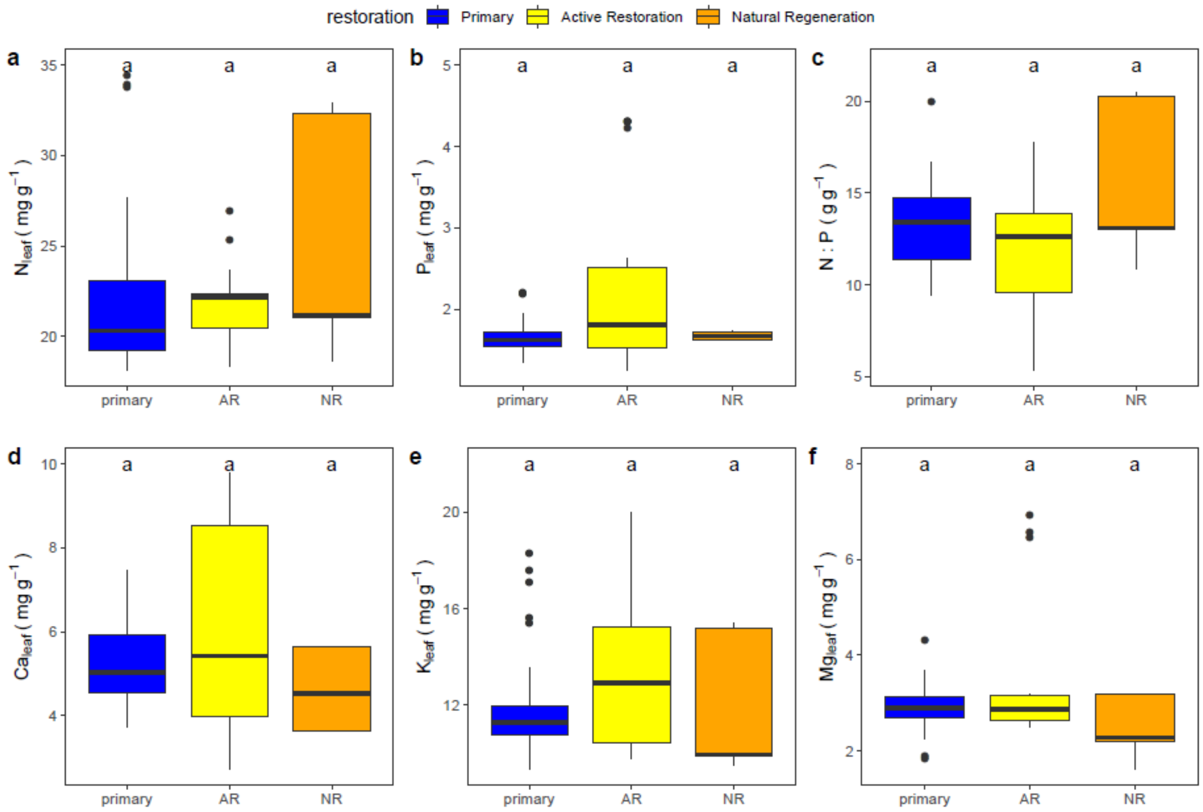
Forest	**Plot**	**Area (ha)**	**Stems**	**Basal Area (m^2)**	**Min Elevation (m asl)**	**Max Elevation (m asl)**
Alluvial	508/1	2.08	2134	61.9	67.2	72.2
Alluvial	508/2	2.45	2787	72.7	69.0	74.0
Mudstone	508/1	1.92	2341	66.0	72.3	86.9
Mudstone	508/2	1.55	1844	47.7	74.0	93.8
Sandstone	292/2	4	3079	71.7	97.1	142.8
Sandstone	508/3	4	6426	171.7	95.1	134.0
Kerangas	508/4	4	9842	138.9	87.9	129.4
Kerangas	508/5	4	8816	133.9	128.0	164.7

Appendix 4: Supporting Information for Chapter 4

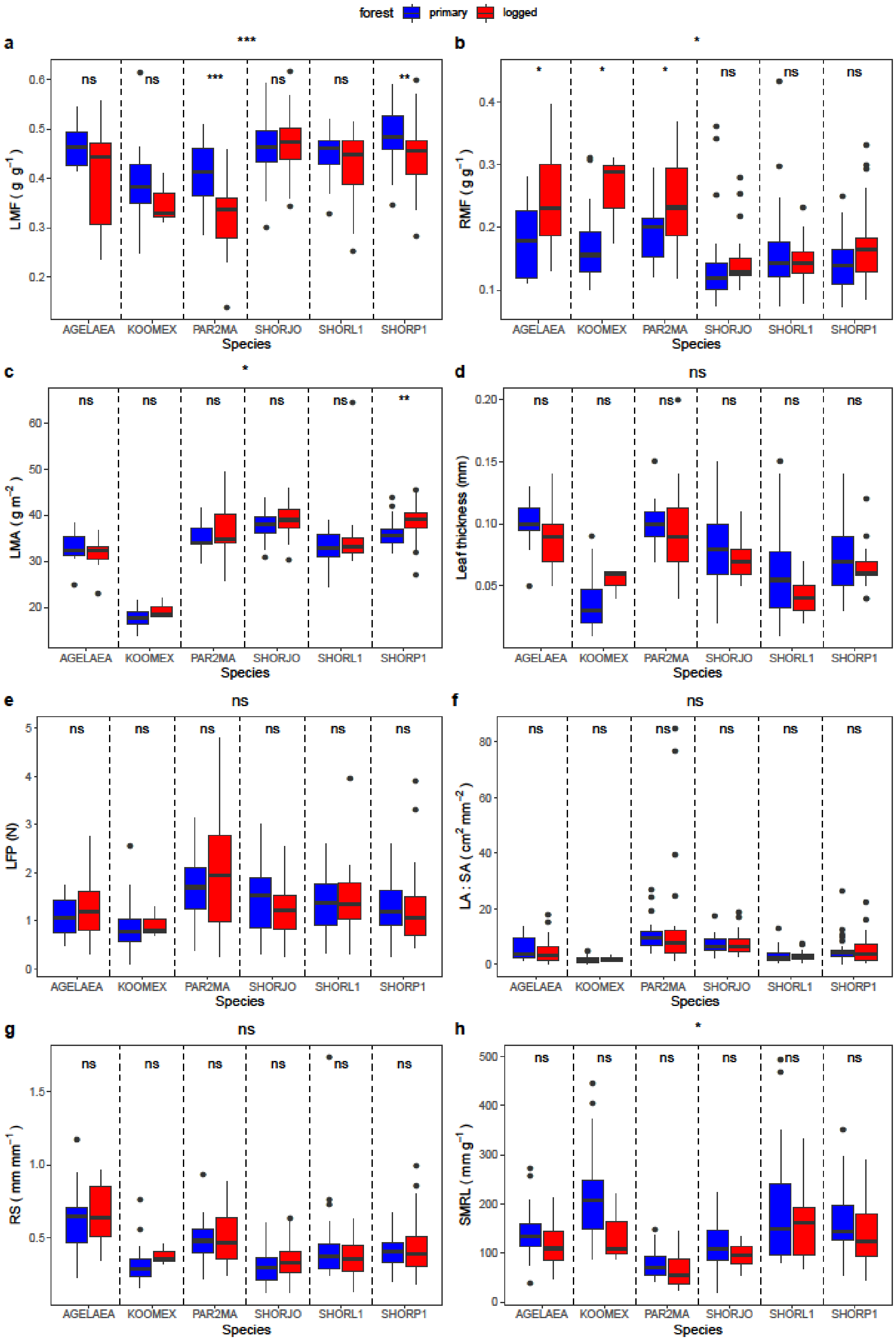
SI Figure 4.1: Community weighted mean trait values for (a) leaf mass fraction (LMF), (b) leaf mass per area (LMA), (c) leaf thickness, (d) leaf force to punch (LFP), (e) leaf area to shoot area ratio (LA : SA), (f) root mass fraction (RMF), (g) root length to shoot length ratio (RS), and (h) specific maximum root length (SMRL) in unlogged primary forests (blue) and logged forests with active restoration (yellow) and natural regeneration (orange). Different letters represent significant differences between forest types from Mann-Whitney tests ($p < 0.05$).



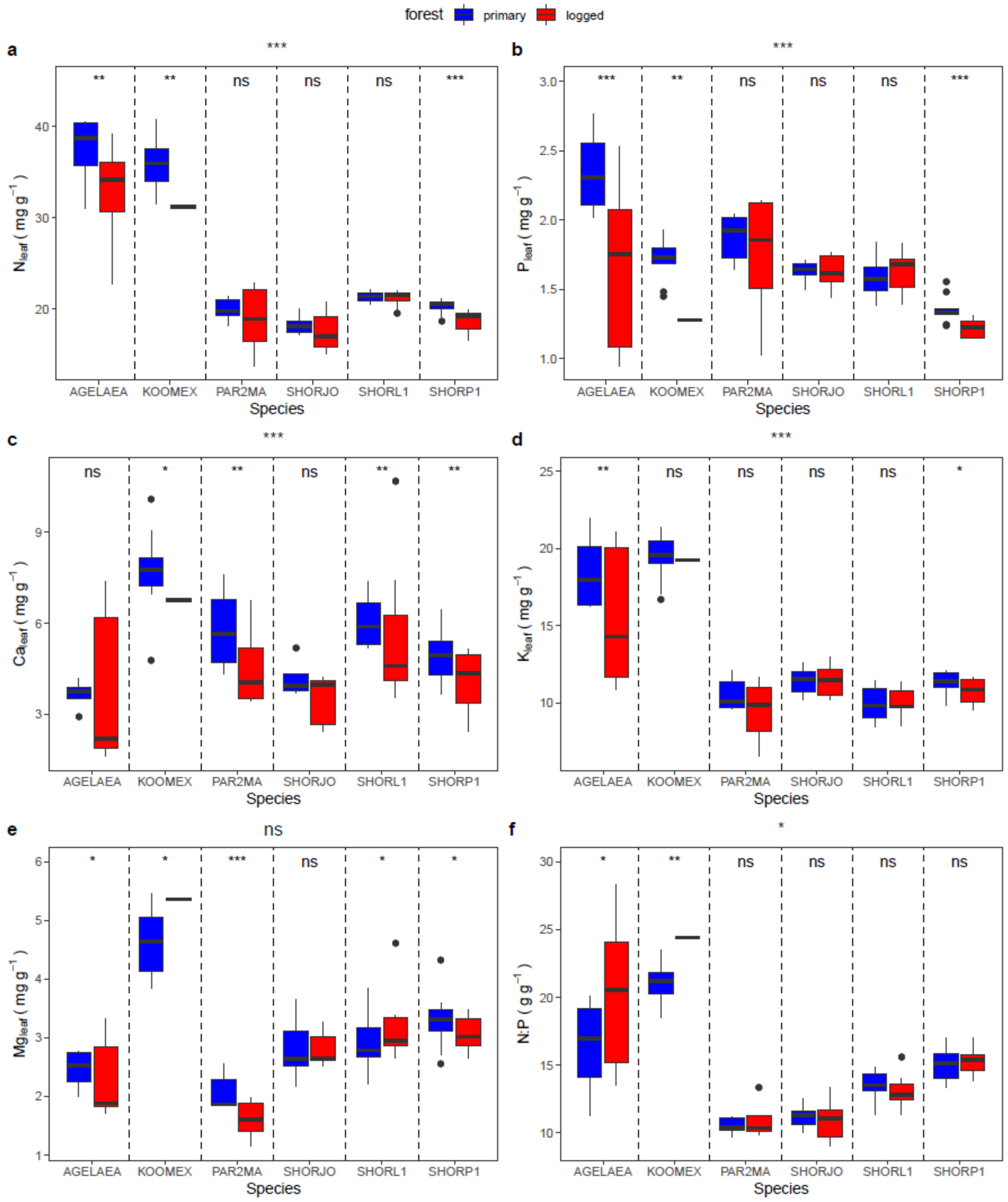
SI Figure 4.2: Community weighted mean trait values of foliar nutrient concentrations in unlogged primary forests (blue) and logged forests with active restoration (yellow) and natural regeneration (orange): (a) N_{leaf}, (b) P_{leaf}, (c) N_{leaf} : P_{leaf}, (d) Ca_{leaf}, (e) K_{leaf}, (f) Mg_{leaf}. Different letters represent significant differences between forest types from Mann-Whitney tests ($p < 0.05$).



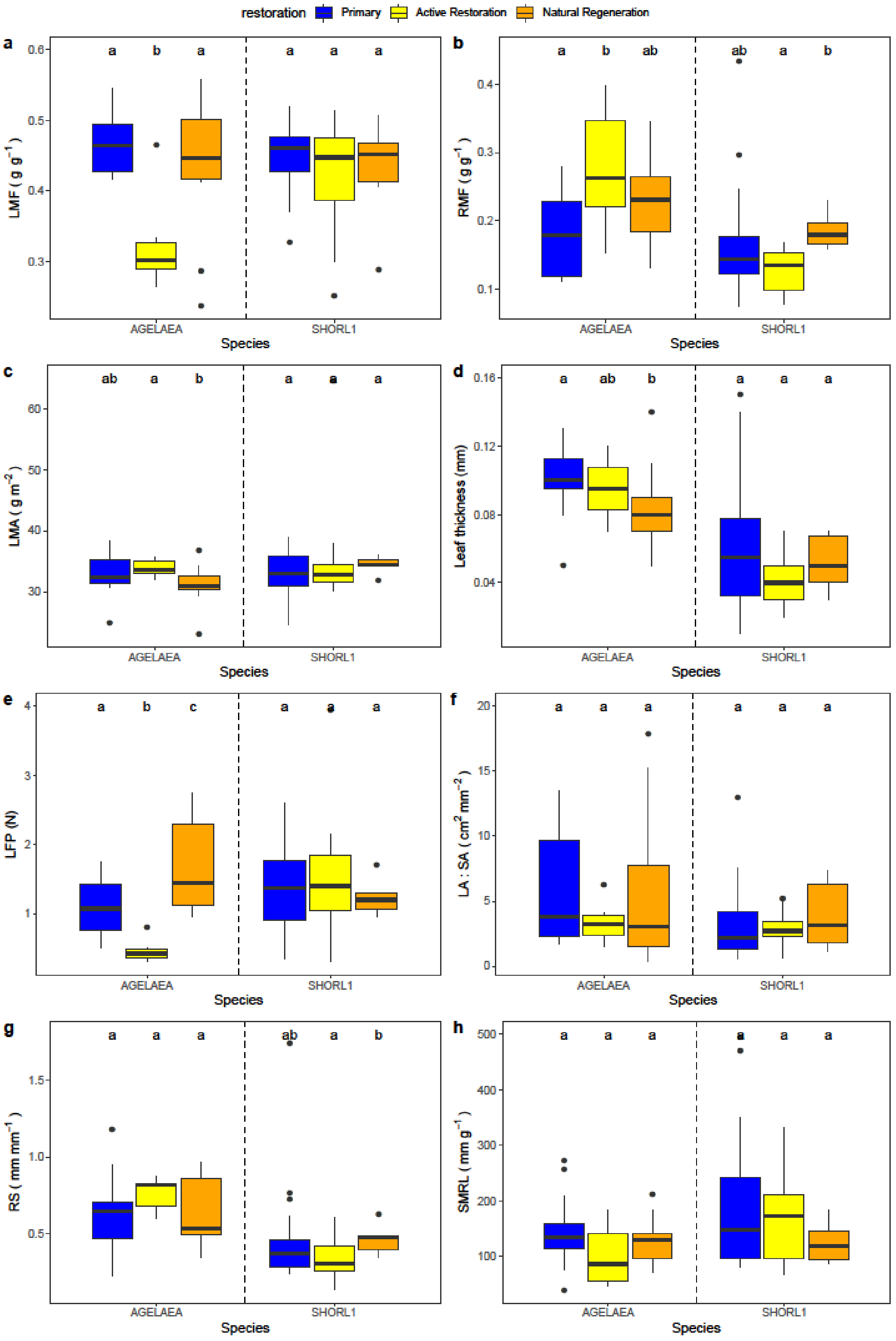
SI Figure 4.3: Intraspecific comparisons of (a) leaf mass fraction, (b) root mass fraction, (c) leaf mass per area, (d) leaf thickness, (e) leaf force to punch, (f) leaf area to shoot area ratio, (g) root length to shoot length ratio and (h) specific maximum root length between primary (blue) and logged (red) forests for the six species sampled in both forest types. Significant differences between forests for all species and for each species separately are shown by asterisks (*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$). See Table 2 for details and species codes.



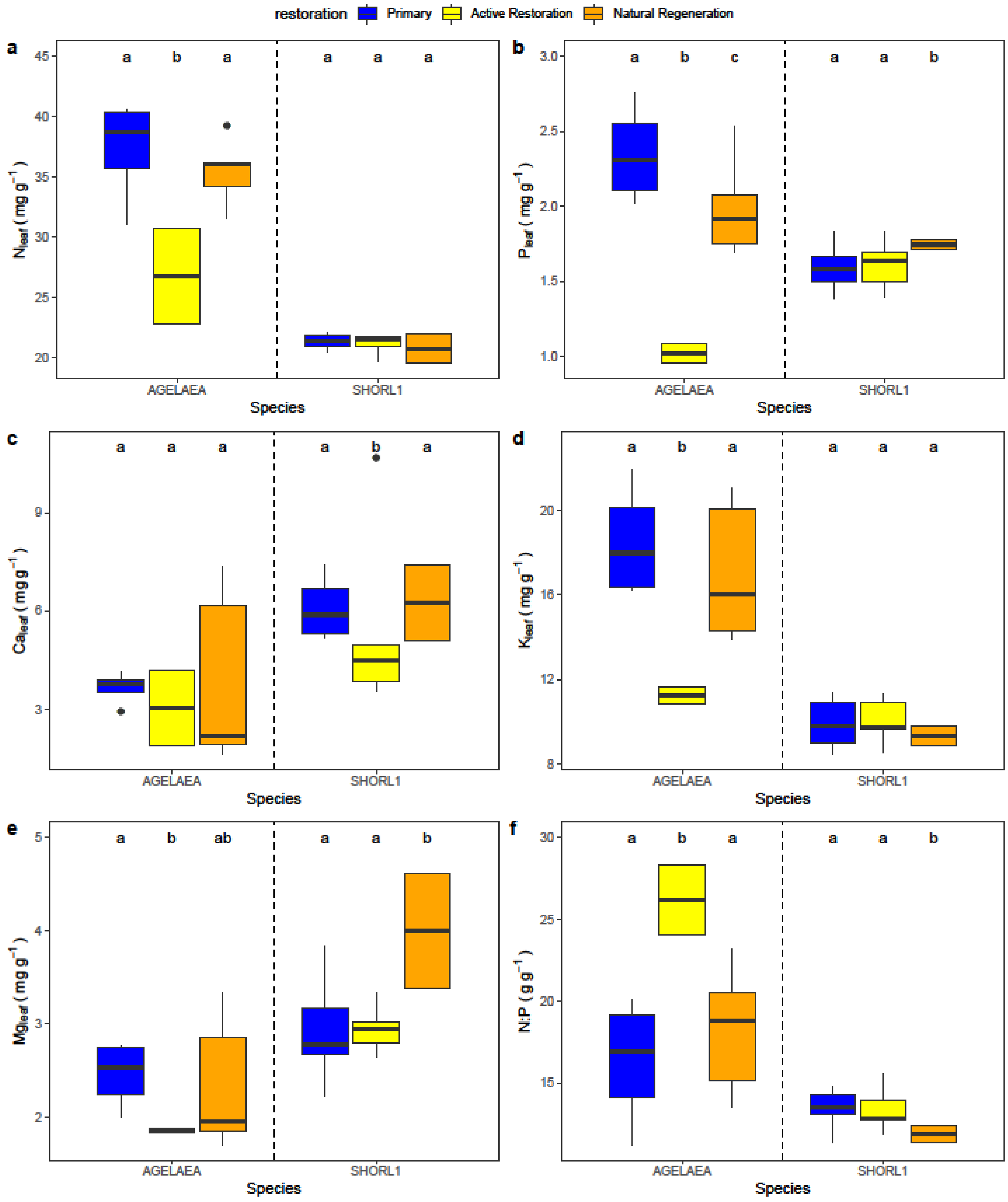
SI Figure 4.4: Intraspecific comparisons of foliar nutrient concentrations – (a) N_{leaf}, (b) P_{leaf}, (c) Ca_{leaf}, (d) K_{leaf}, (e) Mg_{leaf}, and (f) leaf N:P – between primary (blue) and logged (red) forests for the six species sampled in both forest types. Significant differences between forests for all species and for each species separately are shown by asterisks (ns: $p \geq 0.05$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$). See Table 2 for details and species codes.



SI Figure 4.5: Intraspecific comparisons of (a) leaf mass fraction (LMF), (b) root mass fraction (RMF), (c) leaf mass per area (LMA), (d) leaf thickness, (e) leaf force to punch (LFP), (f) leaf area to shoot area ratio (LA : SA), (g) root length to shoot length ratio (RS) and (h) specific maximum root length (SMRL) between primary forests (blue) and logged forests with active restoration (yellow) and natural regeneration for *Agelaea* sp. (AGELAEA) and *Shorea leprosula* (SHORL1). Different letters represent significant differences between forest types from Mann-Whitney tests ($p < 0.05$).



SI Figure 4.6: Intraspecific comparisons of foliar nutrient concentrations – (a) N_{leaf}, (b) P_{leaf}, (c) Ca_{leaf}, (d) K_{leaf}, (e) Mg_{leaf}, and (f) leaf N:P – between primary forests (blue) and logged forests with active restoration (yellow) and natural regeneration for *Agelaea* sp. (AGELAEA) and *Shorea leprosula* (SHORL1). Different letters represent significant differences between forest types from Mann-Whitney tests ($p < 0.05$).



SI Table 4.1: Summary of species selection and the number of seedlings sampled by forest type. Three seedlings were collected per seedling plot except where only one or two seedlings could be located.

Species	Species Code	Family	N	
			Primary	Logged
Agelaea sp.	AGALAEA	Connaraceae	12	21
Buchanania sessilifolia	BUCHSE	Anacardiaceae	0	21
Dryobalanops lanceolata	DRYOLA	Dipterocarpaceae	0	18
Intsia bijuga	INTSBI	Fabaceae	0	6
Koompassia excelsa	KOOMEX	Fabaceae	30	3
Parashorea malaanonan	PAR2MA	Dipterocarpaceae	21	20
Parashorea tomentella	PAR2TO	Dipterocarpaceae	18	0
Pterospermum javanicum	PTERJA	Malvaceae	0	18
Shorea fallax	SHORFA	Dipterocarpaceae	0	3
Shorea johorensis	SHORJO	Dipterocarpaceae	30	22
Shorea leprosula	SHORL1	Dipterocarpaceae	30	27
Shorea macrophylla	SHORMA	Dipterocarpaceae	0	20
Shorea parvifolia	SHORP1	Dipterocarpaceae	30	30
Shorea seminis	SHORSE	Dipterocarpaceae	15	0
Spatholobus sp.	SPAT	Fabaceae	9	0

SI Table 4.2: Percentage contributions to dimensions 1-3 for each trait to the principal component analysis of non-nutrient (a) and foliar nutrient concentration (b) community weighted-mean traits. Significant contributions to each dimension are highlighted in bold. The percentages in brackets below each dimension represent the proportion of the variance in the data explained by that axis.

a)

Trait	**Dimension 1** (37.36%)	**Dimension 2** (26.08%)	**Dimension 3** (14.24%)
LMA	**14.56**	10.82	6.21
RS	0.22	**39.43**	1.93
LMF	4.82	4.21	**29.45**
RMF	2.91	**40.99**	0.51
Leaf Thickness	**21.78**	1.71	0.16
LFP	7.92	0.02	**48.22**
LA:SA	**24.01**	1.72	7.04
SMRL	**23.79**	1.10	6.47

b)

Foliar nutrient	**Dimension 1** (41.76%)	**Dimension 2** (33.41%)	**Dimension 3** (17.98%)
N	1.59	**39.39**	12.47
P	**25.47**	2.49	**26.95**
Ca	**27.76**	2.41	5.76
K	**21.13**	**19.43**	0.68
Mg	12.57	4.11	**52.79**
N:P	11.49	**32.17**	1.36

SI Table 4.3: Species mean annual mortality rates in primary and logged forests. Annual mortality rates were calculated following equation 1 (see Methods). N represents the number of 1 m^2 seedling plots where each species was found. Data were only analysed if the species was found in >1 plot in the respective forest.

Species code	Species	Family	Primary	Logged	N primary	N logged
AGELAEA	*Agelaea* sp.	Connaraceae	0.261	0.443	4	12
BUCHSE	*Buchanania sessilifolia*	Anacardiaceae	-	0.455	-	5
DRYOLA	*Dryobalanops lanceolata*	Dipterocarpaceae	0.764	0.923	2	8
INTSBI	*Intsia bijuga*	Fabaceae	-	1.000	-	3
KOOMEX	*Koompassia excelsa*	Fabaceae	0.642	1.000	27	2
PAR2MA	*Parashorea malaanonan*	Dipterocarpaceae	0.637	0.733	27	8
PAR2TO	*Parashorea tomentella*	Dipterocarpaceae	0.726	-	2	-
PTERJA	*Pterospermum javanicum*	Malvaceae	-	0.583	-	5
SHORJO	*Shorea johorensis*	Dipterocarpaceae	0.476	0.848	61	8
SHORL1	*Shorea leprosula*	Dipterocarpaceae	0.686	0.741	41	14
SHORMA	*Shorea macrophylla*	Dipterocarpaceae	-	0.733	-	2
SHORP1	*Shorea parvifolia*	Dipterocarpaceae	0.674	0.810	45	24
SHORSE	*Shorea seminis*	Dipterocarpaceae	1.000	-	1	-
SPAT	*Spatholobus* sp.	Fabaceae	1.000	-	1	-

SI Table 4.4: Summary of the co-efficient ± standard error and R^2 for the minimal adequate model explaining mortality rates in primary and logged forests. Co-efficients have been transformed using a logistic function as data was modelled with a binomial error structure. Asterisks represent significant co-efficients: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

	Primary	**Logged**
Intercept	0.196 ± 0.94	2.736 ± 1.15*
N_{leaf}	-0.003 ± 0.04	1.48 ± 0.05*
R^2	**0.0004**	**0.3564**

SI Table 4.5: Percentage contributions to dimensions 1-3 for each trait to the principal component analysis of species mean trait values in each forest. Significant contributions to each dimension are highlighted in bold. The percentages in brackets below each dimension represents the proportion of the variance in the data explained by that axis.

Trait	**Dimension 1** (34.34%)	**Dimension 2** (21.41%)	**Dimension 3** (14.14%)
LMA	**14.24**	1.46	0.16
RS	2.81	1.10	**24.07**
LMF	0.49	**24.05**	0.39
RMF	2.51	0.07	**25.99**
Leaf Thickness	**8.79**	4.96	**8.38**
LFP	4.13	**13.52**	2.56
LA:SA	**9.07**	0.05	0.17
SMRL	**14.18**	2.10	4.41
N	5.64	**18.35**	4.85
P	0.13	**16.89**	6.04
Ca	**10.02**	4.19	3.59
K	**10.02**	**12.77**	0.28
Mg	**13.31**	0.49	2.74
N:P	4.67	0.00	**16.39**

SI Table 4.6: Species-level mean ± standard error trait values in logged (L) and primary (P) forests. Sample size for non-nutrient and nutrient traits are presented.

Species	Forest	n		LMF (g g^{-1})	LMA (g m^{-2})	Leaf thickness (mm)	LFP (N)	LA : SA (cm^2 mm^{-2})	RMF (g g^{-1})	RS (mm mm^{-1})	SMRL (mm g^{-1})	N_{leaf} (mg g^{-1})	P_{leaf} (mg g^{-1})	Ca_{leaf} (mg g^{-1})	K_{leaf} (mg g^{-1})	Mg_{leaf} (mg g^{-1})	N : P (g g^{-1})
		Traits	Nutrients														
AGELAEA	L	21	7	0.409 ± 0.021	31.9 ± 0.6	0.09 ± 0.00	1.32 ± 0.17	4.89 ± 1.05	0.244 ± 0.016	0.672 ± 0.042	118.5 ± 9.9	32.93 ± 2.01	1.71 ± 0.21	3.63 ± 0.88	15.41 ± 1.49	2.20 ± 0.24	20.5 ± 2.0
	P	12	4	0.467 ± 0.012	33.0 ± 1.0	0.10 ± 0.01	1.10 ± 0.13	5.71 ± 1.21	0.180 ± 0.017	0.621 ± 0.078	146.3 ± 19.7	37.30 ± 2.21	2.35 ± 0.17	3.65 ± 0.26	18.53 ± 1.37	2.46 ± 0.18	16.3 ± 2.0
BUCHSE	L	21	7	0.445 ± 0.016	27.3 ± 1.1	0.05 ± 0.01	1.59 ± 0.09	0.67 ± 0.06	0.157 ± 0.008	0.491 ± 0.040	372.7 ± 43.1	22.75 ± 1.21	2.40 ± 0.12	9.80 ± 1.38	19.96 ± 0.58	6.91 ± 0.44	9.6 ± 0.6
DRYOLA	L	18	5	0.474 ± 0.034	43.0 ± 3.7	0.11 ± 0.01	2.57 ± 0.22	29.94 ± 2.81	0.154 ± 0.015	0.379 ± 0.034	77.3 ± 26.3	15.69 ± 0.14	1.61 ± 0.04	1.45 ± 0.20	10.23 ± 0.29	2.16 ± 0.04	9.8 ± 0.3
INTSBI	L	6	1	0.044 ± 0.017	60.0 ± 20.7	0.12 ± 0.01	0.40 ± 0.14	6.87 ± 4.62	0.123 ± 0.005	0.165 ± 0.018	37.0 ± 4.5	38.66	4.52	0.93	20.82	2.07	8.6
KOOMEX	L	3	1	0.350 ± 0.030	19.7 ± 1.3	0.05 ± 0.01	0.93 ± 0.19	1.99 ± 0.63	0.258 ± 0.042	0.376 ± 0.042	139.3 ± 41.6	31.23	1.28	6.77	19.26	5.36	24.4
	P	30	10	0.388 ± 0.012	17.7 ± 0.3	0.04 ± 0.00	0.88 ± 0.10	1.66 ± 0.24	0.169 ± 0.010	0.306 ± 0.022	216.9 ± 16.2	35.93 ± 0.82	1.71 ± 0.05	7.74 ± 0.44	19.39 ± 0.48	4.59 ± 0.17	21.1 ± 0.5
PAR2MA	L	20	7	0.321 ± 0.016	37.3 ± 1.3	0.09 ± 0.01	1.97 ± 0.26	16.41 ± 5.33	0.239 ± 0.015	0.499 ± 0.040	63.3 ± 7.5	18.63 ± 1.22	1.74 ± 0.15	4.53 ± 0.52	9.49 ± 0.65	1.61 ± 0.11	10.9 ± 0.5
	P	21	7	0.411 ± 0.014	35.1 ± 0.6	0.10 ± 0.00	1.74 ± 0.16	11.08 ± 1.26	0.190 ± 0.009	0.474 ± 0.036	80.0 ± 6.8	19.88 ± 0.40	1.90 ± 0.06	5.66 ± 0.45	10.40 ± 0.36	2.06 ± 0.11	10.5 ± 0.2
PAR2TO	P	18	6	0.416 ± 0.017	39.2 ± 0.9	0.09 ± 0.00	2.08 ± 0.21	22.81 ± 3.39	0.166 ± 0.013	0.402 ± 0.044	60.7 ± 7.4	18.13 ± 0.55	1.93 ± 0.04	7.42 ± 0.62	9.32 ± 0.32	1.83 ± 0.06	9.4 ± 0.3
PTERJA	L	18	6	0.441 ± 0.011	27.6 ± 0.9	0.07 ± 0.01	1.26 ± 0.16	1.75 ± 0.21	0.189 ± 0.008	0.425 ± 0.029	165.6 ± 13.2	22.28 ± 0.78	4.31 ± 0.35	8.51 ± 0.80	15.21 ± 0.56	2.52 ± 0.14	5.3 ± 0.4
SHORFA	L	3	1	0.423 ± 0.032	43.1 ± 1.8	0.12 ± 0.00	1.57 ± 0.29	75.73 ± 19.09	0.150 ± 0.022	0.331 ± 0.046	45.5 ± 13.0	20.50	1.72	3.55	11.28	2.98	11.9
SHORJO	L	22	6	0.470 ± 0.014	38.9 ± 0.8	0.07 ± 0.00	1.25 ± 0.13	7.67 ± 0.91	0.147 ± 0.010	0.339 ± 0.028	95.9 ± 5.1	17.61 ± 0.88	1.62 ± 0.04	3.51 ± 0.33	11.42 ± 0.40	2.79 ± 0.08	10.9 ± 0.6
	P	30	10	0.462 ± 0.011	37.8 ± 0.5	0.08 ± 0.01	1.44 ± 0.13	7.02 ± 0.60	0.140 ± 0.012	0.296 ± 0.021	114.3 ± 9.7	18.27 ± 0.29	1.63 ± 0.02	4.08 ± 0.14	11.41 ± 0.25	2.79 ± 0.14	11.2 ± 0.2
SHORL1	L	27	9	0.428 ± 0.014	34.6 ± 1.3	0.04 ± 0.00	1.45 ± 0.14	3.12 ± 0.35	0.141 ± 0.007	0.360 ± 0.025	161.6 ± 13.0	21.15 ± 0.31	1.63 ± 0.05	5.65 ± 0.76	9.93 ± 0.31	3.19 ± 0.20	13.1 ± 0.4
	P	30	10	0.448 ± 0.008	33.1 ± 0.6	0.06 ± 0.01	1.31 ± 0.11	3.00 ± 0.46	0.161 ± 0.013	0.437 ± 0.052	185.9 ± 20.5	21.38 ± 0.17	1.59 ± 0.04	6.11 ± 0.27	9.96 ± 0.35	2.90 ± 0.14	13.5 ± 0.3
SHORMA	L	20	6	0.357 ± 0.023	100.8 ± 14.5	0.11 ± 0.01	1.81 ± 0.20	225.90 ± 34.41	0.159 ± 0.026	0.253 ± 0.029	17.8 ± 4.2	16.52 ± 0.25	1.25 ± 0.03	2.48 ± 0.22	8.08 ± 0.39	1.90 ± 0.04	13.2 ± 0.2
SHORP1	L	30	10	0.445 ± 0.013	38.5 ± 0.7	0.07 ± 0.00	1.25 ± 0.14	5.23 ± 0.94	0.170 ± 0.011	0.428 ± 0.037	136.0 ± 11.0	18.72 ± 0.35	1.22 ± 0.02	4.08 ± 0.29	10.72 ± 0.25	3.06 ± 0.08	15.4 ± 0.3
	P	30	10	0.489 ± 0.010	36.1 ± 0.5	0.07 ± 0.01	1.30 ± 0.11	5.23 ± 0.91	0.141 ± 0.007	0.402 ± 0.021	167.6 ± 13.2	20.32 ± 0.26	1.35 ± 0.03	4.93 ± 0.26	11.29 ± 0.25	3.29 ± 0.15	15.1 ± 0.4
SHORSE	P	15	2	0.452 ± 0.021	43.7 ± 1.4	0.10 ± 0.01	1.49 ± 0.13	29.35 ± 3.69	0.128 ± 0.018	0.311 ± 0.025	56.9 ± 19.5	19.39 ± 0.76	1.60 ± 0.06	3.12 ± 0.58	7.70 ± 0.14	1.80 ± 0.43	12.1 ± 0.0

SPAT	P	9	1	0.425 ± 0.043	36.6 ± 1.0	0.13 ± 0.01	1.79 ± 0.19	7.52 ± 0.86	0.182 ± 0.024	0.749 ± 0.063	141.8 ± 33.5	34.26	2.25	4.67	19.65	3.49	15.3

AGELAEA – Agelaea sp.; BUCHSE – Buchanania sessifolia; DRYOLA - Dryobalanops lanceolata; INTSBI - *Intsia bijuga; KOOMEX - Koompassia excelsa; PAR2MA - Parashorea malaanonan; PAR2TO - Parashorea tomentella; PTERJA - Pterospermum javanicum; SHORFA - Shorea fallax; SHORJO - Shorea johorensis; SHORL1 - Shorea leprosula; SHORMA - Shorea macrophylla; SHORP1 - Shorea parvifolia; SHORSE - Shorea seminis;* SPAT -*Spatholobus* sp.

LMF – Leaf mass fraction; LMA – Leaf mass per area; LFP – Leaf force to punch; LA:SA – Leaf area to shoot area ratio; RMF – Root mass fraction; RS – Root length to shoot length ratio; SMRL – Specific maximum root length; N_{leaf} *– foliar nitrogen;* P_{leaf} *– foliar phosphorus;* Ca_{leaf} *– foliar calcium;* K_{leaf} *– foliar potassium;* Mg_{leaf} *– foliar magnesium; N:P – foliar nitrogen to phosphorus ratio.*

Appendix 5: Supporting Information for Chapter 5

SI Table 5.1a: A list of sample sizes and tree heights for sampled species in the control and TFE plots used in the saplings analysis (1-10 cm DBH).

Genus	**Species**	**Control**		**TFE**		**Total n**
		n	**Height (m)**	**n**	**Height (m)**	
Duguetia	*Duguetia cadaverica*	2	3.62, NA	1	6.00	**3**
Eschweilera	*Eschweilera coriacea*	3	3.00, 6.20, 8.23	3	2.90, 3.30, 7.01	**6**
Inga	*Inga heterophylla*	4	5.10, 5.39, 7.22, NA	3	6.42, 8.08, 8.57	**7**
Iryanthera	*Iryanthera laevis*	1	6.17	2	5.22, 15.19	**3**
Licania	*Licania cannescens*	2	4.95, 11.46	3	4.00, 5.90, 8.38	**5**
	Licania egleri	1	7.80	0	-	**1**
	Licania octandra	1	10.76	1	9.46	**2**
Manilkara	*Manilkara elata*	1	4.40	2	5.90, NA	**3**
Minquartia	*Minquartia guianensis*	2	4.85, 18.66	1	3.80	**3**
Ocotea	*Ocotea caniculata*	0	-	3	7.66, 9.89, 16.57	**3**
	Ocotea caudata	3	3.10, 4.00, 4.85	0	-	**3**
Protium	*Protium apiculatum*	1	3.65	0	-	**1**
	Protium krukoffii	2	2.75, 8.08	0	-	**2**
	Protium trifoliuolatum	2	4.95, 8.38	3	8.71, 12.46, 22.99	**5**
Swartzia	*Swartzia racemosa*	3	3.20, 4.15, 5.75	2	4.50, 6.35	**5**
Tetragastris	*Tetragastris altissima*	4	3.00, 4.15, 5.80, 6.25	0	-	**4**
	Tetragastris panamensis	1	9.22	3	2.70, 5.85, 14.92	**4**
Vouacapoa	*Vouacapoa americana*	3	3.00, 5.30, 5.75	3	6.40, 6.50, 17.21	**6**
	Total	**36**		**30**		**66**

SI Table 5.1b: A list of sample sizes for sampled species in the control and TFE plots used in the analysis to compare large tree and sapling responses (1-10 cm DBH).

Genus	**Species**	**Large trees (>20 cm DBH)**		**Saplings (1-10 cm DBH)**		**Total**
		Control	**TFE**	**Control**	**TFE**	
Eschweilera	*Eschweilera coriacea*	2	1	3	3	**9**
	Eschweilera decolorans	0	2	0	0	**2**
	Eschweilera spp.	2	0	0	0	**2**
Inga	*Inga alba*	1	2	0	0	**3**
	Inga capitata	1	0	0	0	**1**
	Inga gracilifolia	0	3	0	0	**3**
	Inga heterophylla	0	0	4	3	**7**
	Inga rubiginosa	1	0	0	0	**1**
Licania	*Licania cannescens*	0	0	2	3	**5**
	Licania egleri	0	0	1	0	**1**
	Licania membranacea	3	1	0	0	**4**
	Licania octandra	1	1	1	1	**4**
Manilkara	*Manilkara bidentata*	2	4	0	0	**6**
	Manilkara elata	0	0	1	2	**3**
	Manilkara paraensis	1	0	0	0	**1**
Minquartia	*Minquartia guianensis*	4	5	2	1	**12**
Protium	*Protium apiculatum*	0	0	1	0	**1**
	Protium krukoffii	0	0	2	0	**2**
	Protium paniculatum	0	1	0	0	**1**
	Protium tenuifolium	2	4	0	0	**6**
	Protium trifoliuolatum	0	0	2	3	**5**
Swartzia	*Swartzia racemosa*	8	5	3	2	**18**
Tetragastris	*Tetragastris altissima*	0	0	4	0	**4**
	Tetragastris nitidum	0	2	0	0	**2**
	Tetragastris panamensis	0	2	1	3	**6**
	Total	**28**	**33**	**27**	**21**	**109**

SI Table 5.2: Parameter estimates for the minimal adequate models explaining small understory J_{max}, V_{cmax}, R_{leaf}, leaf mass per area (LMA), leaf thickness, leaf nitrogen ($[N]_{leaf}$) and phosphorus ($[P]_{leaf}$) concentrations and photosynthetic and respiratory nutrient use efficiency for J_{max}, V_{cmax} and R_{leaf} on a mass basis per unit N_{leaf} and P_{leaf} (n = 66). Treatment represents whether the tree is found in the control or TFE treatment. Coefficient estimates ± the standard error are presented for each fixed effect and refer to the differences between the factor levels indicated in brackets for each column and the overall intercept. The genus intercept is given whenever the genus included as a random intercept effect improved the model fit. Random effect variance for genus ± standard deviation is presented. Total (conditional) R^2 represents the total variation explained by the model and is partitioned into the variation explained by the fixed effects (marginal R^2) and fixed plus random effects (conditional R^2). Asterisks represent the significance level of each variable: . $P > 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Dashes represent variables that were not retained in the minimal adequate model, but were tested in the initial fully saturated model.

Trait	**Intercept**	**Treatment** (TFE)	**Genus Intercept**	**Fixed effect (marginal) R^2**	**Random effect R^2**	**Total (conditional) R^2**
J_{max}	19.94 ± 1.80	*** 14.18 ± 2.65	-	0.347	-	0.347
V_{cmax}	15.79 ± 1.27	** 3.99 ± 1.40	. 7.16 ± 2.68	0.104	0.184	0.288
R_{leaf}	0.36 ± 0.04	* 0.12 ± 0.06	-	0.062	-	0.062
LMA	70.80 ± 4.72	** 10.68 ± 4.04	*** 20.40 ± 4.52	0.056	0.539	0.596
Leaf thickness	0.17 ± 0.01	-	. 0.0005 ± 0.023	-	0.207	0.207
$[N]_{leaf}$	18.80 ± 1.22	-	*** 14.95 ± 3.87	-	0.519	0.519
$[P]_{leaf}$	0.54 ± 0.03	-	** 0.01 ± 0.08	-	0.392	0.392
J_{max}/N_{leaf}	0.017 ± 0.002	* 0.006 ± 0.002	-	0.103	-	0.103
J_{max}/P_{leaf}	0.52 ± 0.03	*** 0.21 ± 0.05	-	0.287	-	0.287
V_{cmax}/N_{leaf}	0.013 ± 0.001	-	-	-	-	-
V_{cmax}/P_{leaf}	0.46 ± 0.02	-	-	-	-	-
R_{leaf}/N_{leaf}	0.055 ± 0.013	-	-	-	-	-
R_{leaf}/P_{leaf}	0.010 ± 0.001	-	-	-	-	-

SI Table 5.3: The R^2, p-value, elevation (or intercept) and slope of standardised major axis regressions between $\log_{10}$-transformed J_{max}, V_{cmax}, R_{leaf}, leaf mass per area (LMA) and leaf nitrogen ($[N]_{leaf}$) and phosphorus ($[P]_{leaf}$) concentrations for the control and TFE treatments. Significant shifts in the elevation and slope between the two treatments are in bold and underlined ($p < 0.05$). NAs represent relationships when the p-value of the SMA was not significant ($p > 0.05$).

y-axis	x-axis	Control				TFE			
		R^2 SMA	p SMA	Elev. SMA	Slope SMA	R^2 SMA	p SMA	Elev. SMA	Slope SMA
J_{max}	V_{cmax}	0.20	0.01	**-0.05**	1.13	0.68	<0.01	**0.15**	1.06
J_{max}	R_{leaf}	NA	NA	NA	NA	NA	NA	NA	NA
J_{max}	LMA	NA	NA	NA	NA	NA	NA	NA	NA
V_{cmax}	R_{leaf}	NA	NA	NA	NA	NA	NA	NA	NA
V_{cmax}	LMA	NA	NA	NA	NA	NA	NA	NA	NA
R_{leaf}	LMA	NA	NA	NA	NA	NA	NA	NA	NA
J_{max}	$[N]_{leaf}$	NA	NA	NA	NA	NA	NA	NA	NA
J_{max}	$[P]_{leaf}$	NA	NA	NA	NA	NA	NA	NA	NA
V_{cmax}	$[N]_{leaf}$	NA	NA	NA	NA	NA	NA	NA	NA
V_{cmax}	$[P]_{leaf}$	NA	NA	NA	NA	NA	NA	NA	NA
R_{leaf}	$[N]_{leaf}$	NA	NA	NA	NA	NA	NA	NA	NA
R_{leaf}	$[P]_{leaf}$	NA	NA	NA	NA	NA	NA	NA	NA

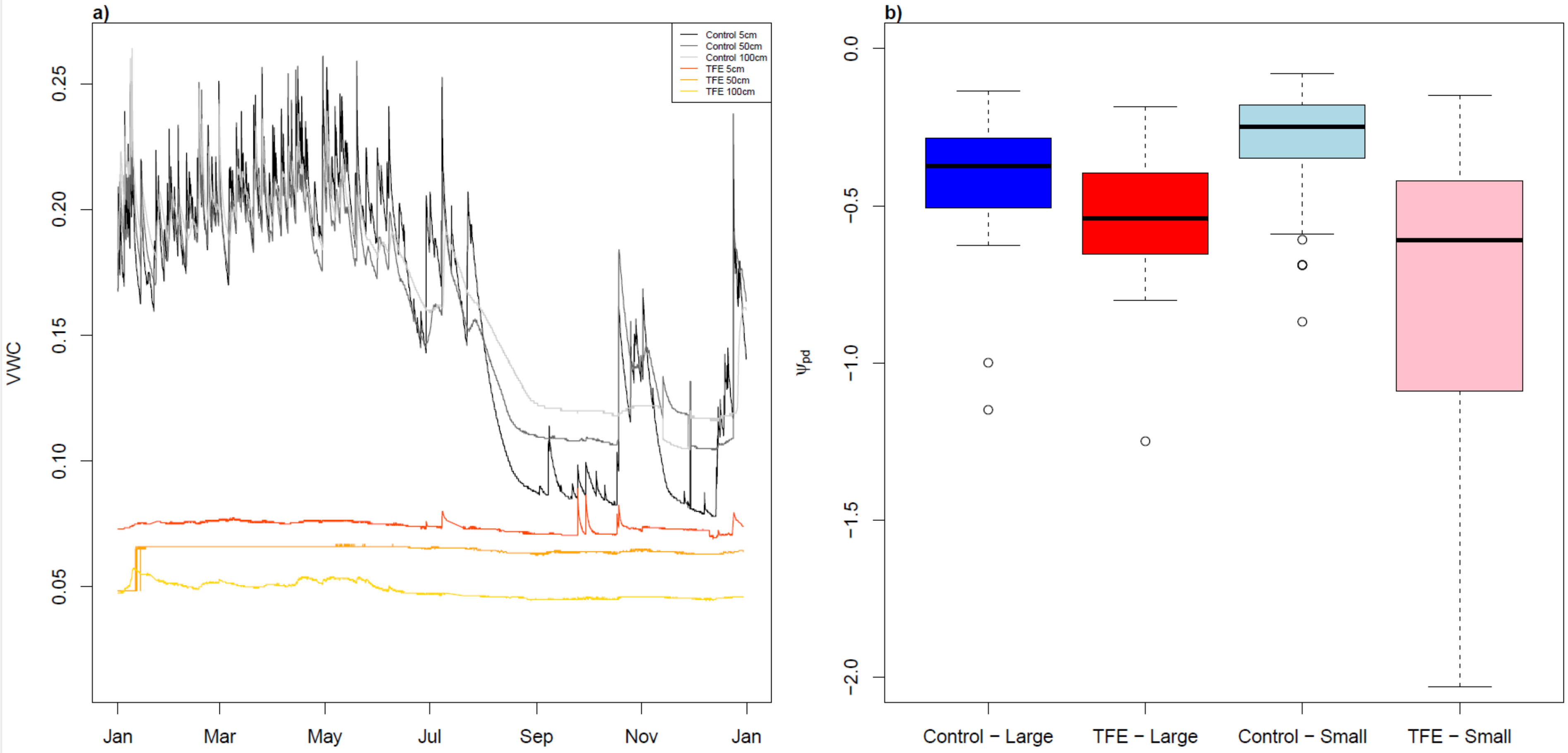
SI Table 5.4: Summary of the model set explaining how J_{max}, V_{cmax}, R_{leaf}, leaf mass per area (LMA) and leaf thickness change with canopy shading (canopy), TFE treatment (plot) and tree size (size). All models tested are presented and the minimal adequate model was selected based on the Akaike Information Criterion corrected for sample size (AICc). The optimal model for each of the traits is highlighted in bold. ΔAICc values represent the difference in the AICc for each model compared to the optimal model. For effect sizes and *P* values, see Table 5.1.

Model	J_{max}		V_{cmax}		R_{leaf}		**LMA**		**Leaf thickness**	
	AICc	ΔAICc	AICc	ΔAICc	AICc	ΔAICc	AICc	ΔAICc	AICc	ΔAICc
canopy + plot + size + plot:size + canopy:size	**717.0**	**0.0**	**632.9**	**0.0**	28.9	4.7	**965.0**	**0.0**	-317.4	44.1
canopy + plot + size + canopy:size	734.2	17.2	640.7	7.7	27.0	2.8	969.2	4.2	-326.0	35.5
canopy + plot + size + plot:size	721.8	4.8	636.2	3.3	27.3	3.0	971.2	6.2	-323.7	37.8
canopy + plot + size	740.2	23.2	644.2	11.3	25.3	1.1	975.3	10.3	-332.3	29.2
canopy + size + canopy:size	735.5	18.5	640.8	7.9	28.0	3.8	975.1	10.1	-336.0	25.5
plot + size + plot:size	742.4	25.4	646.1	13.2	25.9	1.7	974.6	9.6	-333.0	28.5
plot + size	756.8	39.7	652.7	19.8	**24.2**	**0.0**	978.8	13.8	-341.6	19.9
canopy + plot	750.4	33.4	650.8	17.8	26.0	1.7	998.1	33.1	-341.7	19.8
canopy + size	741.6	24.6	644.3	11.4	29.1	4.8	981.2	16.2	-342.4	19.1
plot	799.2	82.2	681.8	48.9	25.3	1.0	1018.7	53.7	-351.5	10.0
size	758.8	41.8	652.9	20.0	40.5	16.3	984.8	19.8	-351.6	9.9
canopy	751.9	34.8	651.1	18.1	29.6	5.4	1003.5	38.5	-351.6	9.9
Null	802.1	85.0	682.5	49.6	42.3	18.1	1026.1	61.1	**-361.5**	**0.0**

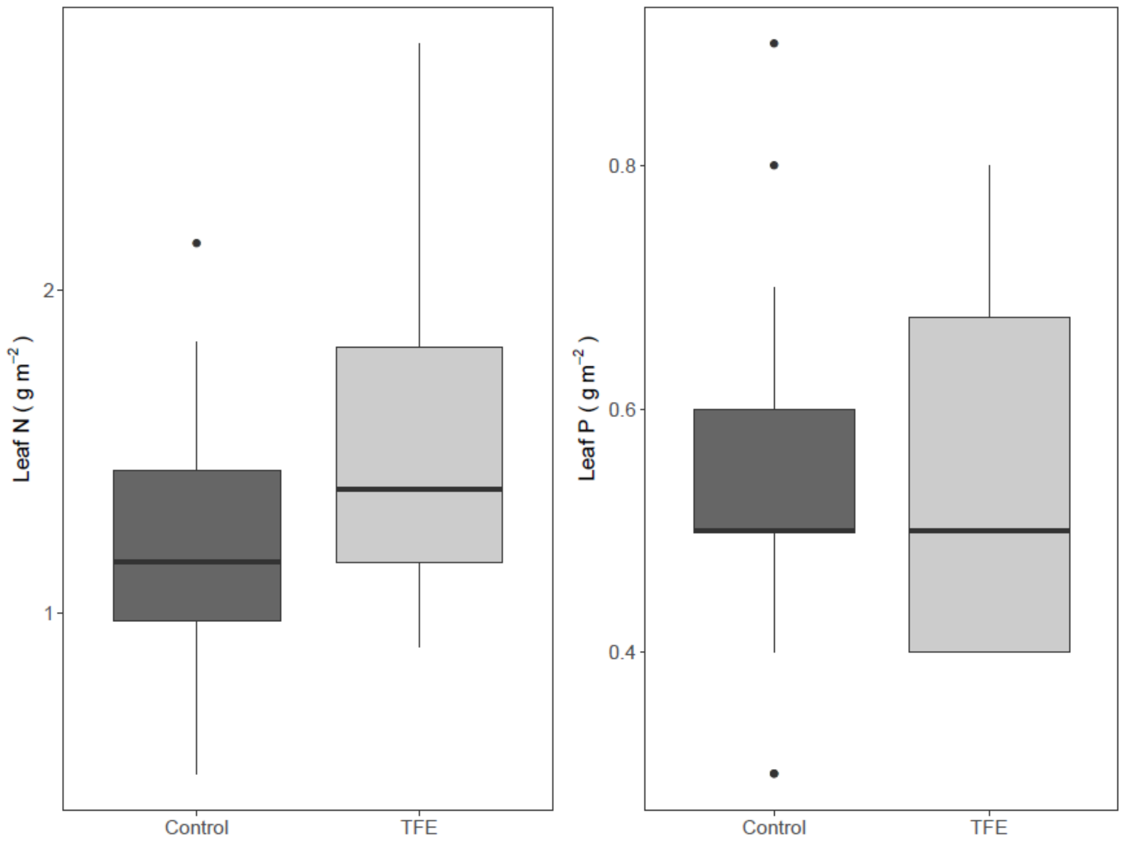
SI Table 5.5: Standard deviation (sd) in trait estimates for J_{max}, V_{cmax}, R_{leaf} and leaf mass per area (LMA) for trees on the control and through-fall exclusion (TFE) plot for each species and for species-level means. The standard deviation for each species represents intraspecific variation in trait values, whilst standard deviation for species-level means represents interspecific variation in trait values. Sample sizes are given (n). Dashes represent cases where there was insufficient replication for standard deviation to be calculated.

Species	**Control**								**TFE**							
	J_{max}		V_{cmax}		R_{leaf}		**LMA**		J_{max}		V_{cmax}		R_{leaf}		**LMA**	
	sd	**n**	**sd**	**n**	**sd**	**n**	**sd**	**n**	**sd**	**n**	**sd**	**n**	**sd**	**n**	**sd**	**n**
Duguetia cadaverica	1.92	2	3.89	2	0.32	2	5.16	2	-	1	-	1	-	1	-	1
Eschweilera coriacea	2.01	2	7.35	2	0.05	3	7.07	3	8.67	2	2.62	2	0.02	3	18.03	3
Inga heterophylla	10.89	3	5.24	4	0.33	4	12.31	3	9.02	3	6.62	3	0.35	3	18.48	3
Iryanthera laevis	-	0	-	0	-	1	-	1	-	1	-	1	0.09	2	0.76	2
Licania cannescens	2.58	2	10.78	2	0.02	2	0.74	2	13.31	2	4.77	3	0.13	3	16.62	3
Licania egleri	-	1	-	1	-	1	-	1	-	0	-	0	-	0	-	0
Licania octandra	-	1	-	1	-	1	-	1	-	1	-	1	-	1	-	1
Manilkara elata	-	1	-	1	-	1	-	1	32.44	2	8.39	2	0.57	2	48.06	2
Minquartia guianensis	-	1	-	1	-	1	7.30	2	-	1	-	1	-	1	-	1
Ocotea caniculata	-	0	-	0	-	0	-	0	13.00	3	10.52	3	0.22	3	30.18	3
Ocotea caudata	0.73	2	6.41	2	0.10	3	12.72	3	-	0	-	0	-	0	-	0
Protium apiculatum	-	1	-	1	-	1	-	1	-	0	-	0	-	0	-	0
Protium krukoffii	4.47	2	2.86	2	0.46	2	2.91	2	-	0	-	0	-	0	-	0
Protium trifoliuolatum	3.03	2	2.03	2	0.21	2	3.49	2	7.94	3	1.61	3	0.04	3	7.94	3
Swartzia racemosa	4.97	2	3.97	2	0.13	3	3.12	2	14.03	2	5.35	2	0.05	2	6.25	2
Tetragastris altissima	1.61	4	0.95	4	0.13	4	14.89	4	-	0	-	0	-	0	-	0
Tetragastris panamensis	-	1	-	1	-	1	-	1	10.67	2	7.17	2	0.55	3	8.69	3
Vouacapoa americana	5.89	3	2.70	3	0.05	3	11.81	3	8.55	3	6.05	3	0.04	3	5.36	3
Species-level means	6.57	16	3.93	16	0.10	17	15.94	17	8.41	13	4.82	13	0.17	13	23.52	13

SI Fig. 5.1: Water availability on the control and through fall exclusion (TFE) treatments in 2017 as indicated by (a) soil volumetric water content at 5 cm, 50 cm and 100 cm depth and (b) pre-dawn leaf water potentials in MPa for large (>20 cm DBH) and small (1-10cm DBH) trees. Data presented in (b) corresponds to trees used in the large versus small tree analyses presented in the main text.



SI Fig. 5.2: Boxplots showing how (a) leaf nitrogen ($[N]_{leaf}$) and (b) leaf phosphorus ($[P]_{leaf}$) on an area-basis differed between the control and TFE plot for small understory trees (1-10 cm DBH). 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 whiskers.



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